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An entomophily syndrome in *Juglandaceae: Platycarya strobilacea*

Ein Entomophilie-Syndrom bei den Juglandaceen: *Platycarya strobilacea*

by

Peter K. ENDRESS

1. INTRODUCTION

Some families and orders of the "Amentiferae", which are so important constituents of temperate deciduous forests, are typically wind-pollinated and have developed elaborate anemophily syndromes (REGAL 1982, WHITEHEAD 1983). However, each group has its exceptions. In Salicales, Salix is entomophilous. In Fagales, some tropical groups of the Castaneoideae are entomophilous; even in the temperate Castanea insect pollination has long been known from Europe (KIRCHNER 1893). A still somewhat controversial point is whether the extant entomophilous members of the Amentiferae are primitively entomophilous or reverted to this state from anemophily (ENDRESS 1977, DILCHER 1979, KAUL and ABBE 1984).
Apparently, it has not been noticed, however, that also the extant Juglandales are not exclusively anemophilous. An evident entomophily syndrome occurs in the temperate eastern asiatic monotypic genus Platycarya. This is all the more interesting since the fossil record of flowers

in *Juglandaceae* is unusually rich. This knowledge of the history of the family, together with an evaluation of structural and functional peculiarities of extant *Platycarya*, enables us to conclude that entomophily in *Platacarya* is most probably a secondary reversion from anemophily which was in itself already a derived state with regard to early angiosperms.

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2. MATERIAL AND METHODS

A tree of *Platacarya strobilacea* Sieb. et Zucc. in the Botanical Garden of the University of Zurich was observed during several flowering seasons (ENDRESS 6548 [Z])). Living material and flowers fixed in FAA were studied with the SEM; the fixed material was examined after critical point drying and Au/Pd-sputtering. Flowers of other *Juglandaceae* cultivated in Zurich were studied for comparison: *Juglans cathayensis* Dode (Endress 4450a), and *Pterocarya* x *rehderiana* Schneider (Endress 6748).

3. OBSERVATIONS

The tree of *Platycarya strobilacea* studied flowers in early July. The inflorescences consist of a cluster of upright spikes. About 7 lateral male spikes surround a terminal mixed spike containing female flowers at the base and male flowers on the top (Figs. 1A, 2). The inflorescences are conspicuous by their yellow colour and strong smell reminiscent of *Tilia* flowers and vanilla. Syrphids and other small dipters have been observed as flower visitors (Fig. 2).
The male flowers are extremely zygomorphic. The pedicel is not developed so that the 4-15 stamens (MANNING 1948) of each flower sit on their subtending bract and on the inflorescence axis above the bract (Figs. 1B,

