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REFLECTIONS ON THE TRANSITION FROM WIND POLLINATION TO AMBOPHILY

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SUMMARY

In western and central Europe a limited number of anemophilous species has been observed to be regularly visited by anthophilous insects. Furthermore, it appears that the visitors may function as pollen vectors in a modest way. In open, wind-exposed environments, the typical habitat of anemophiles, biotic pollination is only of minor importance for their reproduction. On the basis of relevant indications two models are being suggested, visualising a change-over from anemophily to partial insect pollination (ambophily) at the population level. An extant relation of insects to an anemophilous population is regarded to be a necessary starting-point for a development towards ambophily. In addition, the occurrence within such a population of a genetic variant, characterised by a feature furthering biotic pollen transfer, is a prerequisite. Provided these conditions are being fulfilled, two different pathways may lead to ambophily. (1). In a population that is being subjected to conditions of decreased wind-intensity, only the variant is capable of surviving by availing itself of biotic pollen transfers, which may ultimately give rise to an ambophilous biotype. (2). In a population inhabiting an open environment, liable to a moderate action of wind, selective biotic pollination of the variant will cause the spreading of this type within the population, which may likewise lead to the formation of an ambophilous biotype.

The significance of these concepts lies primarily in the possibility of their empirical testing in actual situations, which in some instances has already yielded interesting results.

1. INTRODUCTION

Systematic study of pollination phenomena has led to the recognition of two predominant modes of pollination, *viz.*, anemophily and entomophily, in addition to a few other specific categories which are, however, immaterial to the present context. While the two above-mentioned and clearly defined pollination forms have been thoroughly investigated, pollination systems including both air-currents and insects as obligatory pollen vectors, constitute a less intensively studied aspect of floral ecology. Yet such phenomena, currently referred to by the term ambophily, in my opinion deserve adequate attention, since they may well contribute towards gaining a better insight into the mechanism involved in the change-over from one mode of pollination to another strategy.

The recent ambophilous forms assumedly have been descended both from anemophilous precursors and from entomophilous ones. As examples of the former, representatives of *Pariana* (Poaceae) and *Dichromena* (Cyperaceae) may be mentioned, whereas species of *Artemisia* (Compositae) and *Thalictrum* (Ranunculaceae) provide good examples of the latter. The possibility of evolutionary

developments reverting to a progenitorial mode of pollination may not altogether be precluded, however. Incipient stages tending towards ambophily naturally can not be recognised so readily, but for all that they may be of a more common occurrence than is hitherto assumed.

In the present paper this theme will be approached from the anemophilous premises. On the basis of the scarce, pertinent data in literature and personal investigations, it will be endeavoured to trace some general principles inherent in phenomena of this kind. From a methodical point of view it is deemed desirable to focus our attention in the first instance on the relations of anthophilous insects to real or putative anemophiles, since these may be supposed to constitute the starting-point of developments proceeding to partial insect pollination. Against this background beginning and advanced stages of ambophily can subsequently be subjected to a closer examination.

2. INSECT VISITING OF NOMINAL ANEMOPHILES

Although, generally speaking, visiting of anemophiles by anthophilous insects for the sake of the nutritious pollen is a fairly rare and mostly incidental phenomenon, this relation appears in a limited number of cases to be more or less of a regular character. A perusal of the scanty pertaining data in literature, augmented by personal observations, shows that in western and central Europe the insect visitors chiefly belong to the Syrphidae and, to a lesser extent, to the Muscidae, Coleoptera and Apoidea. Part of the anemophilous species visited, mainly belonging tot the Pinaceae, Taxaceae, Cyperaceae and the so-called amentiferous group, exhibit a manifest spatial segregation of the sexes. Since the female pollination units do not offer any food, they are not attractive to anthophilous insects, thus precluding biotic pollination. It then appears, that only a small number of anemophilous species with hermaphrodite reproductive units and with closely aggregated male and female ones, may be involved in possible, biotic pollen transfers. To this category belong in particular several representatives of the Plantaginaceae, Poaceae and Cyperaceae. These anemophilous species are mainly visited by syrphids, among which *Melanostoma mellinum, M. scalare, Platycheirus clypeatus, P. scambus* and *P. fulviventris* play a prominent part (henceforth to be referred to as the *M.-P.* group). The relations of these species to the anemophiles in question are restricted to those biotopes where they are found sympatrically, namely in more or less humid and open environments. The following survey shows a number of anemophilous species which have been observed to be regularly visited by pollen-foraging insects. The names of the principal (groups of) visitors have been added. The survey refers to my own observations in western Europe (ranging over a space of ten years) and is at least partly corroborated by data in literature.

