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STEPS TOWARD A NATURAL SYSTEM OF THE DICOTYLEDONS: EMBRYOLOGICAL CHARACTERS¹

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ABSTRACT

Embryological character states are mapped on the diagrams of dicotyledons (G. Dahlgren 1989). The often well-defined pattern of distribution forms a basis for discussing and clarifying phylogenetic relations. It is shown how numerous embryological characters, alone or in combinations, support certain systematic constellations, even if the character states may have arisen independently within a varying number of evolutionary lines. Characters presented are: anther wall formation; tapetum types; cells in pollen grains at dispersal; microsporogenesis; ovule morphology; ovule integuments; endothelium; obturator; parietal tissue; embryo sac formation; antipodal cells; hypostase, embryogeny; polyembryony; endosperm formation; persistence of endosperm; ruminant endosperm; endosperm haustoria; perisperm; storage compounds in the endosperm; chlorophyllous embryo; embryo size, seed coat characters; arils; dry and wet stigma types.

Key words: dicotyledons, embryology, phylogenetics, systematics, evolution.

INTRODUCTION

My husband, Rolf Dahlgren, and I began a survey of the embryological literature, with the purpose of using patterns of distribution of embryological character states for clarifying relationships in the dicotyledons at and above family level. My husband, however, tragically lost his life in a traffic accident, and I have continued with the investigation on my own.

My intention has been to show how a great variety of embryological characters can be used to confirm certain systematic constellations and to reject others. The treatment in such a survey must be generalized and concentrated on gross taxonomic features.

The diagram used for the distribution of character states was presented in G. Dahlgren (1989), being a modified version of the dicotyledons in the diagram in Dahlgren (1980a). This new classification, showing orders and families, has been included here (Fig. 1), so that the interpretation of the distribution of patterns in the diagrams, and the discussions, can be more readily followed.

Embryological data have accumulated steadily throughout the years. Some major contributions and compilatory works that have guided taxonomists are Schnarf (1931), Martin (1946), Wunderlich (1959), Davis (1966), Philipson (1974), Alimova et al. (1981), Poddubnaja-Arnoldi (1982), Batygina et al. (1982, 1985), and Johri (1984). Corner's account of seed coat characters (Corner 1976) also provides new evidence to support phylogenetic conclusions. Examples of articles that stress the importance of embryological information for taxonomy are Cave (1962), Maheshwari (1963), Johri (1963), Kapil and Bhatnagar (1980), and Cocucci (1983), although these tend to give illustrative examples rather than elucidate

what embryological data can offer for the clarification of phylogenetic relationships in angiosperms. Even textbooks, such as Maheshwari (1950), rarely give a satisfactory view of the distribution of embryological characteristics or correlations among them, nor do they deal with correlations between embryological and non-embryological characters.

A wealth of embryological literature is available but few comparative studies comprising all of the dicotyledons have been made. Although Warming, for example, as early as 1878, pointed out the correlation between sympetaly and unitegmic ovules, the importance of this information is rarely mentioned in taxonomic textbooks. Wunderlich (1959) presented an extensive survey of integument number, occurrence of parietal tissue, and types of endosperm formation, and to some extent evaluated these characters taxonomically. However, her article has generally been disregarded by English-speaking taxonomists. Quite recently the same subject was treated by Philipson (1974), who stressed the phylogenetic implications of overlapping and nonoverlapping distributions of unitegmic and tenuinucellate ovules. Jensen et al. (1975) correlated iridoids and embryology. Palser (1975) presented a survey of embryological characters that may be useful for taxonomic purpose and also discussed embryological character states at different levels. Further, in their comparative studies of the monocotyledons, Dahlgren and Clifford (1982) used various embryological characters, such as endothelial thickenings, tapetum type, number of cells in mature pollen grains, ovule morphology, type of endosperm formation, storage substance in endosperm, type of embryogeny, shape and relative size of embryo, and seed coat characters, finding that these characters contribute very useful information for estimating phylogenetic relationships.

