

Adaptive radiation and coevolution — pollination biology case studies

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Abstract

The impact of coevolutionary interaction between species on adaptive radiation processes is analysed with reference to pollination biology case studies. Occasional colonization of archipelagos can bring together coevolving partners and cause coradiation of the colonizing species, e.g. the drepanidids and the lobelioids on Hawaii. Permanent reciprocal selective pressure between pairs of coevolving species can lead to a coevolutionary race and rapid evolutionary change. This is exemplified by spurred flowers and long-tongued flower-visitors. The geographic patterning of diffuse coevolution systems can lead to dramatic changes in species interactions. In different populations, interaction between pollinating and seed-parasitizing *Greya* moths and their host plants varies from mutualism to commensalism and antagonism, depending on the presence of copollinators. Asymmetrical coevolution between angiosperms and oligolectic flower-visitors may facilitate rapid reproductive isolation of populations following a food-plant switch, if the oligolectes use their specific food plants as the rendezvous sites. Diffuse coevolution between angiosperm species and pollinating insects may cause frequent convergent evolution of floral traits such as nectar reward instead of pollen reward, floral guides, zygomorphic flowers, or mimicry of pollen signals, since the multiple plant species experience similar selective pressures via the coevolving partners. Patterns of angiosperm adaptive radiation are highlighted in the context of coevolution with pollinators.

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Introduction

Adaptive radiation and coevolution of species are two of the major processes organizing biodiversity. However, the ways in which coevolutionary processes can influence speciation and radiation are among the least understood aspects of reciprocal evolutionary change (Thompson 1982). Much recent progress in this field is related to specific cases in the area of pollination

biology. The mutual interrelations between zoophilous flowering plants and their pollinators encompass:

- (1) obligatory coevolution, for instance the pollination of yucca plants by yucca moths, in which the reproduction of each partner is closely and directly dependent on the other, including extreme one-to-one coevolution systems;
- (2) diffuse coevolution of few to many facultative partners, as in many pollination systems of bumblebees and other polylectic flower-visitors; and
- (3) asymmetrical coevolution with unbalanced reciprocal effects, such as occurs in oligolectic bees specializing on a few related plants as pollen sources.

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Here, I ask whether and how the processes of coevolution and of adaptive radiation are interrelated, focussing on pollination systems in which direct reciprocal selection pressure of the coevolving partners can be recognized by the existence of coadaptations. The coevolutionary process demands and produces some degree of specialization within biological communities (Thompson 1994). The spatio-temporal patterns of coevolutionary partners in pollination systems and the variation in pollinators' visitation rates in response to floral display constrain specialization of the plants to particular pollinators (Thompson 2001) and may promote speciation through specialization.

The angiosperms as a whole group, and in particular some families and genera of the Angiospermae and various taxa of flower-visitors such as syrphid flies (Syrphidae), bombyliid flies (Bombyliidae), pollen wasps (Masaridae), butterflies (Lepidoptera), bees (Apoidea), sphingid moths (Sphingidae), hummingbirds (Apodidae), nectar birds (Nectarinidae), and others are textbook examples of evolutionary success attributable to the mutualistic relationship between the flowering plants and the pollinators. I ask how adaptive radiation both in angiosperms and in flower-visitors is related to coevolutionary interaction between zoophilous plants and their pollinators. I review outstanding case studies of pollination biology, including both adaptive radiation and coevolution between pollinators and pollinated plants. On the basis of data from my own research I present some ideas about coevolutionary interaction in the context of floral signalling of entomophilous angiosperms and flower detection, flower choice, and the cognitive abilities of pollen-feeding insect flower-visitors, and discuss the relevance of these data for the understanding of the natural history of zoophilous angiosperms and pollinators, and the adaptive radiation processes in these groups.

Definition of terms

Adaptive radiation is the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage (Schluter 2000). According to this definition adaptive radiation may be detected by the following four criteria:

- (1) the common ancestry of the component species;
- (2) the key innovations predating the differentiation of an ancestor into an array of species that inhabit a variety of environments and that differ in the morphological, physiological and behavioural traits used to exploit those environments, commonly referred to as the adaptive zone;
- (3) the demonstration of fitness advantages of trait values in their corresponding environments;

- (4) rapid speciation, which can most easily be assessed by the superior species diversity of the taxon in question as compared to the sister taxon.

Coevolution is the reciprocal evolutionary change in interacting species (Thompson 1994). Coevolution can be detected by coadaptations, which are adaptive traits related to the coevolutionary partner as part of the ecological niche. More than two species are involved in diffuse coevolutionary processes. Diffuse coevolution includes single species interacting with various coevolutionary partners, as well as multiple species interacting with multiple coevolving species. One-to-one coevolution has only two component species such that each coadaptation of one species can be related to the selection pressure imposed by the other. The number of coadaptations may be very different among coevolving species. Extreme asymmetrical coevolution largely lacks the reciprocal component, and may thus not be defined as coevolution in a narrow sense (Paulus 1988; Fig. 1).

Mutualism is regarded as any mutually advantageous interaction between the individuals of different species. Mutualism in pollination systems has many facets. Coevolution in animal pollination systems may be based on either mutualistic or antagonistic interaction between the two partners. The pollination system of figs (*Ficus*) and fig wasps (Agaonidae) is one of the rare examples of pollination mutualisms with active pollination (Bronstein 1988; Machado et al. 2001; Weiblen 2002; Molbo et al. 2003). Plant species with deceptive flowers and deceived pollinator species do not obligatorily coevolve: male solitary bees and wasps lured by *Ophrys* (Orchidaceae) flowers mimicking olfactory, visual and tactile stimuli of the conspecific females (see Organisms Diversity and Evolution Electronic Supplement 04–05,

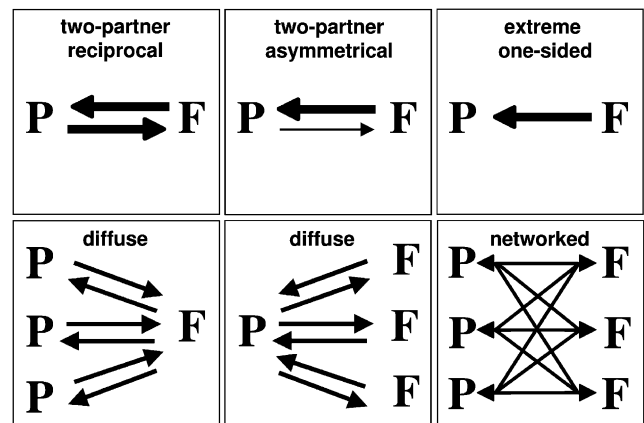


Fig. 1. Schemes of coevolutionary interactions between species. Arrows indicate strength and direction of selective forces on the evolution of coadaptations. F = flowering plant species, P = pollinator species.

Part 1) achieve only fitness costs. The very small reduction of reproductive success is caused by the waste of time during pseudocopulation which may not last longer than a few seconds (Schiestl et al. 1999; Ayasse et al. 2000). However, the males do not ejaculate during pseudocopulation and thus do not waste sperm. Moreover, the males are deceived only a few times and quickly learn to avoid female-mimicking *Ophrys* flowers.

The deadly consequences of the attraction of fungus gnats (Fungivoridae) by fungus-mimicking flowers exemplify antagonistic interactions of coevolved pollination systems. Fungus-mimicking flowers deceive fungus gnats which pollinate the flowers, oviposit in the wrong fungi, and lose their offspring because the latter are unable to feed on the inadequate floral substrate. The severe reduction of reproductive success of deceived female fungus-gnats has promoted the evolution of adaptations. The gnats' sensory filtering mechanisms for identification of the brood substrate have not been experimentally tested. However, the reciprocal selection between the fungus gnats and the fungus-mimicking plants has led to the evolution of some spectacular fungus-mimicking flowers showing multimodal deceptive signals including chemical, tactile and visual stimuli such as fungus-like odour, lamelliform structure, or hat-like shape (Vogel 1978) as in *Aristolochia arborea* (see Barthlott 1992; and Electronic Supplement 04–05, Part 2).

However, most pollination systems do not conform to these extreme types of interaction. The general features of these common pollination systems are as follows. The zoophilous plants attract and manipulate flower-visitors so that the latter transfer pollen within a flower (self-pollination), between flowers of the same plant (geitonogamous pollination), or between flowers of conspecifics (cross-pollination). To achieve cross-pollination the flower is a pollen donor during the first visit of a pollinator, and flowers of conspecifics subsequently visited are both pollen acceptors and pollen donors. Most flower-visitors consume floral resources; these flower-visitors are herbivores feeding on pollen, floral tissues or floral secretions such as nectar and fatty oils. Pollination usually is a passive process, a side-effect of the flower-visitors' activities while exploiting the rewards offered by the flower. Although mutualisms provide fitness advantages for both involved partners, this does not necessarily imply that coevolution has occurred (Schemske 1983).

