THE DESCENT OF THE FLOWERING PLANTS IN THE LIGHT OF NEW EVIDENCE FROM PHYTOCHEMISTRY AND FROM OTHER SOURCES

I. GENERAL DISCUSSION

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SUMMARY

Accumulated phytochemical data partially compiled by Kubitzki in 1969, and evidence from various other sources point to a fundamental heterogeneity of the Flowering Plants, which is interpreted by the present author as an unmistakable indication of a multiple descent of the Angiosperms. The consequences of this viewpoint for taxonomic classifications and for phylogenetic speculations must be faced. In view of the possible misunderstanding of some pointers, and in order to avoid erroneous interpretations of the accumulated evidence, a survey of the relevant data appears to be indicated. Some tentative proposals concerning a future classification of the Angiosperms will be made in the second part of this paper.

1. INTRODUCTION

Recently, KUBITZKI (1969)[1] pointed out that cogent phytochemical evidence renders a close relationship between the *Polycarpicae* or *Ranales (s.l.)* and several other groups of the Dicotyledons most unlikely. The corollary of his discussion is that the Dicots (and, by inference, the Angiosperms) are rather heterogeneous and did not all arise from a *ranalean* ancestral group, and that, in point of fact, the ranalean alliance is more likely to represent a kind of phylogenetic *cul-de-sac*. Most hesitatingly, Kubitzki admits the possibility of a multiple descent of the Flowering Plants, referring to a statement made over fifteen years ago by Metcalfe (who suggested that the assumption of a polyphyletic origin of the Angiosperms may well provide the best explanation of the great diversity of their anatomical features) but, strangely enough, not mentioning more recent contributions dealing with the question of a single *versus* a multiple descent. Especially a number of relevant publications by the present author, in which the isolated, relict character of such groups as the *Magnoliales (s.s.)* and the presence of a plexus of "more successful" dicotyledonous groups including such taxa as *Guttiferae (Clusiales)* and *Cistiflorae (Parietales; i.e.,* the ordines *Dilleniales, Theales* and *Cistales* in TAKHTAJAN's (1969) and *Theales* and *Cistales* in THORNE's (1968) classifications, respectively) were emphasised, might have been adduced for corroborative data. When my earlier papers were written

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[1] The references will be published at the end of the second paper.

(before 1964; for a summary, see MEEUSE 1965, Chapters III, IV and XIV), the phytochemical evidence was not nearly so convincing as it is at present, so that I consider myself entitled to say that the recently procured data from "chemo-taxonomy" or "biochemical (molecular) systematics" *corroborate* the indications from several other sources.

Although Kubitzki's paper barely touches upon relevant morphological and additional, non-chemical, characteristics, there are some points which I consider to be misapprehensions and need some comment, the more so because the morphological evidence, if properly interpreted, is so strongly supported by chemodiagnostic pointers.

I firmly believe that the irrefutable chemical data will compel the leading phanerogamists eventually, but unavoidably, to change their minds and to start thinking (and system-making?) along the lines of a more diversified origin of the Flowering Plants. In order to make it easier for the reader to follow my train of thought, or perhaps even to attempt the new approach himself (or herself), a number of points must be raised concerning the consequences of such a change-over. I have already treated some of these topics in greater detail, especially in my above-cited book on Angiosperm phylogeny, but cases dealt with in a few other recent publications may serve as examples of the effect of a New Look in Flowering Plant Taxonomy on the subjects treated in these papers and of the rather different outlook after an alternative interpretation of the evidence. Several aspects amply discussed in some of my previous works (MEEUSE 1961, 1962, 1964, 1965, 1966) will not be repeated here (for particulars the reader should consult the originals), but only the salient points will be singled out. The evidence is augmented by data gleaned from several recent publications that have some bearing on the subject in question.