To an even greater degree this must also apply to the dicotyledons, where the taxa are far more numerous and the phylogeny far more complicated; moreover, convergence and parallelism, which are frequently encountered in the monocotyledons, can be expected to be so also in the dicotyledons.

A number of embryological character states have well-defined distributions in the dicotyledons. Tobe (1989) listed 48 embryological characters that may all be investigated and used in systematic and evolutionary studies. They may have arisen independently, within a varying number of evolutionary lines, but in combination with other characters states, they can be helpful in characterizing clades. Combinations of two or more embryological characters or embryological and nonembryological character states will be pointed out as being of importance in circumscribing higher taxa.

Character states that have appeared once in the ancestor of a clade may, however, have been lost in some of the derivative taxa. This must be considered a possibility in cases such as when a character state has become functionally superfluous in the course of evolution, e.g., an aril will easily become rudimentary if the fruit becomes indehiscent.

Embryological characters have been regarded as "conservative" in the sense that they have evolved more slowly than have most macromorphological char-

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Fig. 1. Classification of dicotyledons, showing orders and families.

acters. This may well be so. Thus, although ovules vary greatly in number, size and morphology with the reproductive strategy of the plant, they often retain similarities in certain fundamental embryological characteristics such as development of parietal tissue, type of endosperm formation and development of endosperm haustoria. An example of this is seen in *Veronica* and *Orobanche*, both of Scrophulariaceae s. lat., which in spite of considerable differences retain the fundamental embryological characteristics of most Lamianae. It can be added, however, that if one looks at endosperm formation in *Veronica* in terms of cell division patterns there is a variability within the genus and also variability among other closely related genera of Veroniceae (Yamazaki 1957).

EMBRYOLOGICAL CHARACTERS

Anther Wall Formation (Fig. 2)

Details of anther wall formation and definitions of the types of walls are presented by Davis (1966). She reports the type for about 80 dicotyledonous families.

In the *Basic type* both daughter cells of a cell division in the primary parietal layer divide periclinally, resulting in four cells which differentiate into endothecium, two middle layers and tapetum. The *Dicotyledonous type* and the *Monocotyledonous type* are both derived from the Basic type by suppression of the periclinal divisions in the inner and the outer secondary parietal layers, respectively. Thus, in the Dicotyledonous type only cells of the outer secondary parietal layer divide, giving rise to the endothecium and the single middle layer, while the cells of the inner layer develop directly into tapetum. In the Monocotyledonous type periclinal divisions are suppressed in the outer secondary parietal layer which develops directly into endothecium, while the inner layer forms the middle layer and the tapetum. The *Reduced type* is characterized by the suppression of all periclinal divisions in the secondary parietal layer. No middle layers develop, the endothecium and the tapetum forming the only two subepidermal layers.

The most complete type of anther wall, the Basic type (B in the diagram), is generally regarded as ancestral in the dicotyledons, though this is not very clearly reflected in its distribution (Fig. 2). The Basic type is recorded for Winteraceae but is less common than the Dicotyledonous type in Magnolianaes. The Basic type is also known from two taxa in Caryophyllanaes (where likewise other types are commoner), in Theanaes (Hypericaceae, Lecythidaceae), and in scattered taxa of Malvales, Rhamnales, Vitales, and Sapindales.

Far commoner, and scattered in the dicotyledons, is the Dicotyledonous type (D). This is virtually the only type recorded in the Cornanaes, Gentiananaes, Ericanaes (one exception), Lamianaes, Solananaes, Araliaeanaes, and Asteranaes, i.e., in all the sympetalous groups with unitegmatic ovules. Furthermore, the Dicotyledonous type is the only type recorded in Ranunculales, Myrtales, Ebenales, Fabales, and Magnolianaes (except for Winteraceae).