Coevolutionary radiation occurs when evolutionary interaction between species creates new adaptive zones (Givnish 1997). The linkage between the evolutionary process of coevolution and that of adaptive radiation may be detected by coradiations, the simultaneous rise of species diversity in the two associated taxa, and by coadaptations. However, adaptive radiation in only one partner's lineage is also possible without simultaneous

adaptive radiation in the lineage of the coevolutionary partner. Coevolutionary processes are identifiable by the coadaptations of the coevolving species. Radiation processes linked to coevolution between species are thus coadaptive radiation processes.

Case studies

Coevolution and radiation on archipelagos: Hawaiian honeycreepers and lobelioids

Adaptive radiations following the colonization of remote archipelagos by an ancestor are among the outstanding cases of adaptive radiation, probably first recognized in connection with the Darwin's finches on the Galapagos islands (Schluter 2000). It is well known that early colonization of islands, evolution without competitors, and a variety of free ecological niches are features characteristic for extensive adaptive radiation on islands (Osche 1966). The adaptive radiations under these specific conditions have been related to the concept of ecological opportunity, including freedom from competitors and wealth of resources as components (Schluter 2000). An interesting aspect of coevolution is that the random colonization of emerging islands can bring together partners that previously had not been involved in coevolving systems.

Both the Hawaiian honeycreepers (Drepanididae, Aves) and the lobelioids, including the genus *Cyanea* (Campanulaceae, Lobelioideae), probably diversified from a single respective ancestor species colonizing Hawaii. The species diversity of both taxa on Hawaii largely surpasses that of the non-Hawaiian sister taxa (Bock 1970; Tarr and Fleischer 1995; Givnish 1997; Fleischer and McIntosh 2001).

The Hawaiian honeycreepers comprise up to 33 known species, 10 of which are historically documented but have become extinct (Tarr and Fleischer 1995). Howard and Moore (1980) listed 12 genera and 20 extant species, whereas Sibley and Ahlquist (1990) recognized 18 genera and 30 species of Drepanidinae as a subfamily endemic to Hawaii. Some of these honeycreepers are flower-visitors and pollinators (Givnish et al. 1995). The ancestor, a cardueline finch as indicated by DNA–DNA hybridization (Sibley and Ahlquist 1982), was not a flower-visiting species (Bock 1970).

Cyanea is the largest genus of endemic plants on the Hawaiian islands. The ancestor of the Hawaiian lobelioids probably was an ornithophilous species. *Cyanea* comprises 55 species (Givnish et al. 1995) and has undergone adaptive radiations in growth form, leaf shape and floral morphology. *Cyanea* appears to have coevolved with honeycreepers (Drepanididae) and

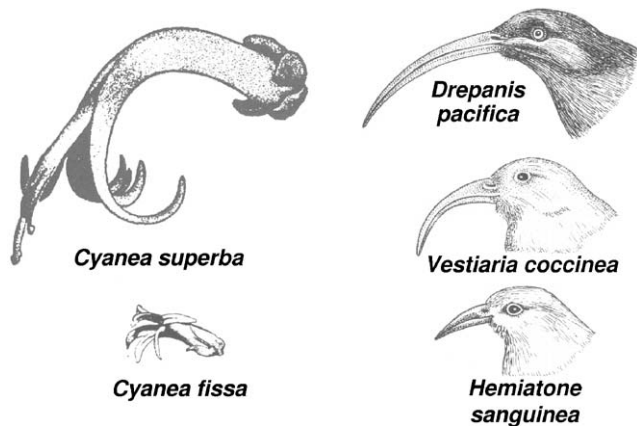


Fig. 2. Curvature as coadaptation: corolla tubes of *Cyanea fissa* and *C. superba*, heads and bills of *Drepanis pacifica*, *Vestiaria coccinea* and *Hemiatone sanguinea*. Modified and combined from Sedlag (1972) and Givnish et al. (1995).

honeyeaters (Meliphagidae), both of which serve as pollinators (Givnish et al. 1995). The most striking coadaptations in the pollination context are the corolla tube length, ranging between 15 and 85 mm, and the curvature of the corolla tube. Both traits seem to be fine-tuned to bill size and shape of the pollinating birds (Fig. 2). The aspect of diversification and radiation in these groups has been studied much more intensively than those of coevolution between them.

Island faunas are often secondarily enriched through extensive speciation. The effect of isolation frequently manifests itself as a paucity of lineages. Rare colonizers of islands potentially open new adaptive zones. There are numerous examples of adaptive radiations on archipelagos, such as the Darwin's finches on the Galapagos archipelago (Petren et al. 1999), and the Silversword Alliance (Compositae; Baldwin and Sanderson 1998) and the drosophilids (Diptera, Insecta; Kambysellis and Craddock 1997) on the Hawaiian archipelago. However, among those there is only one prominent example, the Hawaiian honeycreepers and lobelioids, in which parallel adaptive radiations and coevolution between flowering plants and pollinators play a major role.

Geographical mosaic of coevolutionary interaction: Greya moths and host plants

The mutualism found in the vast majority of pollination case histories is characterized by benefits to both the flowering plants and their visitors. However, flowers ordinarily do not provide easy and full access to all floral resources, and flower-visitors normally do not actively pollinate flowers. Among the outstanding exceptions are some few cases of active pollination known in the obligate mutualistic systems of figs (*Ficus*,

Moraceae) and fig wasps (Agaonidae, Hymenoptera) (Bronstein 1988; Machado et al. 2001; Weiblen 2002; Molbo et al. 2003), and of *Yucca* plants (Agavaceae) and yucca moths (Prodoxidae, Lepidoptera) (Pellmyr and Krenn 2002).

Females of the true yucca-moth genera *Tegeticula* and *Parategeticula* collect pollen and actively pollinate yucca flowers before ovipositing into the carpel on which the larva will feed. The actively pollinating yucca-moth females possess unique tentacles on their maxillary palps, which Pellmyr and Krenn (2002) regard as a key innovation for the adaptive radiation of true yucca moths. The moths use these tentacles to collect pollen on the first *Yucca* flower they visit and to deposit the pollen on the floral styles (active pollination) of this and other flowers visited prior to oviposition. Pellmyr and Leebens-Mack (1999) found evidence for rapid diversification of true yucca moths following the colonization of yuccas 41.5 million years ago (Mya) and an explosive radiation of the *Tegeticula yuccasella* complex 3.2 Mya (Fig. 3). The second radiation coincided with a rapid aridification that extended or created the primary extant habitats for the capsular-fruited yuccas and their moth associates. Twice within the *Tegeticula yuccasella* complex 'cheaters' evolved, species which still possess the maxillary tentacles, but do not actively pollinate flowers at all (Fig. 3).

The evolution of the yucca moths is highlighted by several key innovations accelerating diversification (Pellmyr and Leebens-Mack 1999). It is not clear, however, whether the recent diversification rate can be ascribed to the first or second of the above-mentioned radiations, or to both. It is known that the radiation of the *Tegeticula yuccasella* complex was paralleled by a radiation of the yucca plants. Though phylogenetic data for *Yucca* are still limited, Pellmyr and Leebens-Mack (1999) were able to exclude the possibility that strict cospeciation of true yucca moths and capsular-seeded yucca plants led to parallel radiation.

An insect functioning both as a pollinator and as a floral parasite can be strongly mutualistic, commensalistic or antagonistic in different habitats by means of diffuse coevolution. The studies by Thompson and Cunningham (2002) on pollination in *Lithographa parviflorum* (Saxifragaceae) by the parasitic moth *Greya politella* (Prodoxidae) provide strong evidence that dynamic coevolutionary selection creates a selection mosaic among habitats. Oviposition behaviour and larval development of *G. politella* closely resemble those of the true yucca moths of the genera *Tegeticula* and *Parategeticula*, but pollination by *G. politella* is more passive rather than active. Thompson and Cunningham (2002) showed that in *L. parviflorum* populations relying on pollination by *G. politella* developed capsules were much more likely to have *Greya* eggs than were aborted capsules, whereas in *L. parviflorum* populations with