Plantaginaceae: *Plantago lanceolata*: *M.-P.* group and a few other Syrphidae, *Halictus* spp. and *Bombus* spp. (Apoidea); *P. maritima*: *M.-P.* group and other Syrphidae.

Poaceae: *Alopecurus pratensis, Anthoxanthum odoratum, Festuca pratensis,*

Molinia coerulea and *Phleum pratense*: *M.-P.* group; *Arrhenaterum elatius, Avenachloa pubescens* and *Dactylis glomerata*: *M.-P.* group, and *Thricops semicinerea* (Muscidae); *Glyceria* spp.: *M.-P.* group, and *Neoascia* spec. (Syrphidae).

Cyperaceae: *Carex riparia* and *Eleocharis palustris*: *M.-P.* group; *Scirpus maritimus*: *Lejops vittata, M.-P.* group and a few other Syrphidae.

In addition, in literature have been mentioned a few singular observations of frequent visits to *Brachypodium pinnatum*: *Malachius viridis* (Coleoptera); *Carex acuta, C. nigra* and *Scirpus lacustris*: small beetles, and to *Typha angustifolia*: M.-P. group, *Lejops vittata* and a few other Syrphidae.

Although the preceding enumeration presumably includes the most important of the extant relations of insects to anemophiles in western and central Europe, it may not be ruled out that further inquiries will bring to light even more instances of this sort. No doubt, such explorations in other, and especially tropical, regions, would lead to numerous novel and possibly even surprising finds. LEEREVELD (1982; pers. comm.) examined the contents of the digestive tract of syrphids of the genera *Melanostoma* and *Platycheirus* and some related taxa, hailing from Europe, Russia, North America, New Zealand and Madagascar. He found that most specimens had been feeding on pollen of herbaceous anemophiles. This result indicates that insect visiting of anemophiles is a phenomenon of world-wide occurrence.

Whereas the anemophilous species mentioned before are habitually, or at least regularly visited by insects, other ones occurring in the same habitat, and normally growing in close proximity to the former, scarcely attract any visitors. Thus, on grasses like *Holcus lanatus, Lolium perenne, Cynosurus cristatus* and *Cynodon dactylon,* as well as on species of *Rumex*, I but rarely observed any visitors, although hover-flies of the *M.-P-* group were abundantly about. *Plantago major* I even saw visited only once by a pollen consuming syrphid fly! Conceivably, the specifically distinct nutritional value of the pollen is a critical factor as regards the manifest preference of the insects for certain food sources. Further investigations in this respect seem to be indicated.

3. THE PROSPECTS OF BIOTIC POLLEN TRANSFER IN ANEMOPHILES

Some features inherent in anemophily, to a certain extent, interfere with the possibility of an efficacious pollen transfer by insects. The pollen grains of anemophiles, unlike those of most entomophilous species, exhibit a more or less smooth extexine, *i.e.,* without prominent sculptural elements. In addition, the amounts of *Pollenkitt* on the surface of the pollen wall are comparatively small, or wanting at all (HESSE 1980a, with further references). Consequently, the pollen does not so readily adhere to the insect body. There is the added disadvantage that the habitual dipterous visitors do not possess a proper palynophilous pubescence. Although these conditions necessarily reduce the chances of biotic pollen conveyance, field observations and especially microscopical examination show that insects after visiting the (male) blossoms of anemophiles usually carry away smaller or larger amounts of their pollen.