2. THE PRINCIPAL MORPHOLOGICAL AND ECOLOGICAL IMPLICATIONS OF A MULTIPLE VERSUS A SINGLE DESCENT OF THE ANGIOSPERMS

The postulate of a monophyletic origin of the Flowering Plants has cramped the style of nearly all system-makers, because of necessity all angiospermous taxa were supposed to have originated from a single group of progenitors (a single prototype), usually assumed to be morphologically conformable to a, more or less vaguely circumscribed, proto-ranalean, and, to all intents and purposes, a more or less magnoliaceous, form. It is irrelevant in this connection if, as was sometimes done, a different hypothetical prototype was chosen. The morphological and ecological characters of that hypothetical pre- or proto-angiospermous group of progenitors (and usually in actual practice: of some *recent* members of the *Polycarpicae*!) served, again of necessity, as the archetype (the "primitive condition") of various similar or dissimilar features present in recent angiospermous groups and supposed to be the homologues of that "primitive" character.

If one decides, however reluctantly, to reconcile oneself to the inevitable, one must also face the consequences: the alternative case of a polyphyletic (po-

lyrheithric) evolution implies the occurrence, at one time or another, of a number of *different* contemporaneous prototypes, and each of these may have had some singular characteristics distinguishing it from the other ones, thus largely accounting for the great diversity of the taxonomic characters of the recent Angiosperms. We must get accustomed to the idea that there were several *alternative*, "original" conditions each of which is "primitive" in respect of all features homologous with (derived from) it, but by no means necessarily so in respect of features found in groups belonging to a different lineage (MEEUSE 1966, p. 8). The most important alternative conditions, nowadays present in different angiospermous groups, but (to my mind, at least) by inference already occurring separately in the respective groups of immediate angiosperm progenitors, and having some bearing on the assessment of certain features in Angiosperm taxonomy and phylogeny, include:

1. *phytochemical characteristics*, viz., the absence or presence of certain unequivocally identifiable organoconstituents, indicative of the presence or absence of some genetically controlled, more or less typical synthetic pathway(s);
2. a number of *morphological and other structural features* such as growth habit, leaf shape, floral morphology, morphology of fruit and seed, embryological and palynological characteristics, (wood) anatomy, the type of stomatal apparatus, etc.;
3. *sex distribution* (monocliny *versus* dicliny), roughly correlated with the type of pollination (zoo- or anemophily, respectively);
4. *genetic data*, mainly obtained from karyological ("cytological") studies, and principally chromosome numbers;
5. *host-parasite relationships*; and
6. *fossil records.*

2.1. Chemical features

Kubitzki, following up earlier suggestions made by Bate-Smith, Hegnauer and some other workers, applied the following hypotheses:

a. certain higher hydroxylated compounds are phylogenetically more advanced than corresponding compounds with a lower degree of hydroxylation, so that, generally speaking, the presence of, *e.g.*, ellagic acid and β-trihydroxylated flavonoids (such as myricetin and leucodelphinidin), in not manifestly advanced dicotyledonous groups is supposed to be a derived character, and the presence of lower substituents (or total absence of ellagic acid and of the particular, specific group of phenolic compounds) a more primitive condition (barring the cases of a "secondary loss" of the synthetic pathway in very advanced groups, of course),

b. the occurrence of a certain group of alkaloids is characteristic of many taxa of the greater ranalean alliance, but these compounds are practically non-existent in all other di- and monocotyledonous groups except *Rutaceae* and some associated families; and

c. the capacity of biosynthesising iridoid monoterpenes and their derivative compounds is indicative of a relationship of groups with this capacity, and

conversely, the lack of this biosynthetic pathway, generally speaking, is a nega-
tive indication of taxonomic affinity.

