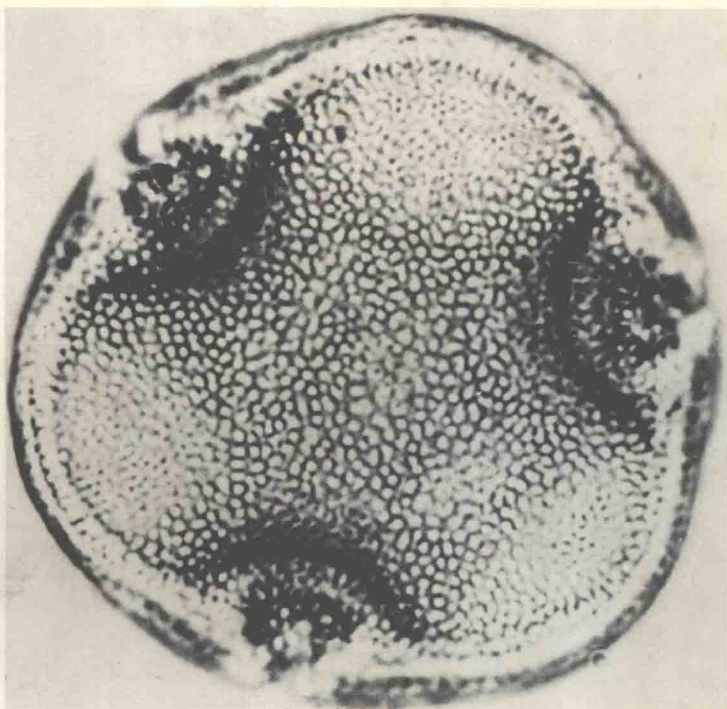


LEIDEN BOTANICAL SERIES, VOLUME 10



S. C. WILLEMSTEIN

AN EVOLUTIONARY BASIS
FOR POLLINATION ECOLOGY



AN EVOLUTIONARY BASIS FOR POLLINATION ECOLOGY

BY

S. C. WILLEMSTEIN



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FOR POLLINATION ECOLOGY

LEIDEN BOTANICAL SERIES

VOLUME 10



*Aan Els
Voor Nicolette en Eveline*

PREFACE

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S.C.W.

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1. INTRODUCTION

Usually pollination ecology is narrative and in many cases even anecdotal, presenting case histories rather than generalizations. There are exceptions however, which are mainly presented in the form of text books, including syntheses of the relations of pollinators and flowers, as Müller (1873 and 1881), Loew (1895), Knuth (1898), Kirchner (1911), Knoll (1921 and 1956), Cammerloher (1931), Meeuse (1961), Kugler (1970), Proctor & Yeo (1973), and Faegri & Van der Pijl (1980). The syntheses in these books, however, are not connected with either the phylogeny of the pollinators or that of the angiosperms.

Evolutionary studies on pollinator-flower relationships are mainly restricted to taxa of lower rank, morphological features, phenology of plant communities, processes (isolating mechanisms; ethology of, mainly, higher bees; and other restricted items). Examples are: Daumann, 1935 (nectaries in the taxonomy of *Iris*), 1966 ("Pollenkitt", pollination mechanisms and phylogeny); Doyle, 1945 (developmental lines in pollination mechanisms in the Coniferales); Mayr, 1947 (ecological factors in evolution); Pennell, 1948 (relation between taxonomy and floral biology); Grant, 1949, 1963 (processes: pollination systems as isolating mechanisms; adaptations); Whitehouse, 1950 (incompatibility and angiosperm evolution); Heslop-Harrison, 1958 (ecological variation and angiosperm evolution); Faegri, 1965 (Proteaceae); Baker, 1966 (evolution of incompatibility systems in Plumbaginaceae); Grant, 1966 (floral colours and hummingbird flowers); Gottsberger, 1967, 1972 (Malvaceae), 1970 (Annonaceae), 1974 ("primitive" angiosperms); Grant & Grant, 1965 (description of several evolutionary lines in the pollination of North American Polemoniaceae, regarding also the taxonomical relationships within the family), 1968 (hummingbirds and flowers); Van der Pijl, 1969 (evolutionary action of tropical animals on plant reproduction); Levin & Anderson, 1970 (processes: competition for pollinators between simultaneously flowering species); Kevan, 1972, 1972a (entomophilous pollination in the high arctic); Bell, 1971 (fine example of developmental processes in micro-evolution of some Apiaceae); Grinfeld, 1973 (anthophilous evolution of the Apoidea); Heywood (Ed.), 1973 (various examples of taxonomy and ecology); Gilbert & Raven (Eds), 1975 (various examples of co-evolution of animals and plants); Frankie, 1975 (tropical phenology and pollinator-plant evolution); Dodson, 1975 (co-evolution of orchids and bees); Chase & Raven, 1975 (evolutionary and ecological relationships in two *Aquilegia* species); Vogel, 1969, 1971, 1974,