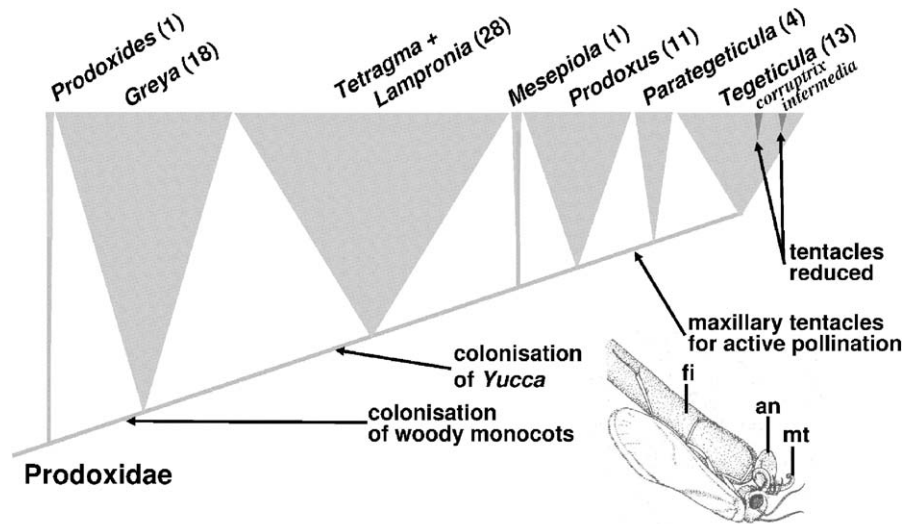


Fig. 3. Phylogeny and key innovations of the yucca moths (Prodoxidae). Species numbers per genus or tribe are given in parentheses (data after Pellmyr 2003). Non-pollinating cheating species with reduced tentacles are marked. Inset: active pollination by a true yucca moth (an = anther, fi = filament, mt = maxillary tentacle). Modified from Knoll (1956, after Riley 1892) and Pellmyr and Krenn (2002).

non-parasitic copollinators the reverse was true: developed capsules were more likely not to have *Greya* eggs than were aborted capsules. They also found *L. parviflorum* populations in which *G. politella* pollination and oviposition had no influence on seed development, indicating major pollination effects by abundant copollinators. The coevolutionary selection mosaic remained stable across multiple generations in populations often less than 100 km apart. It is not known whether the *Greya* moths have evolved coadaptations in response to abortion of capsules. Selection pressure would favour the evolution of strengthened sensory filtering mechanisms for host-plant detection, visitation of freshly opened, not yet pollinated flowers, etc.

The ornithophilous flowers of *Heliconia bihai* and *H. caribaea* show different outcomes of coevolution with the purple-throated carib hummingbird, their sole pollinator. *Eulampis jugularis* represents the hummingbird species with the most extreme sexual dimorphism in bill size and curvature. The *Heliconia* species are monomorphic throughout the Lesser Antillean islands, with flowers of *H. bihai* corresponding to the long, curved bills of *E. jugularis* females, and flowers of *H. caribaea* corresponding to the short, straight bills of males. However, Temeles and Kress (2003) showed that on St. Lucia, where *H. caribaea* is rare, a second morph of *H. bihai* carries flowers that match the bills of the *E. jugularis* females, whereas on Dominica a second morph of *H. caribaea* shows flowers that match the bills of the males.

Geographic variation within species includes populations specialized to different coevolutionary interactions. Driven by geographical differences of

specialization in coevolutionary interactions, coevolution may result in speciation (Thompson 1994, 1999). The theory of complex population-level mosaics of coevolutionary interactions has led to a better understanding of potential ‘hot spots’ for specialization and speciation.

Specialization and generalization in coevolutionary interactions: nectar spurs and long-tongued insects

Flowers with deep floral tubes or nectar spurs are pollinated by flower-visitors with mouthparts of corresponding length. Darwin (1862) was the first to infer that the evolution of deep flowers could be related to an evolutionary race with the pollinators. Nilsson (1998) noted that Darwin’s ingenious conclusion regarding the Madagascar Star Orchid, *Angraecum sesquipedale*, and its predicted pollinator has received only anecdotal attention, even though the sphingid moth *Xanthopan morgani praedicta*, described by Rothschild and Jordan (1903, p. 30), has long been known to match Darwin’s prediction.

Nilsson (1978) collected quantitative data on the pollination success of the orchid *Platanthera chlorantha*, which showed a correlation between floral spur length and pollinaria placement or fruit set. The pollinarium, which contains all the pollen grains of a single flower, is attached to the flower-visitor only if suitable hairless or scaleless parts of the visitor’s head touch the viscid disc when the head is forced against the spur mouth. Nilsson (1988, 1998) has developed a model of a coevolutionary race, which integrates his findings on the functional

adaptation mechanism in the floral nectar spurs, that reproductive success is positively correlated with spur length, and his hypothesis regarding the functional adaptation mechanism in the flower-visitor's proboscis, that reproductive success is positively correlated with proboscis length. Fuelled by the constant selection pressure for elongation of both the spurs of the nectariferous flowers and the probosces of the nectar-sucking hawkmoths, intense reciprocal coevolutionary interaction has led to flowers with spurs of extraordinary length and to flower-visitors with extraordinarily long mouthparts (Fig. 4). In contrast, Wasserthal (1997) questioned the coevolutionary race hypothesis and interpreted the proboscis with extreme length as an organ for keeping at a distance any predators that might be waiting in ambush on flowers. Nectar spurs not only facilitate evolutionary change via elongation caused by permanent reciprocal selective pressure, but also function as a mechanical barrier to short-tongued flower-visitors.

Hodges and Arnold (1995) have demonstrated that nectar spurs are key innovations leading to intense diversification in those plant taxa that had independently developed this feature (in at least 15 cases, see Hodges 1997). Sister-group comparisons are critical for tests of the impact of key innovations on the diversification rate. For eight of the angiosperm taxa that have independently evolved nectar spurs, Hodges and Arnold (1995) were able to determine that the sister group is lacking spurred flowers. Seven out of these eight taxa, each including all extant species related to a common ancestor which independently evolved a nectar spur,

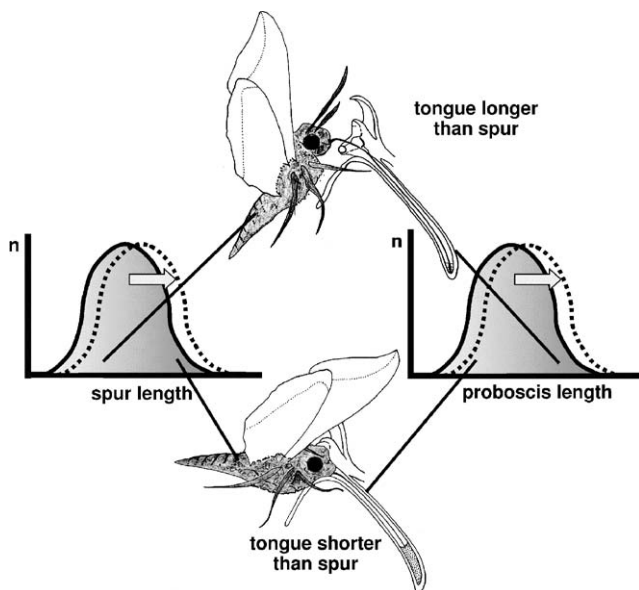


Fig. 4. Coevolutionary race model for a long-tongued sphingid moth and a deep-spurred orchid. Arrows and dotted lines indicate shifts in character distribution of successive generations. Modified from Nilsson (1988).

contain more species than the respective sister taxon without nectar spurs (Table 1).

Although evolution of deep nectar spurs and long tongues is obviously strictly reciprocal, it does not necessarily constitute two-partner coevolution. Hapeman and Inoue (1997) showed frequent changes of pollinators for the orchid genus *Platanthera*, including switches from the initial nocturnal settling moths to nocturnal hawkmoths, diurnal hawkmoths, mosquitoes, butterflies, empidid flies, and bees (Fig. 5). Based on a molecular-systematic study they found, related to the changes of pollinators, convergent changes of flowering time, flower colour, pollinaria placement, and other characters. Hapeman and Inoue (1997) speculated that floral diversification as a result of pollinator-mediated selection has been an important driving force in the radiation of the orchids. The huge diversity of pollination syndromes found within the genus *Platanthera* might have been enhanced by intraspecific variation of floral traits correlated with pollination according to a geographical pattern, and by variation of the pollinator fauna. Local adaptations of populations within species are regarded as an important mechanism that gives rise to new species by divergent selection (Schluter 2001). Diffuse coevolution of a single *Platanthera* species can involve many partner species: Nilsson (1978) listed 28 species, belonging to four families of the Lepidoptera, that serve as pollen vectors of *P. chlorantha*. However, this multispecific system of diffuse coevolution is likely to be a spatio-temporally variable mosaic of more specialized subsystems, and to include populations with a potential for specialization.

Goldblatt et al. (1998) reported on the adaptive radiation in the genus *Gladiolus* (Iridaceae), comprising 250 species. The vast majority of *Gladiolus* species has moderate-sized flowers with obliquely funnel-shaped tubes, which show a close morphological fit between tube shape, diameter and length and the shape and size of the insect pollinator's head and thorax. *Gladiolus* species are pollinated by long-tongued flies (mouthpart length up to 14 mm) and anthophorine bees (mouthpart length between 4 and 10 mm), both of which extract nectar produced at the base of the tube. Narrow, elongate floral tubes thus may act as a key innovation, similar in this respect to nectar spurs.