In addition, other chemical evidence not mentioned by Kubitzki is certainly
admissible. The Monocotyledons have often been supposed to be "derived"
from a more or less "ranalean" group of progenitors, but they lack certain
typical features of the Dicotyledons altogether (such as the normal dicotyle-
donous type of secondary growth) and do not show a striking chemical affi-
nity with magnoleaceous (nymphaeaceous) or berberidalean-ranunculalean
taxa. As I have pointed out on several occasions, certain resemblances in "pri-
mitive" features between Mono- and Dicots, particulary in their pollen mor-
phology (viz., the occurrence of monosulcate grains in a number of magnoli-
aceous genera and in several families of the Monocots), can also be satisfacto-
rily explained by assuming that they represent some ancient cycadeoid charac-
ters retained from their, still gymnospermous, ancestors (in very much the same
way as all bordered pits and corresponding modified types of pitting of all seed
plants including the Angiosperms are most probably derived from the bordered
pits of the Devonian Progymnospermopsida). The occurrence of petiolate and
reticulately veined leaves in Araceae, Dioscoreaceae, Taccaceae, etc., is, like-
wise, not necessarily a clear indication of a relation with Dicots (as HUBER 1969,
has it), because these features are known from several (fossil and living) cy-
cadopsid gymnosperms.

Within the ambit of comparative phytochemistry one would at least expect
some clear chemical affinity between the two major groups of the Angiosperms,
and especially between Polycarpicae and Monocots, but alkaloids of the iso-
quinoline type, so characteristic of the ranalean assembly of taxa, are completely
lacking in the Monocots. Conversely, certain secondary plant products typical
of Monocots, such as certain steroid saponins of wide-spread occurrence in
Dioscoreales and in (other) Liliiflorae, are not clearly matched by related com-
pounds in members of the Polycarpicae or in other groups eligible as primitive
Dicots. It is interesting to note that HUBER (1969) considers the Dioscoreales to
represent the most primitive recent taxon of the liliiflorous assembly and men-
tions some morphological features suggesting connections with early Dicots
(or, more probably, protodicots, as we have just seen). This contention is not
borne out by the phytochemical evidence, however, and, also in the light of
other morphological characters, a close relationship with 'typical' (magnoli-
aceous) Polycarpicae is not very probable.

As Kubitzki's paper infers, the biochemical data are much more compatible
with the postulation of a long, independent and parallel development of several
major angiospermous groups from as many early (possible pre-Cretaceous), and
still gymnospermous, ancestral taxa.

The chemical evidence is not always unequivocal, however. The occurrence
of the betalains in the majority of the families of the "Centrospermae" and in a
few obviously related ones (see WOHLPART & MABRY 1968, for a summary),
but not in the anthocyanidin-producing Caryophyllaceae and "Molluginaceae",
poses a taxonomic problem. An independent origin of the "Centrospermae"

can not be substantiated solely by the presence or absence of the nitrogen-containing, red or purple betacyanins and the related betaflavones, *i.e.*, without a consideration of the taxonomic position of the two, in my opinion, pertaining anthocyanidin families (for a full discussion the reader is referred to my forth-coming book on chemodiagnostics and practical taxonomy). On the other hand, consistent phytochemical evidence pointing to a possible connection between "rosiflorous", hamamelidaceous and amentiflorous taxa seems to be une-quivocal and agrees with the repeatedly mentioned "advanced" condition of some anatomical features of the amentiflorous orders. A common origin of one or of some of the taxa included in the heterogeneous "*Rosiflorae*" (HUBER 1963) and of the other two groups is not at all unlikely, but they are rather divergent and the hamamelidaceous and amentiflorous orders retained some primitive characters (*e.g.*, binucleate pollen grains: BREWBAKER 1967; crassinucellate ovules: DAVIS 1966; integuments with vascular bundles: KUEHN 1928; perhaps also the type of integument initiation: BOESEWINKEL & BOUMAN 1967); SPORNE (1969) rated these groups in his advancement indices as low as 27 (for *Rosaceae*) to 37 (*Juglandales*), or 41 to 44 (if *Salicaceae* and *Casuarinaceae* belong here), in a scale with a maximum of 100, *i.e.*, among the 41 (or 63) dicotyledonous families with the lowest indices (out of a total of 259 families). The corollary of these data is that the hamamelidaceous and amentiflorous orders have hetero-bathmically evolved, their wood anatomy and, to a somewhat lesser extent, their phytochemical characteristics being more or less clearly advanced, but some other (*e.g.*, embryological) features having retained a primitive condition.