1984, 1986 (co-evolution of oil-producing flowers and oil-collecting bees); and many others. Interesting surveys can be expected from e.g. the extensive research on bumblebees and *Pedicularis* (e.g. Macior, 1968, etc.; and Kwak, 1979, etc, see references) and of Agaonidae and *Ficus* (see e.g. Wiebes, 1979, 1982 and his referring to e.g. Corner and Galil).

The main synopses have been given by Van der Pijl (1960, 1961) and Proctor (1978), based on a comparison of Recent ecosystemic conditions.

Some authors have included angiosperm phylogeny and fossil record in pollination ecological research, as Leppik (1957, 1957a, 1971 and 1974) for *Rhododendron* and Crepet et al. (1974) and Crepet (1979 and 1979a).

In case of an approach from plant systematics, the tracing of evolutionary lines (transformation series) is difficult, because the study of the phylogeny of the Angiospermae in the sense of Hennig (1966) is only at its very beginning, despite the several existing classification systems (Takhtajan, 1980; Cronquist, 1981; Dahlgren et al., 1981; Rouleau, 1981; Thorne, 1981). In actual systematics, first the phylogeny is described and it functions as a basis for the classification. Systematic zoology in this respect is ahead of taxonomical botany. This certainly will be due to the fact that morphological variation within angiosperm species is much more extensive than in animal species. But to my opinion it may also be a result of the fact that zoological systematists much earlier started to produce taxonomical monographs (subject of study a whole taxon) than did plant taxonomists. The latter mainly produced geographically restricted floras, which for practical reasons initially were more required than monographs of single taxa, because of the extensive economical importance of angiosperms, but in which in most cases only parts of taxa occur. And, last but not least, the inventarisation of seed plants of a region is much easier than that of insects.

Although the insect phylogeny in the sense of Hennig (1966) is much in development in recent times (see e.g. the many foot notes in the second edition of Hennig (1981)) the link with entomophilous pollination ecology has not yet been made on a more large scale. This may be due to the fact that up to now too few entomologists have shown interest in pollination ecology from a phylogenetic point of view. One of the few examples concerns the Agaonidae (see Wiebes, 1982)

It is, however, hopeful to notice that in the most recent surveys of the Angiospermae (as e.g. Cronquist, 1981) not only morphological character states, but also pollen ecological aspects are, at least, taken into account.

As has been stated above, the insufficient descriptions of evolutionary trends in pollination are mainly due to the imperfectly studied phylogeny of the Angiospermae, but also other facts may have hindered these descriptions. The main interest of pollination ecologists was in first instance drawn to the highlights of insect-flower relationships. In most cases these are highly

developed temporary terminal points of evolutionary lines, and in many cases possibly the definite terminal points. It mainly will be the beauty of these cases which gave them such an important place in pollination ecology as a whole. These and other pollination systems are classified in the, each other excluding, pollination syndromes. These syndromes, however, refer to artificial groupings of taxonomically often unrelated angiosperms. Only when applied within the phylogeny of angiosperm taxa of lower rank, they will throw some light on the evolutionary developments of pollination. Besides, pollination syndromes only cover a part of the angiosperm flowers. Many non-specialized entomophilous flowers do not fit the syndromes, and consequently they were largely overlooked. In analysing the present state of pollination ecology it can be concluded that most evolutionary studies are limited to the pollination syndromes.