Asymmetrical adaptation in coevolved systems: oligolectic bees and angiosperm pollen resources

Many zoophilous flowering plants attract a number of different pollinators, and many pollinating species use a large array of food plants, integrating plant and pollinator species into a diffuse coevolution system. Both the plant and the pollinator species have various coadaptations in the context of flower-visitation and

Table 1. Numbers of species for monophyletic taxa with spurred flowers, and for respective sister taxa with unspurred flowers

Taxa with flowers spurred	Numbers of species	Taxa with flowers unspurred	Numbers of species
<i>Aquilegia</i>	70	<i>Semiaquilegia</i>	1
<i>Delphinium</i> , <i>Aconitum</i>	350	<i>Nigella</i>	14
Fumariaceae	450	<i>Hypericum</i> (Papaveraceae)	15
Tropaeolaceae	88	Akaniaceae (Bretschneideraceae)	2
<i>Noisettia</i> , <i>Viola</i>	401	Subgroup of <i>Hybanthus</i>	<150
Lentibulariaceae	245	Bibliaceae	2
<i>Pelargonium</i>	280	<i>Geranium</i> , <i>Erodium</i> , <i>Nonsonia</i> , <i>Sarcocaulon</i>	399

Note: Modified from Hodges (1997).

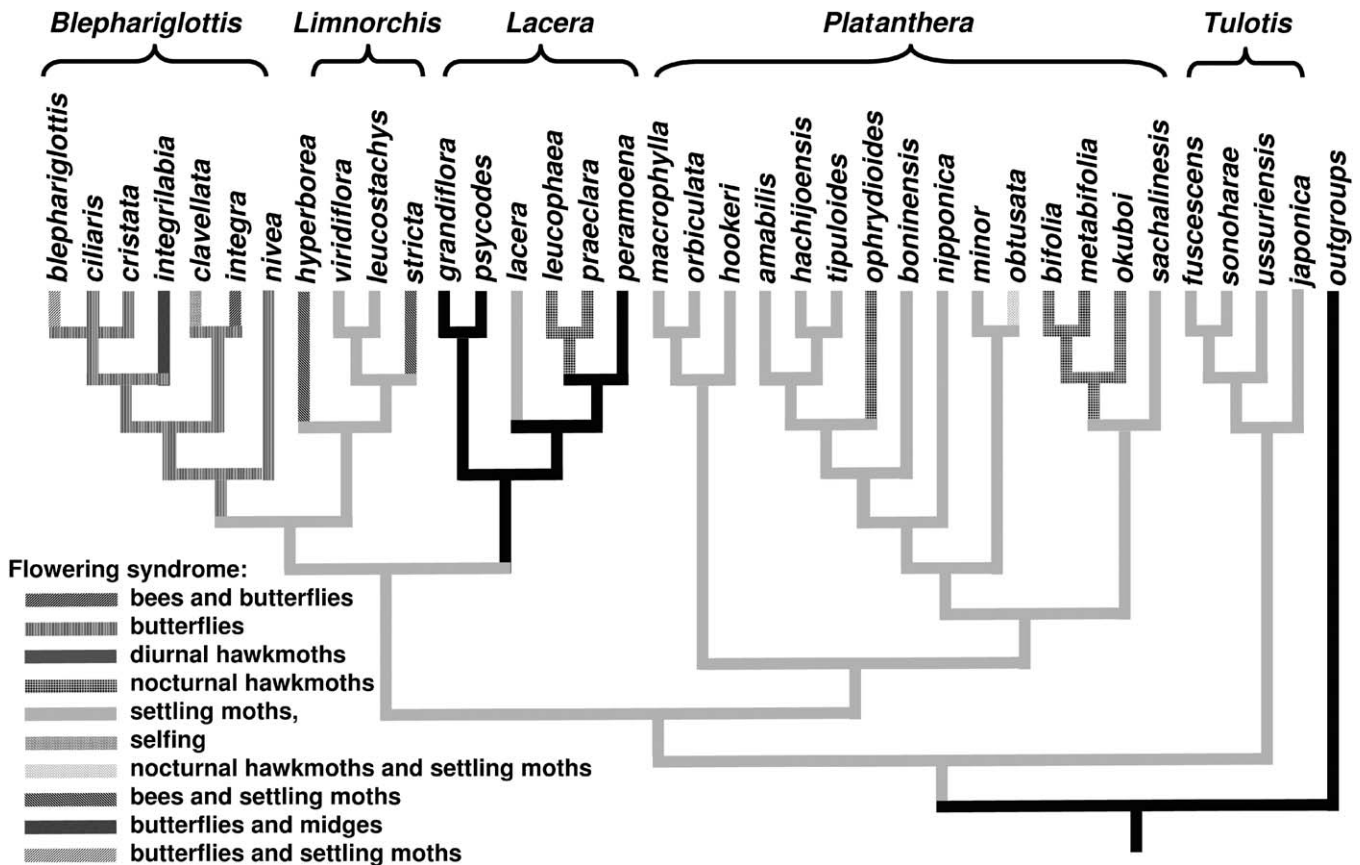


Fig. 5. Pollinators of *P. chloantha*, identified by successful pollinaria removals, superimposed on a cladogram of the genus *Platanthera* (strict consensus tree based on molecular sequence analysis of *m/COI*) with the five major clades indicated: *Blephariglottis*, *Limnorchis*, *Lacera*, *Platanthera*, and *Tulotis*. Modified from Hapeman and Inoue (1997).

pollination. However, in most cases none of these coadaptations can be attributed to a specific coevolving species within the diffuse coevolution system. The unspecialized character state of coadaptations in generalistic pollinators and flowers is typical for generalistic, multispecific pollination systems. A remarkable exception are oligolectic bees, which are generalistic flower-visitors but specialize in a clearly defined small set of related plant species, the pollen of which is used as food.

Bees rely on floral nectar and pollen for feeding and providing food to larval nest cells. They may or may not specialize in specific food plants. Oligolecty, i.e. the specializing in a few closely related plant species as pollen resources, usually in a single genus or family, is characteristic for 23% of the bee species in Germany (Westrich 1990). The origin of oligolecty of solitary bees is not well understood. Oligolecty is regarded as a one-sided adaptation of the solitary bees, because far more adaptations of oligolectes to exploiting the specific pollen

food plants have been found than adaptations of the pollen food plants to facilitating pollination by oligoleges (Thorp 1979, 2000; Müller 1995). Moreover, all of the food plants of oligolectic bees are also visited by polylectic bees and/or other unspecific flower-visitors. Oligolectic bees generally are not more efficient pollinators of their food plants than polylectic bees (but see Schlindwein and Wittmann 1997). These data suggest that oligolectic bee species and their particular food-plant species do not closely coevolve. Instead they are component species of a diffuse coevolutionary system, in which the oligolectic bees exhibit more specific adaptations tuned to pollen collection on their food plants than do polylectic flower-visitors.

Some oligolectic bees have adaptations directly related to oligolecty, such as specialized pollen-collection and pollen-transport structures optimized for pollen gathering from the specific food plants. However, physiological adaptations — sensory adaptations to detect food plants, behavioural adaptations to handle the flowers effectively, and metabolic adaptations enabling the larvae to grow on the supplied pollen — have only occasionally been tested (Bohart and Youseff 1976; Müller 1996; Dobson and Peng 1997).

The assumption that pollen-collecting oligoleges are more efficient than polyleges underlies some hypothetical explanations for the diversity of oligolectic bees (Strickler 1979). Schröder and Lunau (2001) demonstrated that females of the oligolectic *Andrena florea*, a specialist on *Bryonia* (Cucurbitaceae), are collecting pollen in the early morning following synchronous pollen presentation by the staminate flowers. The availability of pollen to other flower-visitors is thereby reduced to 50% before the latter even start foraging (Fig. 6). Only in the absence of *A. florea* females did females of *Lasioglossum* show up early in the morning to collect pollen at staminate flowers. Although there is no

direct evidence for individual adjustment of pollen-collection times in pollen-foraging *A. florea* females, the narrow time slot for effective pollen collection suggests strong selective pressure for adjustment of pollen-collection behaviour. The suggestion that the specialization of oligolectic bees may be correlated with a high nutritive value of the pollen was not confirmed by Roulston et al. (2000). The digestion of pollen may be limited by pollen allelochemicals. Thus, the digestion of pollen rich in allelochemicals may require distinct metabolo-physiological adaptations such as mechanisms of detoxification in the larvae of oligolectic bees (Williams 2003), and help to escape cleptoparasites (Budde et al., 2004, in press).