The SEM technique provides us with an excellent tool to this end. A perusal by this method of more than fifty individuals of syrphids of the *M.-P.* group, gathered immediately after their visiting of *Plantago lanceolata,* revealed that in most specimens some dozens of pollen grains, and incidentally even pollen clumps, were attached to their bodies. Likewise, on a few individuals of *Thricops semicinerea* a good many grains of grasses (and of *Plantago media*) were found to be present. Members of the *M.-P.* group captured after visits to *Molinia coerulea* appeared to carry appreciable quantities of its pollen on their bodies, many grains even adhering directly to the glabrous cuticle. On a few specimens of *Syrphus ribesii* and *Episyrphus balteatus* collected after visiting *Plantago maritima,* the presence of small amounts of its pollen could be demonstrated. To this can be added that KNUTH (1898–1905) reported field observations of beetles, copiously dusted with pollen, while moving across the inflorescences of *Scirpus lacustris.* On the female pollination units of *Typha angustifolia* WAITZBAUER (1976) saw numerous individuals of *Lejops vittata,* most of them covered with its pollen all over. Some pollen of *Sparganium erectum* was found on the bodies of hover-flies after they had visited the male capitulas of this species (PINKESS 1980). In S. Africa RATTRAY (1913) studied the relationships between curculionid beetles of the genus *Phlaeophagus* and the cycad *Encephalartos altensteinii.* Most surprising, the author noticed that up to three days after visiting the male strobili, the beetles carried its pollen on their bodies. It is quite clear that, apart from the adhesive power of the *Pollenkitt,* entanglement of the grains in groups of setae plays an important role in the attachment of the pollen to the insect body. As regards the pollen of gymnosperms the latter is virtually the sole possible mode of adherence to the insect. However, as has recently been demonstrated by CORBET et al. (1982), electrostatic forces may also be instrumental in attaching the pollen to the insect body.

A limited spatial segregation of the sexes and/or the incidence of dichogamy, as peculiar to many anemophilous species, complicate biotic pollen transfer, it is true, but these impediments appear, as a rule, not to be unsuperable. Field observations clearly show that pollen-foraging insects often move across the female zone. By drawing up protocols of insect-visiting of *Plantago lanceolata* I could ascertain that in 621 of the 935 spikes under investigation a visitor remained at least once in the zone with receptive stigmas. In *Plantago maritima* and *P. media,* likewise, visitors were often seen wandering around in the female zone. On the female pollination units of *Carex riparia* I noticed several times hover-flies of the *M.-P.* group. As stated before, WAITZBAUER (1976) observed large numbers of *Lejops vittata* (and other syrphids) on the female spadices of *Typha.* Considering the relatively great distance between the female zone and the male one, such a situation is rather surprising, although it may partly be attributed to the high intensity of visiting. By artificially dyeing pollen of *Plantago lanceolata* and thus rendering it traceable, biotic pollen transfer could be demonstrated experimentally. The results showed that in 60% of the 200 test spikes under investigation, stained pollen had been deposited by visitors on fresh stigmas, or, by conversion, involving about 18% of the total number of mature

stigmas (STELLEMAN & MEEUSE 1976; STELLEMAN 1978). The preceding instances clearly evince that it is above all the typical behaviour of the visitors that allows biotic pollen transfer on a modest scale, in spite of the occurrence of a distinct, although restricted segregation of the sexes.

The joint evidence permits the conclusion that in part of the anemophilous species, biotic pollen transfer, so far as it has not been already corroborated empirically, is actually possible. Without beforehand attributing to such phenomena a mutualistic character, they may be considered to constitute potentially the basis of an anthecological development in the direction of ambophily.