The absence of general descriptions of evolutionary trends in pollination ecology, based on the phylogenies of pollinators and angiosperms, has fascinated and challenged me to try and find out whether these transformation series can be described. To achieve this, the comparatively well-known phylogeny of insects and their extensive fossil record are taken as a starting point and are correlated with the Recent insect feeding-habits and insect-flower relationships. This correlation results in flower-morphological transformation series, which can be dated by the fossil history of insects and comparison with the fossil history of angiosperms in its turn indicates floral developments and consequent developments in pollination ecology.

2. METHODOLOGY AND TERMS

For the description of an evolutionary basis for pollination ecology the following tools are available:

- a) insect phylogeny based on Recent comparative morphology and fossil history;
- b) Recent feeding-habits of insects and their relationships with flowers (inclusive some aspects of insect ethology);
- c) angiosperm phylogeny based on Recent comparative morphology and fossil history.

One of the main aids to indicate the sequence of developments is the fossil record. According to De Jong (1980) the stratigraphical appearance is a valid argument to decide whether a character state is plesio- or apomorphous. It, however, will be subject to constant change. The fossil record of angiosperm flowers is very poor; flowers are temporary parts of the plants and after blossom they drop off in withered parts, which means that even in a habitat favourable for fossilization entire fossil flowers are extremely rare. The main exception is the amazingly rich middle Eocene Claiborne Formation of the U.S.A. (see Crepet, 1979), which provides a good flower-ecological picture of that period. Also in the middle Senonian fluviatile sands and clays from Scania, southern Sweden, several flower fossils are found which demonstrate the definite presence of some flower-ecologically important character states in the Upper Cretaceous (see Friis, 1983 and Friis & Skarby, 1982). In contrast to the floral fossil history that of the adult insects (with their resistant chitinous exoskeleton) is very rich. The description of the evolutionary basis for flower ecology is mainly based on the fossil record of the insects. There are strong arguments for this approach, but it requires some explanation.

The nature of the co-evolution of anthophilous insects and entomophilous flowers

The evolutionary developments of pollination are essentially the result of co-evolution of (anthophilous) insects and entomophilous flowers (except for developments towards anemogamy, hydrogamy and autogamy). The term co-evolution denotes the complex of reciprocal adaptive developments favoured by the complex of reciprocal selective pressures, or reciprocal restrictions to variations. Starting from dystropic pollinators (compare e.g. the interesting publication of Vogel et al. (1984) on ornithophilous flowers pollinated by non-specialized birds on the Canary Islands) the developments to allophilic,

hemiphilic and euphilic flowers and allotropic, hemitropic (hemilectic) and eutropic (eulectic) pollinators respectively occur. In many cases it will be difficult to indicate whether the evolution of anthophilous insects is guided by the evolution of the angiosperm flowers, or vice versa. Both guidances will occur, but in general it can be stated that initially adult insects are less dependent on flowers or certain forms of flowers, than are entomophilous flowers on insects for (cross-)pollination. Many nectarivorous insects can e.g. also feed on non-floral honey-dew; within anthophily long-tongued insects in many cases also can feed on short-tubed flowers. This difference in absoluteness of dependence is caused by the fact that insects are free-living organisms and plants in adult state are sessile, and means that the insects form an essential part of the environment of entomophilous flowers.

In the evolution of pollination this indicates that the developments of floral structures run (somewhat) after the developments in insect morphology; every new floral character state is dependent on the presence, i.e. established development, of corresponding elements of insect morphology. Within the variation of floral character states one of the extremes will succeed if corresponding extremes are present in the "environmental" insect morphology (e.g. lengths of corolla tubes and tongue-lengths of anthophilous insects). Once succeeded, on the other hand selection in one of the extremes of the variation in insect morphology can occur (e.g. anthophilous insects with the longest tongues will meet less feeding-competition on the flowers with the longest corolla tubes than on those with shorter ones). Because initially floral evolution is more dependent on the morphological evolution of anthophilous insects than is the reverse, the stratigraphical presence of these insects may indicate the presence of corresponding floral structures, or the potential presence of them. The stratigraphical presence of floral structures more certainly indicate the presence of insect morphology, but as mentioned before, the fossil record of floral structures is very poor.