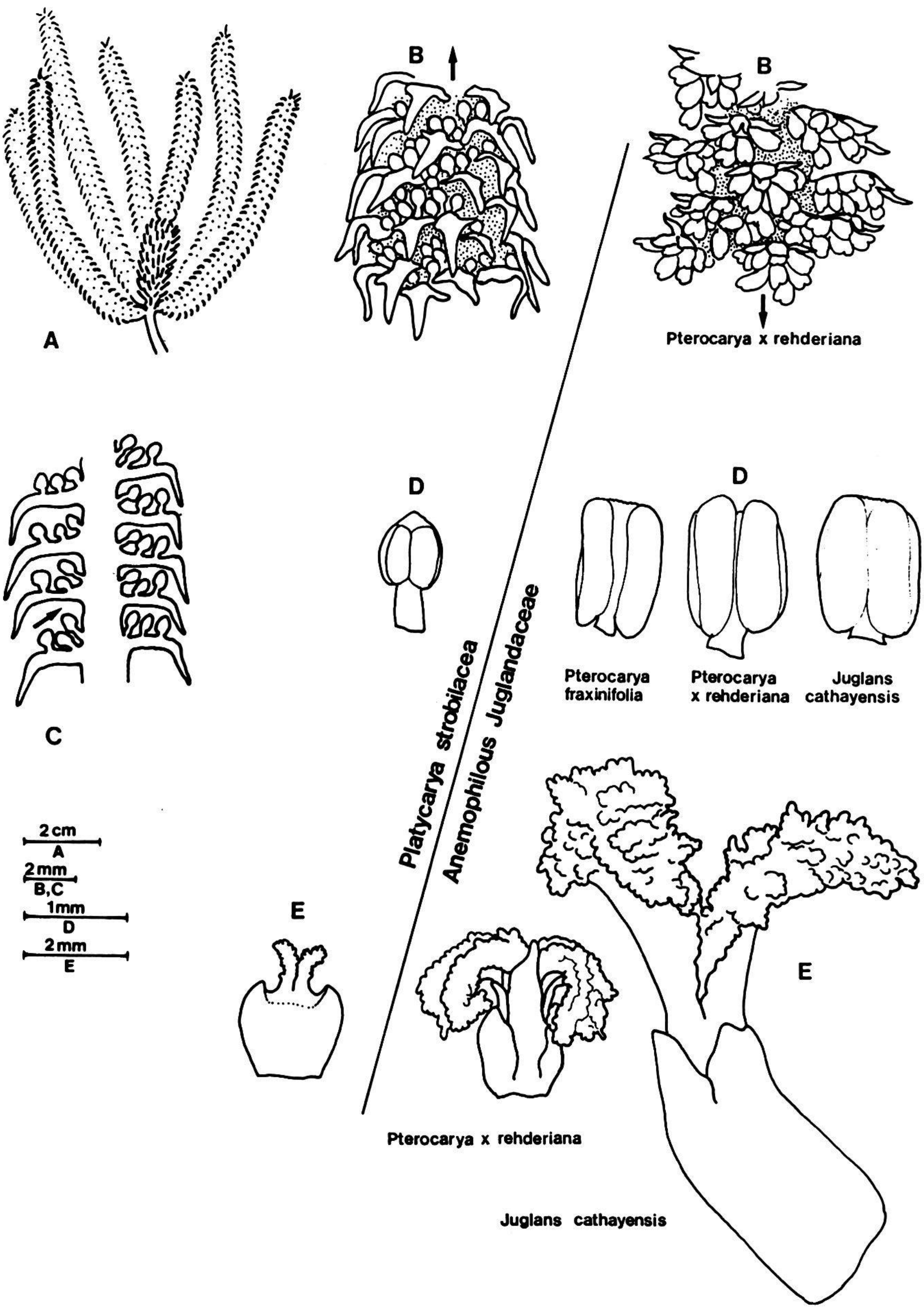
C, 5). The bracts are cuspidate. The tip is upright at first and becomes reflexed at early anthesis; it is red and provides a conspicuous colour contrast with the yellow part of the bract and with the yellow stamens; on the exposed (upper) side it is densely covered with short glandular hairs, which are lacking on the other parts of the bract (Figs. 5, 7, 8). Scent seems to be produced either by the secretion of the glandular hairs or by a secretion of the smooth proximal part of the bract. The bending downwards of the bract tips also allows easy access of pollinators to the pollen and may act as a platform for them. The opening of the anthers of a flower is not simultaneous. The most distal ones on the bract open first; those on the inflorescence axis last (Fig. 1C). The small anthers (0.7 mm long, 0.6 mm broad (Fig. 1D)), contain small pollen (mean diameter about 15 µm, cf. WHITEHEAD 1965, STONE and BROOME 1975), which is very sticky, having abundant pollenkitt on the surface (Fig. 6). The distances between the individual flowers along the inflorescence axis are small and free air interspaces are lacking.

Fig. 1 (p. 103). A. Inflorescence at anthesis. B. Part of male spike at anthesis (arrow: apical direction of spike). C. Diagrammatic longitudinal section of part of male spike with bracts and stamens (arrow: direction of anther opening during anthesis). D. Stamens at anthesis, all in the same magnification (from adaxial side). E. Female flowers at anthesis, all in the same magnification (from abaxial side; stigmatic surface papillose).