4. DEVELOPMENT OF AMBOPHILOUS POLLINATION STRATEGIES

In certain cases the structural and functional organisation of the pollination unit readily permits the attachment of the predicate ambophilous to its pollination system, but in other instances the state of ambophily is less obvious for lack of a clearly recognisable, pertinent syndrome. However, one can ascertain the nature of the pollination system by determining experimentally the reproductive effect of each separate mode of pollen transfer (STELLEMAN 1984). Naturally, the possibility of the incidence of other reproductive systems, such as autogamy (including cleisto- and geitonogamy) and apomixis must be allowed for and, if present, have to be technically incorporated in the experimental set-up. In case that the combined actions of air-currents and insects appear to effectuate a higher reproductive effort than each of the separate modes of pollination, there is sufficient cause for attributing the state of ambophily to the pertaining pollination system.

One can reasonably posit that an anemophilous population, which is being subjected to conditions of decreased wind-action (*e.g.*, by migration, or by microclimatic changes), can but maintain itself lastingly, if it succeeds in developing an alternative pollination strategy, that adequately meets the new ecological conditions. Apart from a development towards autogamy or apomixis (which may already form part of the extant reproductive system, for that matter), another conceivable pathway includes a transition to (partial) insect pollination, the latter being the subject of our further concern.

This hypothesis was put to the test in the reputedly anemophilous and self-incompatible species *Plantago lanceolata* (STELLEMAN 1984). In western and central Europe, at suitable sites, its flowering spikes are habitually visited by syrphids of the *M.-P.* group, which also act as pollen vectors. It could be experimentally established that in open, wind-exposed areas, these being the typical habitat of this species, biotic pollination is only of minor importance for its reproduction. However, in populations occurring in woodland-enclosed meadows in Luxemburg with but weak wind-action (<2 Beaufort), the biotically effectuated share in the reproduction amounts, on the average, to half of the total seed set. Under the prevailing ecological conditions the plantain is apparently dependent on both modes of pollination for as high a reproductive result as possible. In addition, the pollen of the plantains of the forest meadows appeared to pos-

sess a genetically controlled, higher adhesive capacity than that of plants from open habitats. The overall picture points to an adaptation to partial insect pollination at the intraspecific level, which is to be esteemed as an incipient stage of ambophily. From the joint evidence some essential features regarding the mechanism, involved in the transition from wind pollination to ambophily, can be deduced. For one thing it can be established that an extant relation of anthophilous insects to an anemophilous species appears to provide a favourable, if not necessary, predisposition for getting under way a development towards ambophily. Furthermore, the occurrence within a population of a variant (morph), characterised by a feature which is conducive to biotic pollen transfer, is a prerequisite. In the instance of *Plantago* this condition was fulfilled by the comparatively strong adhesiveness of its pollen, but it is quite clear that any other appropriate trait may qualify to this end, such as visual and olfactory signals, nectarial secretion, aggregation of male and female reproductive units, etc.

Since the pollen of anemophiles is not particularly suited for transportation by insects, it is tempting to regard an increase of its adhesiveness if not as a first step, then as a necessary concomitant phenomenon of a development towards ambophily. A preliminary examination of the pollen of several wind-pollinated species, *viz., Plantago maritima, Molinia coerulea* and *Carex riparia,* by the method of KNOLL (1936), suggests that any anemophilous population contains a small fraction of individuals producing pollen with a relatively strong adhesive power (unpublished). POHL (1930) reported corresponding findings in the grass species *Dactylis glomerata* and *Avenachloa pubescens.* It has not been settled, however, whether this feature is genetically fixed, as it is in the case of *Plantago.* If so, it implies that in such populations appropriate variants are constantly available for possible selection in favour of a biotype, adapted to partial biotic pollination. So far this has been examined, in most ambophilous species belonging to otherwise predominantly anemophilous groups, the pollen was found to be rather sticky.