Using the phylogeny of anthophilous insects, based on the classification of taxa in which anthophily developed and their fossil record, requires the presupposition that these insects did not behave otherwise in earlier times in unchanged morphological conditions (e.g. Coleoptera in the Cretaceous had no wider visual sensitivity in the spectrum than they have now). This presupposition is the same as the doctrine of uniformitarianism as used in historical geology. In this study it will be regarded as "vertical" uniformitarianism (in the geological time scale); because the sample taken for the analysis of insect-flower relationships is geographically limited to the central European area, the term "horizontal" uniformitarianism will be also used (see next paragraph).

Correlation of the Recent insect-flower relationships with the phylogeny of insect taxa in which anthophily developed

The least anecdotically compiled survey of flower visits of insects is that of Knuth (1898a, 1899) as far as it concerns the central European area.

A statistical analysis was carried out, correlating these insect visits to flowers with the floral morphology of central Europe, as described by Hegi (1906-1931, 1936 etc. and 1966 etc.) and listed by Ehrendorfer (1973). To correlate the results of this analysis with the fossil record of the insects, the results have to be considered world-wide (e.g. if the bees in central Europe appear to visit significantly more blue coloured flowers than do beetles, they are considered to do so also in other parts of the world), and this requires the presupposition of "horizontal" uniformitarianism (geographically over the world). The geographical restriction of the analysis means that not all insect-flower relationships are covered, which will appear in many examples. The statement of Faegri & Van der Pijl (1980) that pollination ecology is too much based on the observations of the central European area (with, however, still the most detailedly known flora and insect fauna of the world) is avoided as much as possible: only the statistically significant results are taken into account. The correlation of the results of the analysis of Recent insect-flower relationships requires a behavioural "vertical" uniformitarianism (in unchanged morphological conditions).

The phylogeny of the insects is largely based on the principles of phylogenetic systematics as introduced by Hennig (1966). This definition of classification in complexes of sister groups, applied on insect phylogeny (Hennig, 1969 and 1981) has the advantage of the predictive value of stratigraphical presence of insect taxa (the presence of a predictive theory can be considered one of the most important elements of good research programmes, see e.g. Lakatos, 1978): if a representative of a taxon is present in a stratum, demonstrating the presence of one or more synapomorphies, also representatives of the sister-group must have been present in the time corresponding with that stratum.

The results of this correlation are functionally directed developmental lines in floral morphology, or in other words a series of transformation series. E.g., the floral colours yellow and white were much earlier functional in attracting insects than were purple and blue, and therefore probably they were earlier present than the other ones, i.e. yellow and white can be considered plesiomorphous (primitive) floral colours and purple and blue apomorphous (advanced) ones in the evolution of angiosperm floral colours. Regarding the presuppositions stages in the transformation series can be dated by the stratigraphical appearance of the insect taxa in which anthophily developed.

The phylogeny of the Angiospermae in the sense of Hennig (1966) ought to be based on the Recent morphology correlated with the fossil record. The first has not yet been worked out as detailed as that of the insects, or at least is less readily available, and thus the main component of correlation is that of the fossil record. It is possible that the dating of the transformation series on the basis of the stratigraphical appearance of the insect taxa in which anthophily developed, has to be changed by the stratigraphical appearance of angiosperm fossils (hypothetically) or flowers (definitely). This method of reasoning is called spiral reasoning (Hull, 1967, 1979) and is the result of reciprocal illumination (Hennig, 1966; see also e.g. Walker, 1974a).

A survey of the structure of this study is given in fig. 2-1, indicating the sources (with indications of secondary, i.e. derived from literature, and original, i.e. personal observations, statistical analyses and new combinations) and the way of reasoning. It is indicated that application of the results of this study on the phylogeny of the Angiospermae may provide a synergy effect (at any rate at the present state of knowledge of angiosperm phylogeny), i.e. comparison of the description of the evolution of pollination (transformation series, mainly based on insect phylogeny and fossil record) with the phylogeny and fossil record of the Angiospermae will give a result that reaches further than separate descriptions (continuing process of reciprocal illumination).

This study consists of a number of compilations, which are compared with each other. None of these compilations is complete, they merely give a survey of the present state of comparatively easily accessible knowledge, i.e. found in more general surveying articles. Together, however, they throw some light on the evolutionary developments in pollination ecology at a fairly high abstraction level. The general transformation series should be checked on their validity in angiosperm taxa of lower rank, also with regard to falsification. The latter may indicate interesting evolutionary potentials.