Robertson (1925), Linsley (1958), Michener (1979), and Strickler (1979) found that the proportion of oligoleges is highest in species-rich bee assemblages, and suggested that oligolecty reduces interspecific competition for pollen via resource partitioning. Since many oligolectic bees use their specific food plants for rendezvous, courtship and mating, a host-plant switch may lead to strict reproductive isolation and facilitate ecological speciation (Schemske 1983). In this respect, oligolectic bees resemble monolectic or oligolectic phytophagous insects such as tephritid flies for which sympatric speciation has been demonstrated (Filchak et al. 2000).

Promotion of parallel evolution by coevolution: plant–pollinator interactions and angiosperm adaptive radiation

In this section, I shall discuss hypotheses relating the radiation of the Angiospermae to a single key innovation, and alternative hypotheses linking angiosperm diversity to several key adaptations. The focus is on

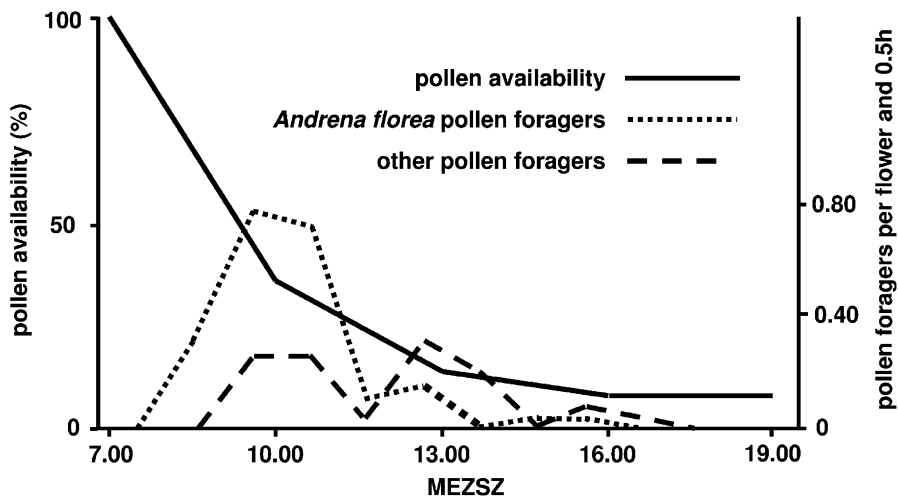


Fig. 6. Development of pollen availability (in per cent of the maximum) in staminate *Bryonia dioica* flowers during daytime, and number of pollen foragers (*A. florea* versus others) per flower and 30 min. Modified from Schröder and Lunau (2001).

angiosperm key innovations related to pollination biology.

Key innovations and angiosperm radiation

In a letter to Sir Joseph Hooker, Charles Darwin stated in 1879: “The rapid development as far as we can judge of all the higher plants within recent geological times is an abominable mystery.” (Darwin and Seeward 1903, pp. 20–21) The timing and causes of angiosperm radiation were summarized a century later by Dilcher (1979), who concluded that the coevolution of angiosperms and insects, once established, underwent an explosive radiation. Recent phylogenetic studies include a renaissance of papers on early angiosperm radiation (Lloyd and Wells 1992; Pellmyr 1992; Sanderson and Donoghue 1994; Crepet 1998, 2000; Qiu et al. 1999; Renner 1999; Frohlich and Parker 2000; Soltis et al. 2000; Zanis et al. 2002; APG II 2003).

The evolutionary success of taxa is often attributed to a single key innovation. The key-innovation concept is controversial, because it is difficult to test hypothesized key innovations and because researchers interpret the concept in different ways (Hunter 1998). The basic idea is that some attributes of organisms have been especially important in evolutionary processes. Key innovations may enhance competitive abilities, open new adaptive zones, promote further evolutionary change, and foster speciation and ecological diversification. Attempts to explain angiosperm diversity have been directed at key innovations such as adaptations regarding the emancipation from water, energetic requirements, and coevolution with animals, some of which are discussed here in more detail. Because angiosperm subtaxa share many angiosperm key characters related to pollination biology, parsimonious hypotheses assume a common ancestor to have accumulated these synapomorphic characters. Here, I ask whether diffuse coevolution could cause convergent evolution of innovations in different angiosperm lines, and develop a scenario in which the transfer of selective pressure among unrelated angiosperm species via the activity of pollinators plays a major role.

Many authors regard biotic pollination as a key innovation of the Angiospermae (Regal 1977, 1982; Raven 1977; Crepet 1984; Midgley and Bond 1991; Pellmyr 1992). More specifically, the directional pollen transfer achieved by insect flower-visits is regarded as a key innovation by Regal (1977) and Crepet (1984). According to Mulcahy (1979), increased sporophytic competition and mate choice caused by animal transfer of pollen confer a decisive competitive advantage over other land plants. He argues that anemophilous flowers are most likely pollinated by single pollen grains from

time to time, whereas zoophilous flowers are pollinated by several pollen grains at a time, causing a large potential for mate choice. The whorled floral structure that facilitates synorganization leading to new structures could have been a key factor in angiosperm diversification (Endress 2001). Some authors designated key adaptations of the Angiospermae that compensate negative effects of animal pollinators, as follows. The angiospermous closed carpels, angiospermy (Stebbins 1981) or the enclosed ovules (Crepet 1984) could have protected plants against the deleterious effects of herbivorous pollinators with chewing mouthparts; stigmas as pollen-capturing areas instead of pollination droplets may have been a necessary prerequisite for animal pollination in that they prevented losses of transferred pollen by pollinators' manipulations of the flowers; and hermaphroditic flowers prevented flower-visitors from specializing in floral morphs such as staminate or pistillate flowers (Crepet 1984).

Although these innovations are generally attributed to the radiation of the Angiospermae as a whole, it has not been explicitly argued that they constitute synapomorphies. This parameter is critical in order to correlate a key innovation with angiosperm radiation. Sanderson and Donoghue (1994) tested whether a significant increase in the diversification rate coincided with the origin of the angiosperms and their synapomorphies, using a maximum-likelihood statistical framework. They drew upon recent phylogenetic analyses which agree that the Gnetales (69 species) are the closest relatives of the Angiospermae (233,885 species). Irrespective of the use of a magnolialian or paleoherb root of the Angiospermae, the results rejected the key-innovation hypothesis for angiosperm radiation, in which the increase in the branching rate matches the evolution of the hypothetical key innovation irrespective of the assumption of a paleoherb ingroup (Nymphaeaceae, 70 species; Chloranthaceae, 70 species; Ceratophyllaceae, six species) or of a magnolialian ingroup (Magnoliaceae, 2847 species). Sanderson and Donoghue's (1994) analysis showed that a large increase in branching rate is required for the remainder-of-angiosperm ingroup, and supports scenarios other than single key innovations to explain the adaptive radiation of the Angiospermae. Due to recent studies, assumptions regarding the basal phylogeny of angiosperms and proximal outgroups have changed (e.g. Qiu et al. 1999; Soltis et al. 1999; Zanis et al. 2002; APG II 2003). In light of recent insights into angiosperm phylogeny, with the more species-rich Gymnospermae as the sister taxon and the monotypic Amborellaceae family as the most primitive angiosperm group, rigorous testing of the correlation between key adaptations and increase of diversification rate suggests that the increase of diversification is obviously not linked to apomorphies of the taxon Angiospermae.

Dilcher (2000) described three major nodes in time that resulted in major radiations of the angiosperms: (1) the Mesozoic initial coevolution between angiosperms and insect pollinators corresponded to the evolution of closed carpels and showy radial flowers; (2) about 60 million years after the origin of the angiosperms, clades with zoophilous species that independently developed bilateral flowers showed increased diversification; (3) the Eocene angiosperm radiations were linked to the evolution of large, stony and fleshy fruits and seeds. There is a problem with attributing species richness of plant families to a key innovation like bilateral flowers, because it has to be shown that bilateral flowers are not a plesiomorphic trait shared with common ancestors nor a trait which developed independently within several subclades, or an apomorphic trait of a subclade. A further problem in this context is how to identify a key innovation: as Schluter (2000) has laid out, there is the problem of circular reasoning here, if we identify a significantly species-rich group and use its apomorphies post facto as key innovations without analysing ingroup diversity. In other words, based on the superior species diversity in a taxon as compared to a sister taxon, it is not possible to conclude that one of the apomorphies of the more species-rich taxon represents a key innovation. Moreover, the key-innovation concept implies everlasting effects of a key innovation on the diversification rate.

A change in the rate of diversification is not necessarily related to a single trait. It is also possible that key innovations are precursors of the evolution of further key innovations that may or may not accelerate the rate of diversification in one of the two ingroups. Whereas hypothetical key innovations such as pollination by animals and the hermaphroditic flower could have opened the way for the evolution of further key innovations without an effect on diversification, other hypothetical key innovations such as a closed carpel or a stigma as the pollen-collection organ could have been breakthroughs and directly promote adaptive radiation.