The Monocotyledonous type (M), which is the type found in nearly all monocotyledons, is particularly common in Caryophyllanaes (found in five families out of

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Fig. 2. Types of anther wall formation. Dicotyledonous: D; Monocotyledonous: M; Basic: B; Reduced: R.

eight investigated) and is the only type noted for Polygonales (Polygonanae). Other orders where the Monocotyledonous type is the only one reported by Davis (1966) are Piperales, Papaverales, Urticales, Capparales, Salicales, Droserales, and Haloragales. It is also known from Geraniales and Santalales, in combination with the Dicotyledonous type.

The Reduced type (R) has been reported for only one species of Ericaceae (Ericales, Ericanae).

The value of this information to phylogeny is of course still very limited. It remains to be shown whether these records are consistent in, or even representative of the families for which they are here reported.

However, the available data show both some homogeneous regions in the dicotyledonous diagram, such as the main sympetalous superorders, with the Dicotyledonous type, and some unexpected differences, such as those between Ranunculales and Papaverales, between Haloragales and Myrtales, and between Winteraceae and the other Magnolianae. The most conspicuous feature is perhaps the common occurrence of the Monocotyledonous type in certain orders, e.g., Caryophyllales and Polygonales.

Tapetum Types (Fig. 3)

Distinction will here be made only between the *Glandular* and *Amoeboid* types of tapetum. In the former the tapetal cells remain *in situ* and are secretory, whereas in the latter type the tapetal walls dissolve and the cell contents ultimately invade the anther cavity as a periplasmodium.

Some authors make a distinction between Amoeboid and Periplasmodial tapetum and Carniel (1963) distinguishes a genuine Periplasmodial tapetum from a false, the latter being the final stage in the degeneration of a secretorial tapetum. In actual fact there is often a transition between different types. For example in some Asteraceae the tapetum is described as cell-amoeboid, in others as periplasmodial. Thus, tapetum types present terminological problems, and even if the use of more detailed distinction could be of further taxonomic importance, it seems too difficult to carry out.

The data presented, preferably taken from Davis (1966), show some interesting features, in particular as regards the Amoeboid type, although this is rather rare in dicotyledons and yields considerably less information than in the monocotyledons.

Exclusively or predominantly Amoeboid tapetum is found in Dipsacales (Dipsacaceae, Valerianaceae, and Caprifoliaceae). In *Sambucus* and *Viburnum*, which are frequently included in Caprifoliaceae but are here treated as separate families (in Cornales), the tapetum is of the Glandular type. Wagenitz and Laing (1984) found a particular type of nectary, situated in the corolla tube, restricted to exactly Dipsacaceae, Valerianaceae, and Caprifoliaceae but found in neither Sambucaceae nor Viburnaceae, a coincidence of phylogenetic importance. This supports the theory that Dipsacales in this circumscription represent a clade with at least two

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Fig. 3. Amoeboid tapetum. Dominant or of common occurrence: hatched; Isolated occurrence: dots.

autapomorphies: Amoeboid tapetum and nectary type. Adoxaceae, in which the nectaries are slightly different (multicellular instead of unicellular), nevertheless has Amoeboid tapetum and it is a matter of conjecture as to whether they belong to the same clade. However, in most other characters they are close to Sambucaceae with which they also share the rare tetrasporic embryo sac. Wagenitz (1987) emphasizes this relationship and both these families are retained in Cornales.

Other families with mainly or exclusively Amoeboid tapetum are Lauraceae (*Cassytha* excluded) in Laurales, Ceratophyllaceae in Nymphaeales (the Nymphaeaceae have Glandular tapetum), Malvaceae in Malvales (Sterculiaceae, Tiliaceae and Bombacaceae have Glandular tapetum), Lecythidaceae in Lecythidales (Theales have Glandular tapetum), Polemoniaceae and Cobaeaceae in Solanales (most Solanaceae and all Convolvulaceae have Glandular tapetum), Bignoniaceae in Lamiales (Gesneriaceae have Glandular tapetum), and Asteraceae in Asterales (Campanulales in Asteranae have Glandular tapetum).