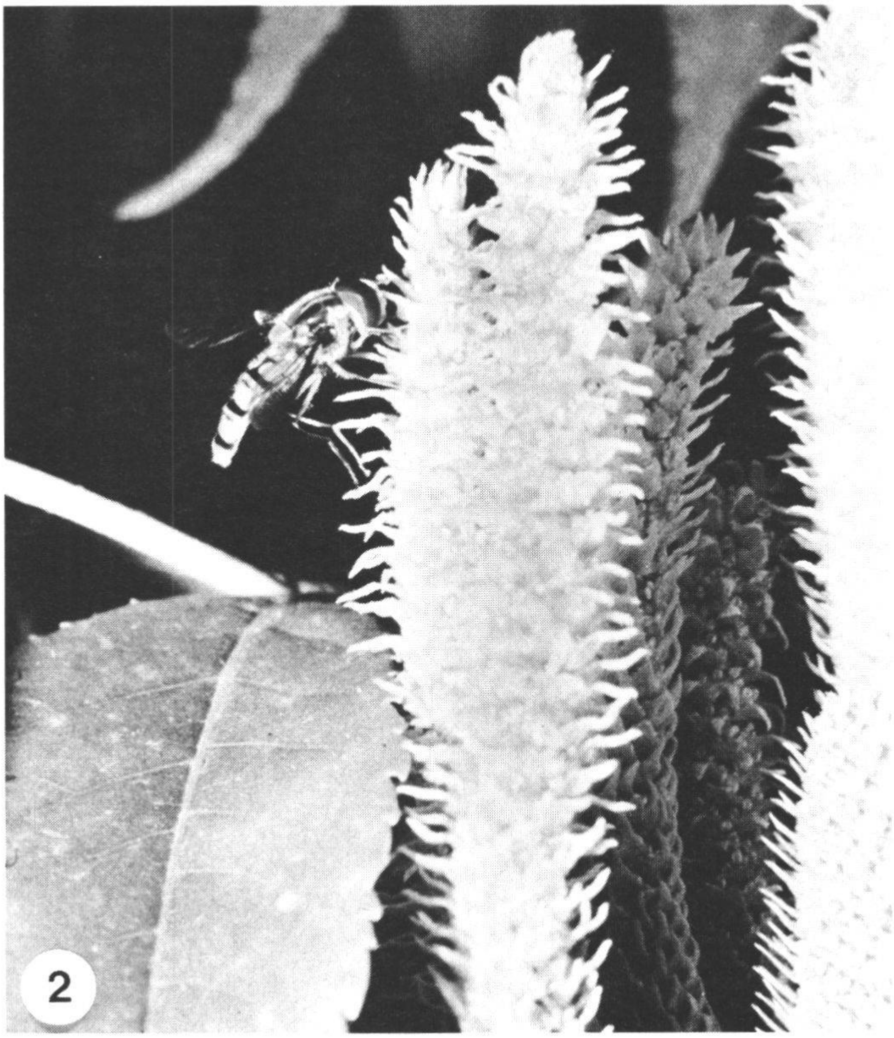
Abb. 1 (S. 103). A. Infloreszenz zur Blütezeit. B. Teil einer männlichen Aehre zur Blütezeit. (Pfeil: Apikale Richtung der Aehre). C. Schematischer Längsschnitt durch Teil einer männlichen Aehre mit Brakteen und Stamina (Pfeil: Richtung der Antherenöffnung in einer Blüte während der Blütezeit). D. Stamina zur Blütezeit, alle gleich vergrössert (von adaxial). E. Weibliche Blüte zur Blütezeit, alle gleich vergrössert (von abaxial; Narben papillös).

Figs. 2-4 (p. 104). Platycarya strobilacea, parts of inflorescence at anthesis.
2. Part of inflorescence with visiting syrphid fly (lower part of the right side: female flowers, other flowers male); x2.
3. Part of female spike; x14. 4. Abaxial side of bract of female flower with scattered glandular hairs; x65.