This study has to be considered no more than a first interim report towards the foundation of a more sound evolutionary basis for pollination ecology, throwing light on both the phylogeny of entomogamous angiosperms and on that of anthophilous insects.

Some remarks on the terminology used in this study

The flower is considered the reproductive structure of the Angiospermae and the term flower is not used for Gymnospermae.

In naming the pollination systems a distinction is made between the flower and the specimen or taxon. A flower can be entomophilous (in case of entomochory, there is no question of a flower anymore). Entomophily in a

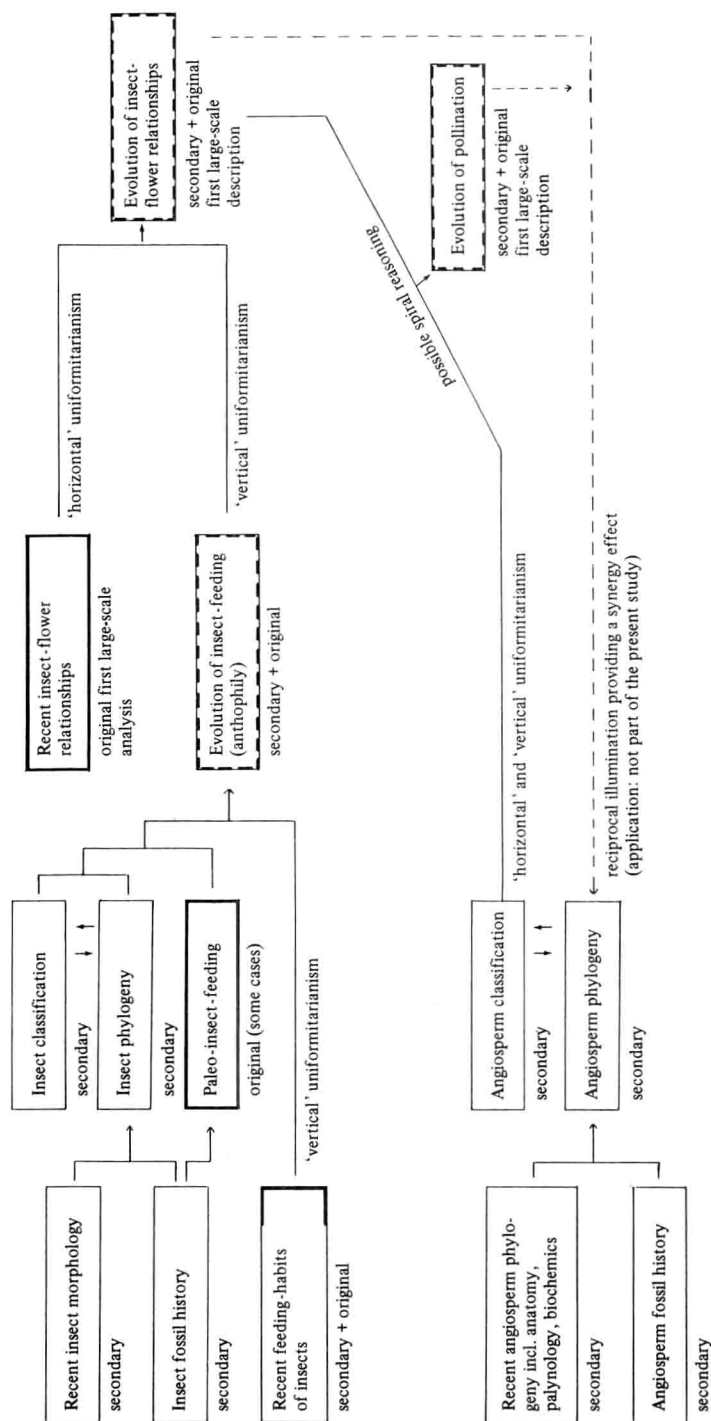


Fig. 2-1. Global scheme of correlations in the present study (way of reasoning). Explanation: thin continuous lines indicate secondary data; thick lines indicate original data; and the discontinuous lines indicate possible application (not part of the present study).