Another complication, apart from the secondary absence due to the "dis-appearance" of a group of bioconstituents (NOOTEBOOM 1966) is the possibility of a phytochemical convergence or parallelism, *i.e.*, the independent develop-ment of synthetic pathways leading to the same type of secondary plant pro-ducts in different taxa. The accumulated data have taught us that in the cases under discussion complications of this kind can be disregarded, allowing for the possible "loss" of, *e.g.*, the capacity to synthesise benzylisoquinoline bases in groups derived from ranaleans in which these alkaloids are of common occur-rence.

2.2. Morphological and other structural features

HUBER (1963) and SPORNE (1969) have shown that a number of primitive macro- and micromorphological characters are not only found in taxa belonging to the large ranalean assembly, but also in such groups as *Dilleniales*, *Theales* (*Cisti-florae*), *Rosales* s.l., *Hamamelidales*, *Clusiales* (*Guttiferae*), *Parietales* (*Bixales*, etc.), and even (Sporne) *Myrtales*. I have (*e.g.*, MEEUSE 1965, 1966) pointed out that the androecial morphology of several of these groups is essentially different from that of the *Polycarpicae* and is often associated with centrifugal (instead of centripetal) stamen maturation. This can be interpreted as a fundamental morphological difference between the ranalean assembly and the other dicoty-ledonous groups indicative of an indepedent and divergent evolution of these taxa (it was, for this reason, used as an additional argument by MERXMUELLER

& Leins 1967, to dismember the "*Rhoedales*" by placing the *Papaveraceae* near the *Berberidaceae* and *Ranunculaceae* in the *Polycarpicae*, and the remainder, as *Capparidales*, somewhere near or in the *Parietales*).

There are no cogent reasons to postulate a single "primitive" habit form for *all* angiospermous groups (Meeuse 1968). It is interesting to note that, their rather singular growth form notwithstanding, the *Dioscoreales* are considered to be the most primitive order of the large liliiflorous assembly by Huber (1969). Several ranalean and associated groups are climbing or rambling (*Lardizabalaceae, Menispermaceae, Schisandraceae, Aristolochiaceae*, some *Annonaceae, Piperaceae* and *Ranunculaceae*; other examples among non-ranalean groups with an advancement index between 27 and 48 (Sporne) are: *Actinidiaceae, Connaraceae, Passifloraceae*, some *Dilleniaceae, Leguminosae* and *Sapindaceae*. This evidence is compatible with the assumption that some of the protoangiospermous groups were predominantly arborescent and erect, some of a low stature to semi-herbaceous, and some climbing, thus reflecting an early diversity or pleiophyly.

Although I feel that the "advancement index", as calculated by Sporne and (for Monocots) by Lowe (1961), is not an absolute yardstick and can be critisised in several respects, the results obtained by these workers can not altogether be without significance. Their data do not unequivocally pinpoint a single group as the "most primitive" one, but suggest a certain equivalence of advancement of several not closely related taxa, *i.e.*, a parallel and independent phylogenetic history rather than a divergent one from the same ancestral group. Lowe's data also suggest a wide range or advancement of certain orders, which does not help to single out the more primitive group or groups, a point stressed by Bate-Smith (1968b). The same conclusion can be drawn from the occurrence of a number of embryological and related features: crassinucellate ovules with vascularised integuments, and at maturity binucleate pollen grains, for instance, are by no means restricted to one (ranalean) group, and within orders there may be a range of representation of a character.

Even if one regards the evidence as inconclusive, it would not contradict more positive indications of an ancient heterogeneity of the Angiosperms, such as diverse phytochemical patterns. One of the most interesting anatomical characters, recently discovered by Behnke (1965, 1969a, 1969b, and in the press), is the fine structure of protoplasmic inclusions in the sieve-tubes. These plastid-like elements are of three types which appear to be correlated with the taxonomic arrangement. In all Monocots investigated up to now, these elements contain in electron-optical section wedge-shaped proteinaceous bodies (Behnke 1969b, lists 24 species out of 21 families from all orders but one, but the number of species has since risen to 26 representing 22 families: Behnke, private comm. dated 7/10/1969). The families include the *Dioscoreaceae* which is a clear indication of the status of this taxon: in spite of "dicotyledonous" trends (such as the presence of a lateral cotyledon, or perhaps of even two cotyledons, and the arrangement of the vascular bundles in young stems) it seems to belong to the Monocots, a conclusion that can also be drawn from its phytochemical characteristics.