Both amoeboid and glandular tapetum are found in isolated species of Dilleniaceae, Droseraceae, Euphorbiaceae, Gentianaceae, Loganiaceae, Ranunculaceae, Solanaceae, and Winteraceae.

The information on types of tapetum is still far from complete. Further information may reveal whether or not tapetum type can be used to clarify circumscriptions of families where there are intermediate or uncertain groups, such as for Malvaceae versus Bombacaceae.

Cells in Pollen Grains at Dispersal (Fig. 4)

The distribution of 2- and 3-celled pollen grains at the time when the pollen is shed has been investigated in particular by Brewbaker (1967). The data used here have mainly been taken from him, but also from Davis (1966) and others. Taxonomic implications of this character have been briefly commented on by Dahlgren (1975).

Two-celled pollen grains, which are considered to represent the plesiomorphic state, are always present in Magnolianae, Nymphaeanae, Ranunculanae, Rosanae (Droserales excluded), Proteanae, Vitanae, and Santalanae.

Three-celled pollen grains are found in all investigated taxa of Caryophyllanae, Polygonanae, Plumbaginanae, Araliales, and Pittosporales in Aralianae, Asterales in Asteranae, and probably all Dipsacales in Cornanae.

In all these groups both states are of phylogenetic significance. Thus, the consistently 3-celled pollen grains in Dipsacales are of interest in combination with the character states mentioned under Tapetum, although it is to be noted that 3-celled pollen grains also occur in Viburnaceae and Sambucaceae in Cornales.

The presence of 3-celled pollen grains in Araliales, Pittosporales, and Asterales, in combination with a number of other shared character states, chemical (e.g., polyacetylenes, triterpenes) as well as morphological, might indicate that these orders belong to the same clade. However, this proves to be doubtful, since the pollen grains in the Asteranean Campanulaceae are 2-celled and those in Lobe-

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Fig. 4. Pollen grain dispersal in 2-celled (unshaded) v. 3-celled (dotted) state; mixed: hatched.

liaceae either 2-celled or 3-celled. It is more probable that Asteraceae evolved within the Campanulalean clade with 3-celled pollen grains (Bremer 1987).

The shared occurrence of 3-celled pollen grains in Caryophyllanae, Polygonanae, and Plumbaginanae would be the result of convergence within two or three independent evolutionary lines, but some authors consider that these groups are a single clade; they make up one subclass in the classification of Cronquist (1981).

Many families are heterogeneous for this character, some of the genera studied having 2-celled pollen grains, others 3-celled. Thus, each of the major families of Gentianales (Loganiaceae, Gentianaceae, Apocynaceae, Asclepiadaceae, and Rubiaceae) and several families of Lamiales have both 2-celled and 3-celled pollen grains.

Two-celled pollen grains are the commonest in the Families of Rutales, but 3-celled grains are reported in some genera. A similar heterogeneity is encountered in the orders Lecythidales and Vitales and in the families Euphorbiaceae (Euphorbiales), Celastraceae, and Staphyleaceae (Celastrales), Mimosaceae (Fabales), and others (Fig. 4).

In Solanales the pollen grains are always 2-celled in Solanaceae; they are mainly 2-celled, though sometimes 3-celled, in Convolvulaceae; in Cuscutaceae they are always 3-celled. In Boraginales the pollen grains are 2-celled in Hydrophyllaceae and in Ehretiaceae and in *Heliotropium* in Boraginaceae, but 3-celled in other Boraginaceae (16 species studied by Brewbaker).

Whereas there are 2-celled pollen grains in Saxifragales, the pollen grains of Icacinaceae and Escalloniaceae, both of which were previously included in Saxifragaceae, are 3-celled (these families have now been placed in Cornales).

In other families, for example in Geraniales and Linales, 3-celled pollen grains dominate but 2-celled grains occur in one or several families. Further, Brassicaceae have 3-celled pollen grains, while other families in Capparales have 2-celled. Melastomataceae differ from other Myrtales in the same way.