Studies of angiosperm fossils support the hypothesis that the increase of angiosperm species diversity occurred long after the angiosperm origin, and in parallel in different lines. An analysis performed on 197 macrofossil floras reveals a pattern of angiosperm diversification that can be approximated by a logistic growth model, with moderate increase of species richness in the Jurassic and after the mid-Cretaceous, and a major rise in angiosperm diversity in the lower Cretaceous, from 110 to 90 Mya. Some non-angiosperm groups, such as cycadophytes and pteridophytes, show pronounced shifts of diversification in association with the angiosperm radiation, which suggests competitive displacement (Fig. 7; Lidgard and Crane 1988). The improved fossil record for insects (Grimaldi 1999) and for angiosperms (Lidgard and Crane 1988) in conjunc-

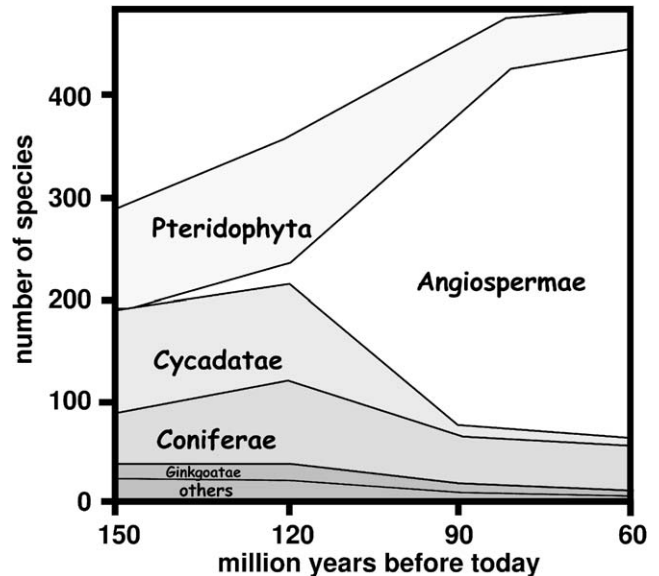


Fig. 7. Change in numbers of species of Pteridophyta, Angiospermae, Cycadatae, Coniferae, Ginkgoatae, and other land plants from 150 to 60 million years before the present, calculated from 197 fossil floras. Modified from Lidgard and Crane (1988).

tion with data on the phylogeny of flower-visitor taxa provides evidence for a parallel radiation in angiosperms and various groups of insect flower-visitors. Based on the interpretation of Mesozoic fossils, Grimaldi (1999) showed that the radiations of major anthophilous groups of insects, such as bees (Apoidea), pollen wasps (Masaridae), syrphid flies (Syrphidae), bombyliid flies (Bombyliidae), and butterflies (Lepidoptera) took place in the mid-Cretaceous, and paralleled the increase of diversification of angiosperms (Fig. 8).

Analysing the fossil record and molecular sequence data for the anthophytes, Crepet (2000) presented additional evidence that the temporal pattern of radiation in the Angiospermae is consistent with the radiation pattern of anthophilous insects, exemplified by a compelling similarity in the rate of floral innovations per time, and an increase in diversification 110–90 Mya. Evidence from the fossil record suggests that floral innovations related to pollination such as bilateral symmetry, the corolla tube, nectar flowers, staminodal nectaries, a single style in combination with multiple carpels, and viscin threads appeared first in the Turonian, 90 million years before now and 40 million years after the presumed origin of angiosperms, and developed in parallel in different lines (Crepet 1996).

Benefits and costs of animal pollination

The scenario developed here takes as its starting point the numerous cases of parallel evolution in the cognitive

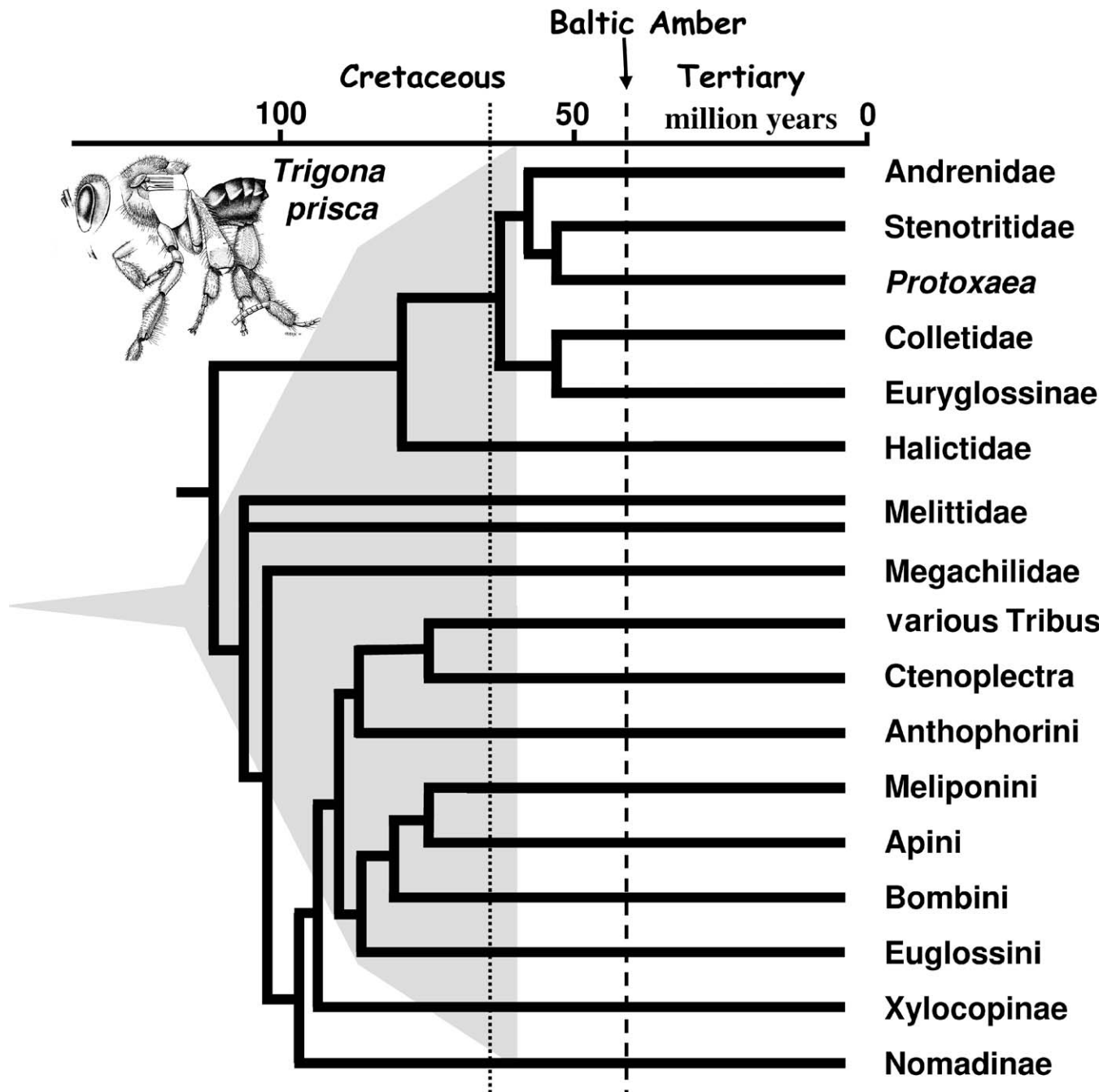


Fig. 8. Cladogram of bee taxa based on morphological and molecular data. Fossil records are indicated by dark lines. Area shaded in grey indicates species diversity of Angiospermae as calculated from fossil records according to Lidgard and Crane (1988). Inset: The 'oldest' bee, *Trigona prisca*. Modified from Grimaldi (1999).

abilities of flower-visiting animals and in the signalling apparatus of angiosperm flowers, as recognized by Baker (1963) and Stebbins (1970). The anemophilous ancestors of the Angiospermae had unisexual flowers with different nutrient-rich organs that might have attracted herbivores. The staminate flowers produced pollen, and the carpellate flowers possessed ovaries and probably sugar-containing pollination droplets (Osche

1983; Lloyd and Wells 1992; Lunau 2000). Flower-visitors exploiting either pollen of staminate flowers or pollination droplets and/or ovaries of carpellate flowers were herbivores without any beneficial effects on plant reproduction. Plants benefited from flower-visitors only when their services as a pollen vector overcompensated for the costly and harmful effects of feeding on floral resources. The evolution of bisexual flowers was thus a

necessary prerequisite to benefiting from otherwise harmful herbivores. It had a large impact on reproductive success, because bisexual flowers facilitated self-pollination and self-fertilization. Floral hermaphroditism results in conflicts and compromises in the parental roles of plants during pollination and mating (Barrett 2002). The reduction of and compensation for costs associated with sexual interference, self-pollination and self-fertilization is a largely underestimated selective pressure which could have had great impact on the evolution and diversification of zoophilous angiosperms. Self-fertilization can be reduced by self-sterility mechanisms which probably evolved in angiosperm ancestors (de Nettancourt 1977; Weller et al. 1995). Reduction of sexual interference and self-pollination required separation of the staminate and pistillate functions of flowers either in time or in space: the separation of the staminate and pistillate floral functions in space is correlated with the evolution of secondary polymorphisms such as secondary dichliny, dimorphic and trimorphic heterostyly, and enantiostyly (Barrett 2002); the separation of the staminate and pistillate floral functions in time is correlated with the evolution of flowering phases associated with dichogamy or temporal herkogamy (Lunau 2000).