In the majority of the dicotyledonous orders the plastid-like bodies do not show much structure in electron micrographs. This S-type plastid of Behnke was found in an appreciable number of cases (in about two dozen species belonging to about 15 orders including the *Polygonales*), with the notable exception of the centrospermous taxa of which BENHKE (1969b, and unpublished results) records 18 examples from 10 families including representatives of the *Cactaceae, Caryophyllaceae,* and *Didiereaceae.*

In the centrospermous assembly the sieve-tube inclusions are of a singular type. They appear as almost spherical bodies (the other two types, the "monocotyledonous" K-type and the common "dicotyledonous" S-type, are usually more ellipsoid) with, in electron-optical cross section, a dark outer zone and a more hyaline centre. This character sharply distinguished the *Centrospermae,* with the associated families *Cactaceae* and *Didiereaceae* and including the *Caryophyllaceae,* from all other Dicots including the *Polygonales.* This is a clear indication of the "isolated" position of the *Centrospermae* in respect of other Dicots.

Additional conclusions to be drawn from the distribution of these plastid types concern (1) the position of the *Nymphaeales* and *Nelumbonales* in respect of the *Monocotyledones* and (2) the position of the *Helobiae* in respect of the *Ranunculaceae* and some related ranalean taxa. In the past a possible close relationship between *Nymphaeaceae* and Monocots has repeatedly been suggested but the presence of ellagitannins in *Nymphaea* and in *Nuphar,* and of certain alkaloids related to the alkaloids of the ranalean assembly in *Nelumbo,* combined with the occurrence of sieve-tube inclusions of the S-type in the nymphaeoid forms, plead strongly against this idea. Another alleged "link" between Mono- and Dicots by way of the groups *Helobiae (Alismatales)-Ranunculales* must, likewise, be rejected. Behnke's painstaking researches have contributed another cogent argument in favour of a heterogeneity, *i.e.,* of an independent origin of Monocots and Dicots, apart from emphasising the isolated position of the *Centrospermae* in respect of all other dicotyledonous groups.

2.3. Sex distribution

Many workers have not only postulated a monophyletic origin of the Angiosperms, but also a single form of sex distribution, *viz.,* the exclusive incidence of monocliny (bisexual flowers) in the immediate progenitors of the Angiosperms. As I have pointed out (MEEUSE 1965, Chapter IX), there is a distinct discrepancy between this idea and the almost universal dicliny observed in all fossil and recent gymnosperms, and in order to explain this one had, furthermore, to assume that, at one time or another, a change-over from dicliny to monocliny took place. I hold the view that indeed this change-over occurred, presumably induced (or at least facilitated) by selective pressure exerted by pollinating insects, and substantiated this (*l.c.*) by referring to the morphological and occasionally even functional monocliny of the *Chlamydospermae* as a probable intermediate stage. However, I most emphatically deny that this was the *sole* pathway of floral evolution. The very fact that wind pollination is,

or was, quite common among gymnospermous groups, combined with the regular occurrence of anemophily in a number of angiospermous groups (palms, pandans, amentiferous orders, etc.), renders it plausible that not all pre-angiosperms "switched over" from dicliny to monocliny but retained their original mode of pollination and passed it on to their descendants, the *primarily anemophilous* angiospermous groups. This is one of the most striking examples of the hindrance of the old hypothesis of a monophyletic descent of the Flowering Plants to ideas concerning morphological and ecological floral evolution; as stated in the introductory paragraph of the present paper, this hypothesis permits *only a single* structural and functional prototype, *viz.*, a "bisexual" flower. It is quite clear that the alternative postulation of several, and for a considerable length of time independent, evolutionary lines leading to as many angiospermous groups is in good agreement with the contemporaneous occurrence of anemophilous (palms) and entomophilous taxa since at least the early Cretaceous.