Abb. 2-4 (S. 104). Platycarya strobilacea Infloreszenzausschnitte zur Blütezeit.
2. Teil einer Infloreszenz mit Schwebfliege als Blütenbesucher (rechts unten weibliche Blüten, übrige männlich; 2x.
3. Teil einer weiblichen Aehre; 14x. 4. Unterseite der Braktee einer weiblichen Blüte mit zerstreuten Drüsenhaaren; 65x.



A
B
B
Pterocarya x rehderiana
C
D
D
Pterocarya fraxinifolia
Pterocarya x rehderiana
Juglans cathayensis
Platycarya strobilacea
Anemophilous Juglandaceae
2cm
A
2mm
B,C
1mm
D
2mm
E
E
E
Pterocarya x rehderiana
Juglans cathayensis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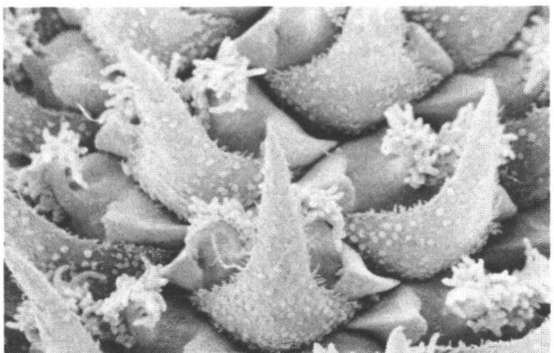
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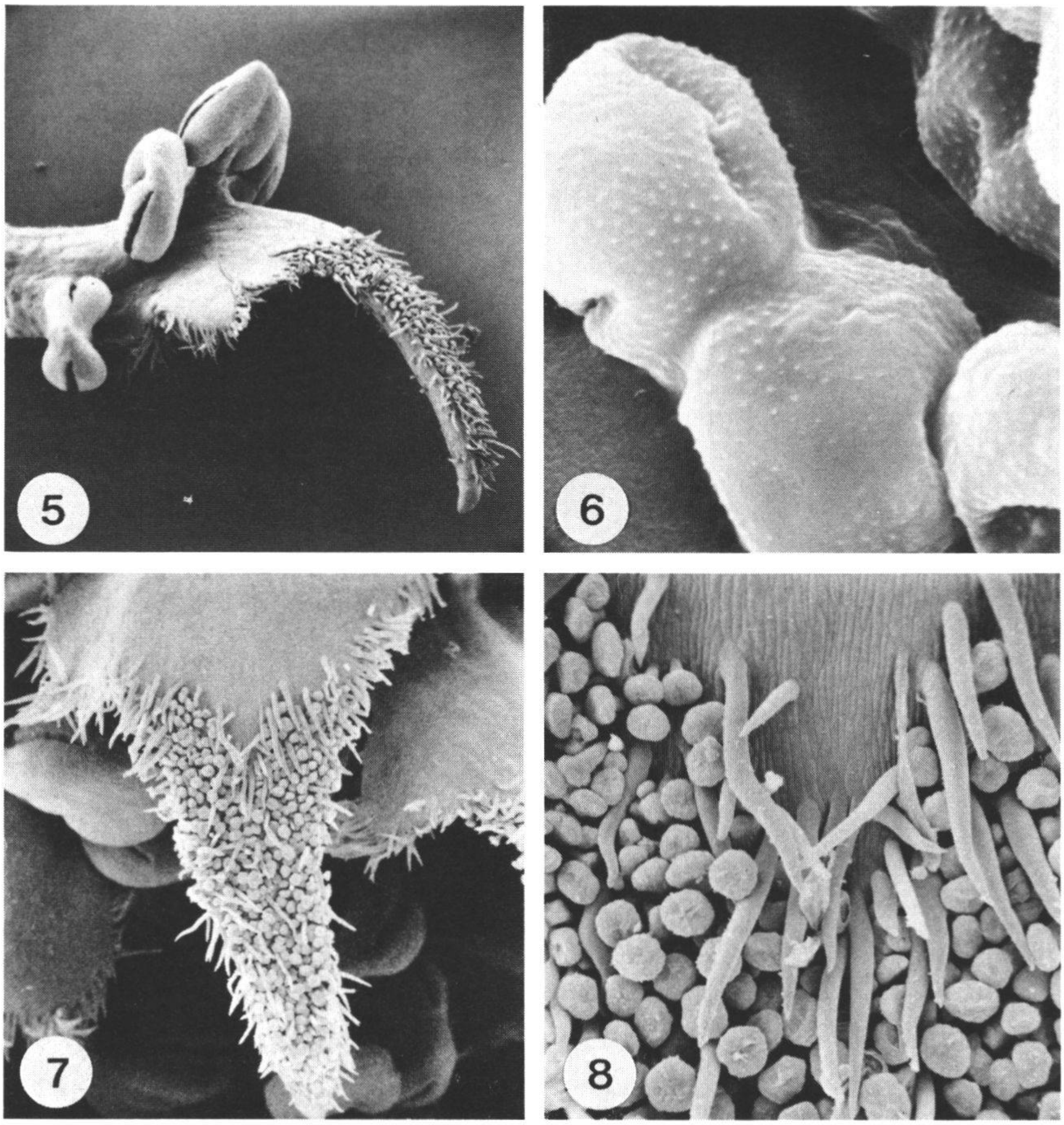