An apparent adaptation to an almost completely wind-still environment is encountered in grasses of the genus *Pariana,* which occur in the lower stratum of the neotropical rain forest. RICHARDS (1952) mentioned wind-velocities from nil to 0.02 m/s for some places in rain forest areas. *Pariana* is visited by a variety of insects, including Meliponinae, or so-called stingless bees (SÖDERSTRÖM & CALDERÓN 1971). The conditions strongly point to the necessity of preponderant insect pollination, not precluding the possiblity of attendant autogamy, however. The numerous, bright yellow anthers most likely function as optical signals. The floral characteristics (*inter alia,* many stamens, two stigmas and a spike-like inflorescence) as well as the leaf structure, indicate a derived position of this genus within the Poaceae. Several rain forest sedges of the genera *Mapania* and *Hypolytrum* with conspicuous involucral bracts, no doubt, are dependent on partial insect pollination as well. In Ivory Coast LOROUGNON (1973) noticed the presence on their inflorescences of ants, beetles and Tenthredinidae, but so far records of more mobile insects are lacking. I think it highly probable that

several other reputedly anemophilous taxa inhabiting the tropical rain forest, such as the Gnetales and a few Cycadales, are likewise largely if not wholly dependent on insect pollination for their reproduction. It may be mentioned in passing that VAN DER PIJL (1953) observed visits of pollen-gathering bees (*Trigona* spec.) to *Gnetum gnemon*, outside its natural habitat. In this connection reference must be made to the incidence of ambophily in *Ephedra*, which latter shows approximately the same reproductive organisation as *Gnetum* (see below). RATTRAY (1913) described visits of beetles (*Phlaeophagus* spec.) to both the male strobili (lured by smell?) and the female ones (for oviposition) of *Encephalartos villosus*, a forest dwelling cycad of S. Africa. Since, as we have seen, these beetles may act as pollen vectors, biotic pollination is quite feasible.

The instances of stabilised ambophily in wind-protected habitats are fully compatible with the view that the particular conditions of decreased wind action determine to a high degree the change-over from anemophily to ambophilous pollination strategies, eventually resulting in perfect entomophily. Reduced to a simple level, it can be posited that appropriate variants of an anemophilous species, which invade a wind-sheltered habitat, are capable of surviving by establishing a mutualistic relationship with anthophilous insects. This process primarily leads to the rise of an ambophilous biotype. Since the settling population becomes segregated from the mother population, favourable opportunities arise for subsequent speciation. Examples of comparable phenomena induced by climatic alterations on a small scale are unfortunately not available, but it may not be ruled out, that on closer and directional investigation they will prove to be extant, at least at the population level.

In the previous cases the ambophilous pollination system could conveniently be associated with wind-still conditions, but matters are less obvious with respect to the incidence of ambophily in open habitats, liable to the impact of air-movement. As instances of such ambophilous species, belonging to otherwise preponderantly anemophilous taxonomic groups, may be mentioned: *Paspalum dilatatum* (Poaceae); *Dichromena ciliata, D. latifolia, D. colorata* and *Rhynchospora cephalotes* (Cyperaceae); *Plantago media* (Plantaginaceae), as well as *Ephedra campylopoda* and *E. aphylla* (Ephedraceae). Since anemophiles are of normal occurrence in the habitats of these species, it can be inferred that the prevailing wind-intensity is sufficiently strong to enable abiotic dispersal of pollen.

The pollination system of the self-compatible grass species *Paspalum dilatatum* was studied by ADAMS et al. (1981) in Oklahoma (USA). It could be demonstrated that in addition to autogamy, pollination by halictid bees contributed substantially to the seed set, whereas pollination by wind appeared to be only of minor importance. The proportionately large pollen grains showed a notable adhesiveness. The conspicuous, purple anthers and stigmas, as well as the overall shape of the inflorescence most probably function as visual attractants. Considering that the subfamily Panicoideae, to which the genus *Paspalum* belongs, is not a primitive one, there is apparently a relatively recent development in the case under discussion. In the above-cited species of *Dichromena* the partly or completely white upper leaves surrounding the inflorescence function as se-