Now that the phytochemical pointers and other considerations (compare Huber, Kubitzki) clearly favour a pleiophyletic origin, it is high time for students of most probably primarily anemophilous taxa to give these points serious consideration. A few recent examples: A tentative reconstruction of the ancestor of the palms by CORNER (1966, p.264, fig. 118), and one of an early pandanaceous inflorescence by STONE (1969. p. 501–3, figs. 2, 3, 4) are both based on the conventional dictum that all Angiosperms were, at one time or another, monoclinous. Corner attempted to make his reconstruction resemble a magnoliaceous prototype (conventionally *all* Flowering Plants *including the Monocots* somehow have to be derived from an arborescent ranalian form!), but it is still a far cry from a *Magnolia*. By the simple procedure of drawing a monoecious or dioecious unisexual version of Corner's reconstruction one obtains something that is rather similar to suggestions and to pictorial representations relating to the morphology of primitive Monocots as made by the present author (MEEUSE 1965, Chapter XII, figs. 9, 10, 13, 14; 1966, Chapters 10 and 18 with figures). The same applies to Stone's proposed *bisexual* prototype of a pandanaceous "flower": unisesexual versions of his drawings approach mine in several essential respects. And what a difference it makes!

It is noteworthy that Sporne found a positive correlation between several primitive characters and the presence of unisexual flowers, and used this for his calculations of the advancement index. If one applies this character (dicliny) only to presumably *ab initio* diclinous families the relative advancement index most probably will not turn out to be higher but possibly lower, and this confirms my contention that some primitive groups have always remained diclinous or, conversely, that the presence of unisexual flowers is by no means always indicative of a derived condition.

2.4. Genetic data

The only important contribution is a recent article by EHRENDORFER *c.s.* (1968), but in my opinion the interpretation of their findings is not conclusive either

way. The supposed origin of all primitive Angiosperms from progenitors with x = 7 (if this primary assumption is correct, which remains to be seen) does not shed any light on the problem under discussion: this basic number x = 7 may be the basic number in woody ranaleans, and perhaps in *Amentiferae*, but was this number carried through by a single evolutionary line or by several parallel lineages and to all primitive Monocots as well as to all early Dicots? The statement (op. cit., p. 350) that the ancestral group with x = 7 was pteridospermous is non-committal, to say the least, and does not suffice to refute a *subsequent* pleiophyletic descent (as postulated by the present author). One would also like to learn more about chromosome counts in other groups, such as *Dioscoreales* and *Pandanales* among the Monocots, and *Piperales, Berberidales-Ranunculales, Rosales, Theales, Cistales,* etc. among the Dicots. The authors take too much for granted: that Monocots are derived from Dicots of a magnoliaceous type, that *Annonaceae* and some *Piperales* are descendants of forms with x = 7 by ascending, and *Aristolochiales* and *Paeoniaceae* by descending disploidy, that such chromosome numbers as x = 19 arose from 7 + 6 + 6, etc. *Piperales* differ chemically rather strikingly from *Magnoliales, Ranunculales-Berberidales, Laurales* and *Aristolochiales* in that they do not produce alkaloids of the benzyl-isoquinoline type and this may signify a somethat distant relationship between piperalean and more typically ranalean forms.

Other characters apart from the chromosome numbers, such as the pollen morphology, suggest a great heterogeneity among the *Polycarpicae* and although they hang together mainly by their phytochemical characteristics, this diversity is conceivably indicative of ancient divergent lines. I think the paper by Ehrendorfer *c.s.* does not sufficiently substantiate their claim of a *long-lasting* monophylesis in Angiosperm evolution and does not *per se* refute the alternative hypothesis.