Figs. 5-8. Platycarya strobilacea, parts of male spikes at anthesis.
5. Distal part of male flower with recurved bract tip; x20. 6. Living, untreated pollen grains, coherent by abundant pollenkitt; x3000. 7. Tip of bract (upper side) with crowded glandular hairs; x35. 8. Part of Fig. 7, enlarged; x130.

Abb. 5-8. Platycarya strobilacea, Teile männlicher Aehren zur Blütezeit.
5. Distaler Teil einer männlichen Blüte mit zurückgebogener Brakteenspitze; 20x. 6. Lebende, unbehandelte Pollenkörner, miteinander verklebt durch Pollenkitt; 3000x. 7. Oberseite einer Brakteenspitze mit zahlreichen gedrängten Drüsenhaaren; 35x. 8. Ausschnitt aus Abb. 7, vergrössert; 130x.

The female flowers produce much less scent than the male ones. They have relatively small stigmas (Fig. 1E). In contrast to the male flowers the bracts remain erect throughout anthesis. They are green, and glandular hairs are only sparsely distributed on the **lower** surface (Figs. 3, 4).

4. DISCUSSION

4.1. THE ENTOMOPHILY SYNDROME OF PLATYCARYA

Platycarya is the only juglandaceous genus with female and male flowers occurring on the same spike. In all other representatives of the family they are on different spikes, or even on different shoots. Although anemophilous plants are often visited by pollen collecting insects, too, especially by syrphids (cf. STELLEMAN 1984), their contribution to pollination is negligible if male and female flowers are not adjoining. Also the feature of stiff, erect male spikes is exclusive for Platycarya (MANNING 1938, 1978), in all other genera they are lax and pendulous catkins (Fig. 1B). In Platycarya the space between individual flowers along the inflorescence axis, both male and female, is smaller than in the wind-pollinated groups of the Juglandaceae, since air flow between the flowers needs not to be facilitated (Fig. 1B). The small or lacking interspaces and the stiffness of the spike axis are both due to a less pronoundced elongation shortly before anthesis. The correlation between the lax, pendulous catkin axis and its pronounced elongation shortly before anthesis has been shown for several wind-pollinated Amentiferae by HELLER (1935).