maphylls. In populations of *D. ciliata,* in El Salvador, LEPPIK (1955) could establish the presence of several types of involucres, varying among themselves in the number of white upper leaves. The author noticed an obvious tendency to development of a five- to six-leaved, more or less radiate involucrum. The inflorescences were mentioned to be visited in particular by *Bombus mexicanus* and stingless bees. In the south-eastern part of N. America UPHOF (1932) observed regular visiting of *D. latifolia* and *D. colorata* by *Bombus* spec. The pollen of these species is reported to be sticky. PORSCH (1910) noticed in Dalmatia visiting of *Ephedra campylopoda* by a variety of insects for the sake of the sugar-containing micropyle droplet, secreted by both the ovules of the female strobilus and the sterile ovules present in the male one. Besides, its pollen appeared to be in demand of visiting hover-flies. In Israel, in the strictly dioecious species *E. aphylla,* both the male and female strobili were found to be regularly visited by various insects (BINO et al. 1984). The visitors appeared to consume the sugary liquid exudated by the outer cover of the ovulate and staminate organs. The nature of perception-stimulating devices attracting prospective visitors has as yet not been sufficiently elucidated. Although the pollen of *Ephedra* most probably lacks *Pollenkitt* (compare: HESSE 1980b), its pollen was found to be present on most insect specimens examined (BINO et al. 1984). It may not be ruled out that the deep, longitudinal grooves of the pollen wall, as well as smearing of the visitor with the viscous exudates partly account for the attachment of the pollen to the insect body. The Ephedrales all but certainly constitute a primary anemophilous group (MEEUSE 1981), so that trends towards ambophily within this taxon necessarily reflect derived conditions.

The interesting question arises by which pathway ambophily may have come about in open, wind-exposed environments. Taking into account that in at least part of the ambophilous species mentioned before, conspicuous visual devices are present and apparently function in enticing insects (and in the other species possibly olfactory attractants do the same), it is a plausible conclusion that the development of these provisions must have been prominently involved in the evolutionary process leading to the present state of ambophily. This inference may provide a clue to a satisfactory, although hypothetical explanation of the advent of ambophily in open habitats.

As a starting-point of an explanatory model a relation of anthophilous insects to an anemophilous population is supposed to be extant. It is to be expected that within this population incidentally mutant morphs arise, characterised by a feature that renders them more attractive to insects than the parental type does. Such a variant stands a better chance of being visisted by insects than the prevailing, widespread type. Provided the newly acquired feature does not hamper pollination by wind, the increased visiting will readily result in a higher rate of seed set. Preferential pollination may thus induce the spreading of the pertinent characteristic within the population in the next generations, eventually even superseding the ancestral type. This process may lead in the first instance to the rise of an ambophilous biotype. Paradoxically, the above trend will be increasingly corroborated by pollination by wind. It is clear that, apart from

attraction cues, any other trait furthering biotic pollination, while not impeding pollen transfer by wind, qualifies as a target for selective pollination. Interestingly, in a few populations of the grass *Glyceria fluitans* I found both individual plants with palish yellow anthers and with purple ones, the latter being visited by insects more frequently than the former. Under appropriate conditions, conceivably, the latter type might well function as a preadaptation for a progression towards ambophily. In *Plantago lanceolata* I incidentally came upon female (gynodioecious) plants with spikes which showed purplish stigmas instead of the typical whitish ones. Whilst normal female spikes barely draw the attention of insects, the spikes with purplish stigmas appeared to be regularly approached by foraging hover-flies. MÜLLER (1873) distinguished at least two different forms of *Plantago media*, of which the one type with short, reddish stamens was observed to be visited more often than the other form, exhibiting longer and palish stamens. In this connection the various types of *Dichromena ciliata*, referred to before, may also be mentioned. In entomophilous species a good many instances of polymorphy and assortative pollination are on record (see: KAY 1978).