2.5. Host-parasite relationships

Of consequence to the issue under discussion are the summaries of EHRLICH & RAVEN (1965, 1967). They pointed out that earlier workers, such as Dethier, Merz, and Gordon, have suggested relations between physiological specialisations of the parasites and a "reaction mechanism" by the host plants, some of these authors even going so far as to attribute the rapid rise of the (early) Angiosperms to the development of successful repellent mechanisms (such as the synthesis of poisonous substances, *e.g.,* alkaloids), thus surviving by escaping from attack by herbivorous parasites. In any event, the interaction between the progressive adaptation of the cadging animals and the biosynthetic pathways developing in the host culminated in a "specialisation" of certain groups of insects nowadays exhibiting a manifest food plant preference. The ultimate result is a co-evolution of the food-providing plant group and the parasitic taxon, the parasites continually adapting themselves to noxious substances produced by the host and showing a divergent evolution more or less parallel with the diversification of the hostal taxon. The relations between *Pieridae* (the cabbage white family) and the mustard-oil producing *Capparidales,*

between the *Papilionidae* (swallowtail butterfly family) and *Polycarpicae*, and between the *Nymphalidae-Danainae* and the *Asclepiadaceae* and *Apocynaceae*, are striking examples of this form of co-evolution.

Conversely, the host-parasite relationships may serve as taxonomic (and phylogenetic) pointers, but this is partly a case of circular reasoning if one combines the data from comparative phytochemistry (such as the distribution of the isothiocyanate glycosides in *Capparidales* s.s.) with the ecological evidence, and this may lead to exaggeration: the observation that *Tropaeolaceae* contain mustard oil glycosides so that they attract *Pieridae* is by itself insufficient proof of a close taxonomic relationship between the nasturtium family and the *Capparidales* s.s. As pointed out by, *e.g.*, Ehrlich & Raven, phytophagous insects originally became tolerant of host-produced noxious phytoconstituents acting as poisons or deterrents, but eventually these injurious substances became "attractants" guiding gravid female specimens to the adequate, potential host plant. The mere occurrence of such "attractants" in *unrelated* plant taxa may lead to a "switch-over" to another group of host plants (populations of the common cabbage white "switched" from *Brassica* and other *Cruciferae* to *Tropaeolum majus*), but in taxonomy such a "secondary" host-parasite relation has little demonstrative force. Without good experimental evidence we can not decide if a substance is only tolerated or also acts as an attractant (as in the case of *Pieridae* and thioglycosides), and conceivably plants containing noxious but specifically tolerated constituents may produce other substances acting as attractants or may possess other, or additional, forms of defence (*e.g.*, mechanical: rough hairs, thick epidermis, the presence of excessive sclerenchyma or raphides, marginal leaf spines, etc.) that render them unpalatable as experimentally shown (see Ehrlich *c.s.*).

The problem is that we can not always distinguish between these various alternatives: although we know that the European *Pieris brassicae* "switched over" from *Cruciferae* to the introduced neotropical *Tropaeolaceae*, we may not infer from this that the South American pierids in the larval state normally feeding on *Tropaeolaceae* also "switched over" at a fairly late stage of their evolution. If *Capparidales* and *Tropaeolaceae* are related (which I think is rather likely), these butterflies were perhaps associated with *Tropaeolaceae* ever since these plants evolved from a common, and already pierid-infested, ancestor of both the nasturtiums and the capparid-cruciferid alliance.

Nevertheless, the host-parasite relationships can certainly act as pointers. As Ehrlich *c.s.* pointed out, the nymphalid genus *Atella* is associated with *Flacourtiaceae* and *Salicaceae*, and there is every reason to follow up this possible clue (the *Salicales* are not necessarily related to amentiflorous orders such as *Betulales*, *Fagales* and *Juglandales* !). The fact that the papilionid butterflies are clearly associated with both the ranalean and some related or probably allied groups (*Aristolochiaceae*, *Piperales*, *Nepenthaceae*), and also with *Rutaceae* and presumably related groups (*Sapindales*, *Malpighiaceae*), for instance, is not without significance. MUNROE & EHRLICH (1960) have argued that the most primitive true papilionids are the *Troidini*, which are typically associated with

the *Aristolochiaceae*. Speculations concerning the taxonomic position of the *Aristolochiaceae* must start from one of two assumptions, *viz.*,

a. both the *Aristolochiaceae* and the early papilionids evolved early and by in-
    ference the former taxon is an ancient one not necessarily "derived" from
    Magnoliales (= "woody ranaleans"); or

b. the early papilionids became adapted to *Aristolochiaceae* rather late and the
    Aristolochiaceae are possibly derived from traditionally more primitive *Po-
    lycarpicae*.