It is seen that groups considered as "primitive" are consistently 2-celled when the pollen grains are released, while others such as Asterales and Caryophyllales are consistently 3-celled, the character thus being of taxonomic significance here. In other orders the variation is great, both types sometimes occurring even in the same genus, e.g., *Euphorbia*, *Drosera*, *Lamium*, and *Plantago* (Brewbaker 1967), the character here being of little or no taxonomic value. The transition from the 2-celled to the 3-celled state must have occurred many times and in many groups scattered over the system.

Microsporogenesis (Fig. 5)

Microsporogenesis, the process by which the microspore mother cells develop into microspore tetrads by two meiotic divisions, can be either successive or simultaneous (Maheswari 1950). In the *successive type* centrifugal cell plates are laid down at the end of meiosis I and II resulting in the formation of four microspores in one plane. In the *simultaneous type* centripetal constriction furrows divide each mother cell into four microspores after meiosis II. The microspores

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Fig. 5. Microsporogenesis. Successive type: dotted.

usually form a tetrahedral configuration. However, centrifugal cell plate formation has also been recorded in the simultaneous type at the end of meiosis II, e.g., in *Helleborus* (Waterkeyn 1962). Sampson (1969) described these three categories, and Longly and Waterkeyn (1979) further investigated the number and the structure of the cell plates, although absolute differences in the way the divisions occur remain unclear. Which of the two basic types is primitive has been a matter of conjecture. I shall return to the phylogenetic aspects after presenting the distribution among the dicotyledons.

The simultaneous type dominates in the dicotyledons, where it occurs in more than 95% of the families investigated. The successive type is known in the following families: Lauraceae (Laurales), Aristolochiaceae (Aristolochiales), Annonaceae and Myristicaceae (Annonales), and Rafflesiaceae (Rafflesiales). At least in the first three families the simultaneous type also occurs. It occurs in Ceratophyllaceae and Cabombaceae, but not Nymphaeaceae (Nymphaeales); in Podostemaceae (Saxifragales, Rosanae) and in Asclepiadaceae and Apocynaceae (Gentianales, Gentiananae), together with the simultaneous type. The distribution of the successive type could suggest a relationship Aristolochiaceae–Rafflesiaceae and Annonaceae–Myristicaceae.

Can the successive type be considered the original one from its concentration in families of Magnolianae and Nymphaeaceae, i.e., groups near the monocotyledons? This is doubtful, because it occurs in families such as Lauraceae, Annonaceae, and Myristicaceae rather than in otherwise more primitive families of these orders. That both successive and simultaneous patterns occur among taxa in these superorders perhaps signifies a certain developmental and evolutionary lability in this grade.

It is to be noted that the successive type has also been reported in some groups placed on the opposite side of the system, viz., Podostemaceae (Saxifragales) and some genera of Apocynaceae and Asclepiadaceae (Gentianales), families which are considered advanced as regards most other features.

Contrary to the dicotyledons the successive type is the commoner in monocotyledons, the simultaneous type occurring in only a few families such as Orchidaceae, Taccaceae, Iridaceae, Dioscoreaceae, and many Arecaceae. If Dioscoreaceae is one of the basal clades of the monocotyledons it is possible that the simultaneous type is primitive for the monocotyledons. This could be further supported, if Nymphaeaceae is the sister group of the monocotyledons.

The simultaneous type in which cell plate formation still occurs, e.g., *Helleborus* in Ranunculaceae, Ranunculanae (Waterkeyn op. cit.) and *Illicium* in Illiciaceae, Magnolianae (Hayashi 1960) probably represents an intermediate stage between the common simultaneous type with constriction furrows and the successive type.

Ovule Morphology (Fig. 6)

Only a few comments on ovule types and their distribution will be presented here. *Anatropous* ovules are distributed throughout the angiosperms and are usually regarded as representing the plesiomorphic state.