Comparatively low pollen production in Platycarya is reflected by a low stamen number per flower (4-15) in contrast to up to 105 in Juglans species (cf. MANNING 1948). In addition, the successive anther opening within a flower has the consequence that at a given time relatively few pollen is available. Pollen size of most Juglandaceae is in the range of the anemophily syndrome, i.e. between 20 and 40 µm diameter (WHITEHEAD 1983). Only in Platycarya (and in Engelhardia roxburghiana) it is considerably lower (WHITEHEAD 1965, STONE and BROOME 1975); accordingly anther size is smaller (about half length) compared with other genera of the family (Fig. 1D).

Although pollen of Platycarya is very sticky by abundant pollenkitt on the surface, it has the same smooth exine as the wind-pollinated groups of the Juglandaceae (cf. STONE and BROOME 1975). In the wind-pollinated Juglans with dry pollen (HESSE 1978, 1981) found pollenkitt to be present but restricted to the exine cavities and not covering the surface.
In typically wind-pollinated Juglandaceae the stigmatic surface is much larger than in Platycarya (Fig. 1E).
In most anemophilous Juglandaceae anthesis occurs in a leaf-less phase of the trees. This is not only true for temperate deciduous genera but even for tropical evergreen members such as Engelhardia in Malesia where flowering is often (always?) accompanied by a short leaf-less phase (cf. JACOBS 1960). On the other hand, Platycarya flowers when it is in full foliage, although it is decidous.
Another Juglandacea worthy of closer inspection as a potential candidate for entomophily is the already mentioned Engelhardia roxburghiana (= E. chrysolepis) which has very small pollen (WHITEHEAD 1965, STONE and BROOME 1975), smaller anthers than in other Engelhardia species (JACOBS 1960), very small stigmas (MANNING 1940, JACOBS 1960) and (peripheral) male and (central) female spikes on the same shoots (MANNING 1938).
The traits constituting the entomophily syndrome in Plarycarya strobilacea are listed in Table 1. Taken together, these features show that Platycarya stands in sharp contrast to groups with an anemophilous syndrome (cf. DGEBUADZE and SOLNTZEVA 1977 for Carya illinoinensis). On the other hand the structural differences of each trait taken individually is more quantitative than qualitative, and the evolutionary step necessary from the one to the other side does not seem to be major.

4.2. PRIMARY OR SECONDARY ENTOMOPHILY?

The unusually rich record of fossil juglandaceous flowers helps in reconstructing the phylogeny of the family and in evaluating the evolutionary status of Platycarya. Inflorescences from the Tertiary have unisexual flowers and do not reveal evident traits of entomophily (CREPET 1979, CREPET et al. 1975, 1980, WING and HICKEY 1984, MANCHESTER and DILCHER 1985). Of still more interest is the spectacular discovery of flowers from the Upper Cretaceous with clear juglandalean affinities (FRIIS 1983, 1985). They are bisexual, radially or bilaterally symmetric

Table 1. Features of the entomophily syndrome in Platycarya strobilacea.
Tab. 1. Merkmale des Entomophilie-Syndroms bei Platycarya strobilacea.

1. Female and male flowers on the same spike (Fig. 1A).
2. Inflorescences strongly scented.
3. Male spikes yellow with red tips of the floral bracts.
4. Male spikes stiff and erect at anthesis (Fig. 1A).
5. Flowers densely packed without free air spaces between, anthers not exposed (Fig. 1B,C).
6. Anthers within individual flowers opening successively over a longer period, at a given time relatively few pollen available (Fig. 1C).
7. Stamens relatively few (4-15) per flower.
8. Pollen (and anthers) relatively small, below range of anemophily syndrome (Fig. 1D).
9. Pollen sticky by excessive pollenkitt on surfaces (Fig. 6).
10. Stigmas relatively small (Fig. 1E).
11. Flowering time in July, when trees are in full foliage.

and have a low number of stamens (5-6). These features point to possible entomophily or at least to entomophilous ancestry. However, the stamens contain Normapolles pollen which is generally interpreted as adapted to anemophily (BATTEN 1981). In this context it is interesting to note that bisexual flowers have often been reported as exceptional formations in extant Juglandaceae, mainly in Platycarya and the related Pterocarya and Engelhardia (e.g. MANNING 1940, 1948, 1978, HJELMQVIST 1948, IL'INSKAJA 1953, LEROY 1955, JACOBS 1960, SU and HE 1984, and several earlier authors).