Costs for flowering plants specifically associated with pollen arise when the pollen is eaten by illegitimate flower-visitors and by pollinators, or collected by either sort of visitor, and as a result of clogging, i.e. the occupation of receptive areas on the stigma by inappropriate pollen grains, which prevents appropriate grains from germinating. Other losses of pollen are related to cleaning behaviour of flower-visitors, low flower fidelity of flower-visitors leading to pollen wastage, and climatic conditions such as rain, wind, or insolation associated with mutagenic UV-radiation and overheating. The costs to flowering plants associated with pollen can be reduced by providing nectar instead of pollen as a reward, by portioning pollen release via secondary pollen presentation and poricidal anthers, employing pollinaria (a compact pollen-transport form that is not eaten or collected by flower-visitors as food), the functional separation of pollination anthers and feeding anthers, or by the concealment of stamens and pollen in the floral tube or in other floral structures. These adaptations not only help reduce the costs of hermaphroditic flowers and pollen reward, but also have a strong impact on the coevolution with pollinating insects, because the signalling function of pollen is affected (Lunau 2000).

Pollen-eating insects are able to detect pollen and/or pollen-bearing anthers by signals of various sensory modalities: tactile (Gack 1981), olfactory (Dobson 1988; Lunau 1992), gustatory (Schmidt 1985; Wacht et al. 1996, 2000) and visual (Lunau and Maier 1995; Lunau 1996). Inexperienced flower-visitors are known to

possess innate mechanisms to locate and detect pollen. In naive syrphid flies (*Eristalis tenax*) the innate proboscis extension is released by visual stimuli and precisely tuned to the spectral reflection properties of yellow pollen of the natural food plants (Lunau and Wacht 1994, 1997). Bumblebees possess a neurosensory filtering mechanism tuned to a common colour pattern of bee-visited angiosperm flowers, which enables naive bumblebees (*Bombus terrestris*) to spontaneously respond to a distinct set of floral signals (Lunau 1991; Lunau et al. 1996; Gumbert 2000), placing their antennal tips in contact with stamens in response to visual signals prior to landing. Besides the shape of the anthers, their colour purity and contrast with the corolla efficiently release the antennal reaction (Lunau 1991; Lunau et al. 1996). The landing behaviour is cued to pollen scent emitted from the surfaces contacted during the antennal response (Lunau 1992). Analysis of spontaneous-choice behaviour of naive bumblebees shows that two-coloured artificial flowers not only attract the approaching bees towards a central, pollen-yellow spot, but also attract more approaches than single-coloured artificial flowers (Fieselmann and Lunau, unpublished; Heuschen et al. unpublished).

Their innate search images guide these bee and syrphid flower-visitors towards the places on flowers that they then inspect more closely in search of food. Some pollen flowers visually display pollen to attract flower-visitors. If pollen is not a floral reward and/or not visually displayed, pollen-mimetic structures may replace the actual pollen as signals (Osche 1983; Lunau 2000). It is obvious that fixed, innate search images of pollen signals constrain the evolution of the flowers' signalling devices and lead to the standardization of floral signalling components, i.e. the colour signals of pollen, anthers, stamens, androecia, and of pollen- and stamen-mimicking organs (Osche 1983; Lunau 2000). In the genus *Iris*, for example, the flowers have evolved a variety of morphological features that mimic stamens (see Electronic Supplement 04–05, Part 3), e.g. a beard of white hairs with yellow, swollen apices (*Iris germanica*), a semi-plastic arch (*I. reticulata*), a comb-like structure (*I. cristata*), a lobed yellow patch (*I. japonica*), a velvet-like cushion (*I. marginata*), or a patch contrasting mostly at UV wavelengths (*I. pseudacorus*).

Flower constancy is a foraging strategy in which individual flower-visitors use associative learning abilities to discriminate between plant species and preferentially visit rewarding species, usually only a single, most rewarding species even though other species are flowering in the same habitat (Waser 1986). Bees in particular have a highly developed capacity to learn visual stimuli (Menzel and Erber 1978; Menzel 1979, 1983, 1985). Pollen signals are not excluded from associative learning. Bumblebees (*B. terrestris*), for example, in experiments with artificial flowers rapidly

and accurately learn to choose the ones that provide a reward, on the basis of pollen signals (dummy anthers). In reciprocal training experiments, however, they can also learn the opposite behaviour: they can just as readily be trained to land on artificial flowers without pollen signals rather than on those that have them, when offered a choice (Gack 1981). Syrphid flies (*Eristalis pertinax*) can be similarly trained to land on targets either with or without pollen signals, but their maximal level of accuracy is lower (Lunau 1988).

The above-mentioned floral polymorphisms and flowering phases associated with heteranthy, absence or presence of pollen and stamens, or pollen depletion, enable flower-visitors to optimize foraging by exhibiting preferences for distinct floral morphs or flowering phases. Floral-morph and flowering-phase preferences are likely to decrease the reproductive success of the plants. Several studies, reviewed by Goulson (1999), confirm that flower-visitors use their sensory and learning capabilities to assess reward availability of individual conspecific flowers. Schemske et al. (1996) showed that *Bombus ephippiatus* preferentially visited male-phase inflorescences and the larger and pollen-rewarding staminate flowers of the neotropical monocious *Begonia oaxacana*. Pellmyr (1988) showed that bumblebees (*Bombus honshuensis*) assess pollen availability in *Anemonopsis macrophylla* through the floral shape, which systematically varies with floral age, and select young flowers that offer a good pollen reward rapidly without alighting. On *Dodecatheon conjugens* flowers, bumblebees (*Bombus* spp.) were not able to visually assess pollen availability, because pollen is gradually released from introrse anthers, but were able to monitor pollen-removal success during flower visits and buzzed pollen-rich flowers significantly longer than pollen-poor flowers (Harder 1990). In the tristylous *Pontederia cordata* (Pontederiaceae) the floral morphs do not differ in nectar reward, but differences in the number and size of pollen grains produced by the three anther levels result in differences of the amount of pollen available to flower-visitors. Monitoring of flower-visitation in *P. cordata* shows that nectar foragers (*Bombus* spp., *Melissodes apicata*) exhibited morph preferences less frequently than did pollen foragers (*Apis mellifera*) (Wolfe and Barrett 1987).

The evolution of floral signalling in angiosperms is accompanied by a remarkable evolution of flower detection mechanisms in flower-visitors. Flower fidelity, innate search images and flower constancy are associated with fixed or flexible preferences for certain flowers in the flower-visitors. Moreover, the capacity for associative learning provided flower-visitors with the ability to optimize foraging on flowers by the development of preferences for species, morphs, flowering phases, and amount of reward available. The discriminatory abilities of flower-visitors require the flowers to

become more uniform and to evolve signalling strategies in which the floral display is uncoupled from floral reward, from flowering phases, and from flower morphs. Concealment of nectar and pollen resources within the floral tubes, replacement of pollen reward by reward with nectar and oil, secondary pollen presentation (Erbar and Leins 1995), heteranthy associated with pollination stamens and feeding stamens, staminodes and false stamens all have a double impact, leading to both uniform floral reward and uniform floral signalling.

The angiosperm families with the greatest numbers of species have developed remarkable floral rewarding and signalling strategies. In the Orchidaceae (> 20,000 species), the pollen is not exploited by flower-visitors; many orchids offer nectar, fragrances or resins, or even deceive flower-visitors (Dafni 1984). The inflorescences of the Asteraceae (20,000 species) resemble a single flower; the disc florets often are yellow-coloured like pollen; pollen reward is prolonged by subsequent opening of florets, and even single florets possess a mechanism of secondary pollen presentation and portioning of pollen reward (Erbar and Leins 1995). The Fabaceae (18,000 species) have flowers in which the pollen reward is completely concealed in the keel. In the many (approximately 2000) species of the genus *Solanum* the flowers are nectarless; the pollen release is limited by poricidal anthers; the stiff and non-wilting anthers produce a constant pollen-yellow signal. That is why bumblebees must land on the flowers and buzz to assess pollen returns. However, Buchmann and Cane (1989) showed that the bumblebees' sonication responds positively to pollen-feedback. Poricidal anthers are known in more than 20,000 species belonging to 544 genera, 72 families, and 27 orders of the Angiospermae, and evolved in parallel in many cases (Buchmann and Cane 1989).