As regards (b), one may well ask from what group of original host plants the early troidinids and the related primitive parnassiids "switched" to *Aristo-lochiaceae* and why they did not co-evolve with the latter plant family right from the beginning. I realise that this would imply that the *Aristolochiaceae* are phylogenetically "old" in spite of having some reputedly "advanced" characters (their advancement index is 47 according to Sporne) and may be as "primitive" or even "older" than several members of the *Magnoliales*, which may sound like heresy to traditionalists, but HUBER (1969) comes to a comparable con-clusion concerning the position of the, likewise, morphologically rather singular *Dioscoreales* as the most primitive members of the liliacean alliance.

The relation between papilionid butterflies and *Rutaceae* (and related *Sa-pindales*, etc.) could be purely fortuitous by being the result of a phytochemical convergence (benzylisoquinoline bases occur in several *Rutaceae*). This is ques-tionable and I believe that rutalean-sapindalean taxa are indeed related to *Po-lycarpicae* (see under 4). The same conclusions concerning taxonomic relations can, *mutatis mutandis*, be drawn from examples of co-evolution found in the relations between host plants and parasitic fungi. However, one of the most detailed accounts (LEPPIK 1955) fails to indicate more than some generalities, such as a sequence leading from "ancient ferns" as primitive hosts to Conifers (*Abietaceae*) as secondary, to *Amentiferae* and *Salicales* as tertiary, and to some other angiospermous as quaternary hosts, which does not necessarily reflect co-evolution. As Leppik himself admits, the picture is incomplete and I believe that, at this scale at least, the evidence is inconclusive.

2.6. Fossil records

Pre-Cretaceous macro-fossils of angiospermous plants are almost entirely lack-ing (or perhaps remained unrecognised), but various types of fossil sporomorphs may represent the pollen grains of protangiospermous or early angiospermous plants. In a recent session paper read during the XIth Intern. Bot. Congress in Seattle, MULLER (1969) summarised the data. In older deposits the monosulcate grains prevail and in younger ones gradually other pollen types make their appearance. Muller concluded that apparently gymnospermous monosulcate grains served as prototypes for all other types of angiosperm pollen and that this is indicative of a monophyletic evolution of the Flowering Plants. This is open to doubt because various angiospermous groups have retained monosulcate pollen and this means that monosulcate fossil sporae dispersae are not neces-sarily all gymnospermous but may partly be early angiosperms.

The origin of the tricolpate type prevailing among the Dicots is still a mystery, but it is feasible that this type developed more than once from more primitive types. The difficulty is that various readily recognisable pollen types seem to appear all of a sudden. The presence of unmistakable palmaceous pollen can not be established with certainty before the Upper Cretaceous, and what, then, was its preceding phylogenetic history? Considering that several authorities, such as Corner, believe that palms are a very ancient group, and repeatedly reports have appeared of pre-Cretaceous fossil occurrences of palm-like plants (fossils said to be Triassic palm stems were shown during the XIth Botan. Congress), one may at least assume that angiosperms which were to all intents and purposes palms already existed before the characteristic palmaceous pollen morphology came into being in the Upper Cretaceous. I believe that the divergence of the angiospermous pollen types took place rather late and that parallelisms can not be ruled out, so that the fossil evidence is inconclusive.

3. PRELIMINARY CONCLUSIONS

Several, and partly independent, sources of information are either indicative of a multiple descent of the Angiosperms, or do not stand in the way of such a hypothesis. The available data strongly suggest that several groups, particularly the *Aristolochiaceae* and the *Dioscoreaceae*, are much more primitive than was hitherto generally assumed. The important question is whether the evidence is sufficient to recognise the rough framework of a system of classification which is more consistent with the new findings than the conventional ones. The present author is of the opinion that the answer is in the affirmative.

(To be continued