All this makes it probable that the cretaceous ancestors of Juglandaceae had bisexual flowers and the anomophily syndrome of the group became refined in the early Tertiary. This clearly contradicts MEEUSE's assertion (1975) that the juglandaceous flowers are primitively unisexual and not homologous with those of Magnoliidae and Rosidae. Apparently, the overall trend in Juglandaceae went from primary entomophily to anemophily, and in Platycarya back to secondary entomophily. It is obvious in Platycarya that the entomophily syndrome has developed from an anemophily syndrome, since the differences of the single features that make up the syndrome are not major, in contrast to the differences from the features of a primary entomophily syndrome with bisexual flowers.

This may be seen as the result of reversible evolution which is probably an important but much neglected factor in angiosperm evolution. Reversible in this case was the development from entomophily to anemophily, not the concomitant morphological changes of the single traits. Therefore, the reversion to entomophily did not include a simple reversion of the evolutionary pathway in every respect, but evolution did work with the actual framework of traits at disposition. In the secondarily entomophilous Platycarya for example, the inflorescence is bisexual but not the flowers, and the floral bracts are attractive but not a perianth, presumably in contrast to the primarily entomophilous ancestors of the Juglandaceae.

It is to be hoped that these observations will stimulate a study of the pollination biology of Platycarya in its natural habitat.

SUMMARY

The eastern asiatic Platycarya strobilacea has an evident entomophily syndrom within the Juglandaceae, which are generally regarded as anemophilous throughout. These features are: spikes partly bisexual, showy, scented, stiff, erect; stamens relatively few, anthers small, opening successively within a flower, not exposed; pollen sticky, relatively small, with a size below the range of anemophilous plants; stigmas relatively small; flowering time when trees are in full foliage. Dipters have been observed as flower visitors.

On the basis of the rich paleobotanical record of juglandalean flowers from the Upper Cretaceous and Tertiary, and morphological and biological features of extant Juglandaceae it is concluded that the immediate ancestors of Platycarya were anemophilous, but the cretaceous ancestors of the Juglandaceae with bisexual flowers were probably entomophilous. Hence, the development from entomophily to anemophily within the early Juglandales was reversible in Platycarya, but the reversion took another pathway with regard to the single traits of the syndrome than the initial progression to anemophily.

ZUSAMMENFASSUNG

Die ostasiatische Platycarya strobilacea zeigt als Ausnahme unter den anemophilen Juglandaceae ein Entomophilie-Syndrom: Aehren teils zweigeschlechtig, auffällig in Farbe und Duft, steif, aufrecht; Stamina relativ wenige, Antheren klein, sich nicht gleichzeitig öffnend innerhalb einer Blüte, nicht exponiert; Pollen klebrig, relativ klein, in der Grösse unterhalb der Variationsbreite windblütiger Pflanzen; Narbenoberfläche relativ klein; Blütezeit während voller Belaubung der Bäume. Als Blütenbesucher wurden an einem (in Mitteleuropa) kultivierten Exemplar verschiedene Dipteren beobachtet.

Aufgrund der Merkmale der relativ reichlich vorhandenen fossilen Blüten der Juglandales aus Oberkreide und Tertiär sowie morphologischer und biologischer Eigenschaften der rezenten Juglandaceen wird geschlossen, dass die unmittelbaren Vorfahren von Platycarya windblütig waren, dass

aber die kretazischen Vorfahren der Juglandaceae mit Zwitterblüten wahrscheinlich insektenblütig waren. Die Evolution von der Entomophilie zur Anemophilie innerhalb der ursprünglichen Juglandales war also reversibel bei Platycarya, aber die Rückkehr zur Entomophilie vollzog sich im Einzelnen auf einem anderen Weg als die ursprüngliche Progression zur Anemophilie.

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