A subsequent selection in favour of variants producing relatively sticky pollen (the latter possibly being a phenomenon of regular incidence), would greatly enhance a development towards facultative insect pollination. Since a higher degree of adhesiveness renders the pollen less suited to pollination by wind (on account of a tendency to form aggregates), this negative effect must be adequately compensated by the increased and more efficient biotic pollen transfer. Only the small dispersal units may be carried away by air-currents. If the hypothesis of MULCAHY (1973) is true, that the joint deposition by insects of large numbers of pollen grains on stigmas involves selective advantages, this ancillary phenomenon would likewise contribute to a development towards ambophily.

Selection by preferential pollination may in particular stand a fair chance of succeeding in climatic areas marked by a moderate wind-intensity, the effect of which is, however, inadequate to ensure a complete seed set. Theoretically, the latter is required even essentially to allow an ambophilous development. As far as can be ascertained, such climatic conditions indeed prevail in the distributional ranges of the ambophilous species cited before. It is worth mentioning in this connection that in *Plantago lanceolata*, occurring at open sites in Luxemburg with a prevailing, moderate wind-force of 2–3 Beaufort, a wind-effectuated fruit set of an average of 70% was found. In the wind-exposed coastal plain of Holland, on the other hand, the average fruit set resulting from pollination by wind, amounted to 90%. In addition, it could be determined that pollen transfer by insects generally results in a higher rate of seed set per fruit than pollination by wind (STELLEMAN 1984).

Admittedly, the proposed models visualising the development of an ambophilous biotype, emanating from an anemophilous stock, are speculative in a measure, but cogent arguments for alternative pathways are hardly available. The hypothetical significance of these concepts is primarily implied in the possibility of their empirical testing at the population level, that is to say, in actual situations. In the extant ambophilous species of anemophilous descent developments

towards their present state assumedly have proceeded initially in much the same way as indicated before. A reconstruction of the complex of factors, that have effectuated their subsequent speciation, lies beyond the scope of our present knowledge, however. At best the nature of the isolation mechanisms involved might be surmised. VOGEL (1981) plausibly argues that the genetic potential for floral diversication in monocots is restricted. The author further suggests that the widespread occurrence of ambophily in this taxon might reflect a primary development, emanating from an anthecologically more or less ambivalent, primitive stage. On account of the genetic limitations, developments may have proceeded by anomalous pathways (*e.g.*, the formation of extra-floral semaphylls), ultimately leading to imperfect zoophily. Such a view is hardly compatible with the taxonomically relatively advanced position of at least the ambophilous monocots dealt with before and hence, to my mind, none too likely.

Plantago media shows a distinct ambophilous syndrome and MEEUSE (1984) proved experimentally its dependence on both modes of pollination for as high a rate of seed set as possible. Most taxonomists assume that the systematically isolated and preponderantly anemophilous Plantaginaceae have been descended from an entomophilous, ancestral stock within the order of the Scrophulariales (see: DIETRICH 1970). It is, therefore, quite conceivable that the ambophilous condition in *P. media* reflects a transitional phase of a progression towards anemophily (HAMMER 1978). On the basis of palynomorphological considerations Dietrich is rather inclined, however, to regard its pollination system to be indicative of a development towards secondary entomophily (pers. comm.). Irrespective of the intricacies as to the main line of development, several forms of this species have been recognised, probably expressing diverse tendencies in the mode of pollination (MÜLLER 1873; HAMMER 1978). Comparable problems regarding the direction of anthecological evolution arise in several other ambophilous taxa, belonging, *inter alia*, to the Salicaceae, Fagaceae and Palmae. For this reason such cases of ambophily, however interesting these may be, have been left out of account in the present study.

From the previous disquisitions it clearly emerges that sundry facets of ambophily need closer investigation. In addition to a deepening of the knowledge already obtained, future efforts should aim at tracing and studying possible, still unknown cases of ambophily. It is, furthermore, desirable to ascertain the nature of the attraction cues of anemophilous species which are regularly visited by insects, more in particular with a view to the role these devices could play in preferential pollination. The study of changes in pollination systems at the intraspecific level should also include the population genetic aspects, in order to gain an insight into the quantitative significance of the phenomena involved. All in all, a wide, unexplored field awaits future investigation.

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