Floral signalling, coevolution, and reproductive isolation: monkeyflowers, hummingbird, and bee pollinators

The three major mechanisms promoting specialization in pollination systems are mechanical barriers limiting the access of flower-visitors to plant resources, metabolo-physiological barriers diminishing the palatability of floral resources for flower-visitors by repellent or toxic ingredients, and sensory barriers controlling the plant's attractiveness by matching or not matching the flower-visitors' search images, sensory capabilities, or preferences. Mechanical barriers are frequently found to control the access to pollen resources of flowers, for example in narrow-tubed and long-spurred flowers, in the mask flowers of the genera *Linaria*, *Anthirrhinum*, *Nemesia* (Scrophulariaceae) and

Utricularia (Lentibulariaceae) (Osche 1983), and in flowers with trigger mechanisms. Toxic ingredients are only occasionally found in nectar (Detzel and Wink 1993) and pollen (e.g. pyrrolizidine alkaloids in the pollen of *Senecio jacobaeae*; Budde et al. in press). Mismatches between the floral signalling apparatus and the search images of certain flower-visitors probably have been underestimated as a strategy to reduce pollen feeding and improve pollination.

Flower-visitors have search strategies that may be determined either by innate preferences for one distinct set of floral signals, or by modifiable learned preferences dependent on experience and reward. Floral signalling is well suited to exclude flower-visitors, allowing sensory barriers to act as a potential pre-mating reproductive isolation mechanism for the flowering plants. In a study with two closely related monkeyflower species, *Mimulus cardinalis* and *M. lewisii*, pollinator discrimination resulted in strong pre-mating reproductive isolation in sympatric populations of the two interfertile species (Schemske and Bradshaw 1999). By comparing the flower-visitation rates for the two species with those of F1 and F2 hybrids, expressing various quantitative floral traits such as nectar content, flower size, carotenoid content, and anthocyan content at different levels, Schemske and Bradshaw (1999) found strong preferences of bees (mainly *Bombus vosnesenskii*) for *M. lewisii*, and of hummingbirds (*Calypte anna*) for *M. cardinalis*, and intermediate preferences for the hybrids. They calculated from the relative visitation rates for the hybrids and their quantitative trait expression that bees preferred large flowers and that hummingbirds preferred anthocyan-rich and nectar-rich flowers.

Conclusions

The ‘adaptive zone’ is a key component of the ecological theory of adaptive radiation (Schluter 2000). It is defined as a collection of ecological licences in the sense of ecological niches that may be used by a set of species varying in phenotype but descendant from a common ancestor. The ecological niches may become available via opportunities to colonize remote islands or by the acquisition of key innovations (modified after Schluter 2000).

Coevolutionary interaction may fuel adaptive radiation in different ways.

- (1) Coadaptations, i.e. adaptations evolved in response to selective pressure from the coevolutionary partner, can promote adaptive radiations just as other key innovations do. This has been demonstrated for nectar spurs.
- (2) Two-species coevolution as well as diffuse coevolution may cause rapid evolutionary change by the

permanent reciprocal selective pressure acting on the two partners in a coevolutionary race, if both of them evolve coadaptations in the same context. A coevolutionary race between the parallel elongation of the nectar spurs of flowers and of the proboscis of pollinators has been proposed by Nilsson (1988). The resulting specialization is not directly linked to speciation, but facilitates resource partitioning among species.

- (3) Pollination systems can be connected via shared partners, in the network of the pollination market. An acceleration of evolutionary change and diversification may arise if two or more species share selective pressure via a coevolutionary partner species. The transfer of selective pressure between unrelated species through shared coevolutionary partners might have effected an enormous amount of parallel evolution in the signalling systems of flowers and inflorescences, as demonstrated for bilateral flowers and mimicked stamens.
- (4) Diffuse coevolution enables flowering plants to interact with different pollinators in different geographical regions, and may facilitate geographical patterning of coadaptations due to local specialization and local shifts of pollinators or food plants. The existence of a geographical mosaic of populations is thought to represent a major prerequisite for ecological speciation (Schluter 2001). If different populations of flowering plants end up sharing the same pollinating species, reproductive isolation occurs and facilitates ecological speciation.

It is generally accepted that key innovations can have positive impact on the diversification rate. It is not clear, however, how many subsequent speciation processes can be attributed to a single key innovation (Fig. 9). In other words, it is not clear how to determine the limited number of niches in an adaptive zone that can be attributed to a single adaptive radiation process. Within the framework of the definition used here, a species, e.g. *P. chlorantha*, may be a component of different adaptive radiation processes, e.g. the adaptive radiation of the land plants, that of the angiosperms, that of the orchids, and that of the genus *Platanthera*.

One weakness of the key-innovation concept lies in the focus on a single adaptive trait which is an apomorphy of the radiated group. This aspect of the concept ignores additive and synergistic effects from different adaptive traits. Moreover, the diversification in one lineage is compared to that of the sister group; this purely comparative approach represents another weakness of the adaptive radiation concept. Radiations will go unnoticed if adaptations in the sister clade caused a similar diversification, and consequently the radiation process is linked to an apomorphy of the superordinate

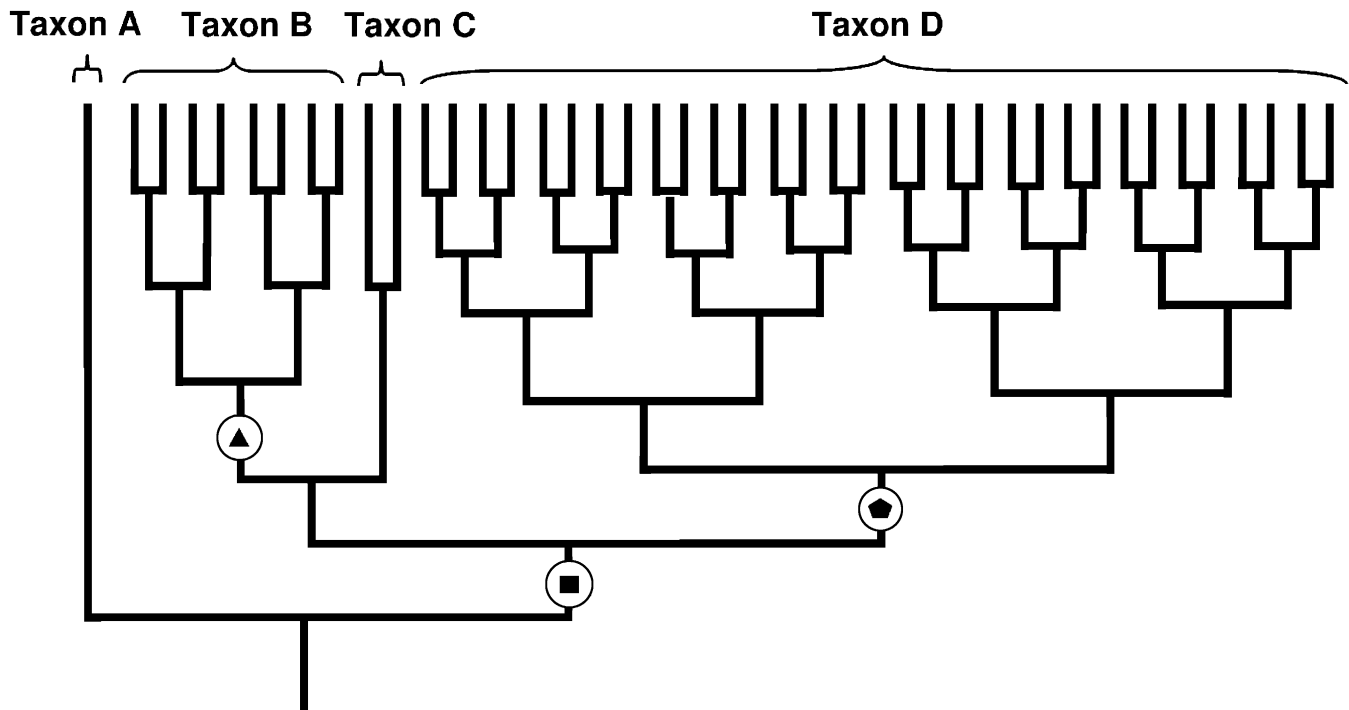


Fig. 9. Model cladogram to illustrate consequences of the criterion of relative species number for adaptive radiation. Taxon B has the key-innovation 'triangle', and more species than the sister taxon C. Taxon D has the key-innovation 'pentagon', and more species than the sister taxon B + C. Taxon B + C + D has the key-innovation 'rectangle', and more species than the sister taxon A.

taxon. A further problem is the requirement of a known phylogeny to ensure that the species richness of a taxon is not linked to a species-rich ingroup of this taxon.

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