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Fig. 6. Occurrence of orthotropous ovules in the dicotyledons: dotted.

Transitions between anatropous and *campylotropous ovules* occur within a number of independent lines, and campylotropous ovules dominate in some orders such as Caryophyllales, or in families such as Brassicaceae in Capparales.

Orthotropous ovules are rare in the dicotyledons. A probable case of synapomorphy with regard to orthotropous ovules at ordinal level is Juglandales-Myricales. There is a considerable amount of evidence that these together represent one clade. Orthotropous ovules also occur in Hydnoraceae and Rafflesiaceae p.p. in Rafflesiales (Magnolianaes). In this case as well it is probable that the orthotropous ovules represent a synapomorphy.

Otherwise the occurrence of orthotropous ovules in the dicotyledons is scattered (Fig. 6). Sometimes their derivation from anatropous ovules seems to be obvious, e.g., in Saururaceae and Piperaceae in Piperales, in Rafflesiaceae (Rafflesiales), and in Urticaceae (Urticales). Against this stands, however, the suggestion that Saururaceae and Piperaceae are basal angiosperms according to rRNA phylogenies. The orthotropous ovules in Polygonales apparently represent an autapomorphy.

The orthotropous ovules in Chloranthaceae (Chloranthales) and Saururaceae-Piperaceae (Piperales), which are similar in habit, could possibly also be considered as a synapomorphy, though this is highly dubious, since there are great differences between these orders with regard to the general structure of the seeds. The storage tissue in the seeds of Piperales consists mainly of perisperm (i.e., with little endosperm), but in Chloranthales it consists entirely of endosperm (no perisperm). Endress (1987) studied reproductive structures of Chloranthaceae and discussed their phylogenetic position. In addition to deviations in seed characters he also presented deviations from the Piperales as regards floral features. He suggests that Chloranthaceae fit best within Laurales though a possible evolutionary pathway to the families of Piperales can be seen in ovule characters, Chloranthaceae thus being a link between the two orders.

Bitegmic, Unitegmic and Ategmic Ovules (Fig. 7)

Bitegmic ovules, which undoubtedly represent the plesiomorphic state in the dicotyledons, are present in most superorders, with some notable exceptions. Unitegmic ovules are derived, and a transition to this condition has clearly occurred within quite a number of evolutionary lines. It has also been demonstrated that the unitegmic condition was derived by different, nonhomologous pathways (Bouman and Calis 1977).

The situation in the dicotyledons is unlike that in the monocotyledons, where unitegmic ovules are rare and of scattered occurrence and never present in an entire family. Figure 7 shows some interesting features in the distribution of unitegmic and ategmic ovules in the dicotyledons. In a large section of superorders on the right-hand side of the diagram the ovules are almost exclusively unitegmic, viz., the superorders Araliales, Asterales, Solanales, Ericales, Lamiales, Loasales, Cornales, and Gentianales. Of these only the Fouquieriaceae, here referred to Ericales, have bitegmic ovules. It may be noted that Fouquieriaceae is a family

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Fig. 7. Bitegmic (unshaded), unitegmic (dotted) and ategmic (hatched) ovules.

whose position is highly controversial! Perhaps they more likely have their origin in basal Rosanae where bitegmic ovules are present.

This major complex coincides largely, but not entirely with the Sympetalae (Asteridae), Araliae, and Cornanae added to the classical Sympetalae (Dahlgren et al. 1981). The occurrence of unitegmic ovules in these groups had already been pointed out by Warming (1878). Most of them are also characterized by other apomorphic character states, e.g., sympetaly, tenuinucellate ovules (without a parietal cell), and cellular endosperm formation, which supports the view that these superorders together could be interpreted as representing a single major clade (i.e., a monophyletic complex). This combination of character states has been particularly stressed by Wunderlich (1959), Philipson (1974), Dahlgren (1975), and Bouman and Schrier (1979). The picture is more complicated, however, and the coincidence of the character states mentioned is by no means complete. On the basis of the different chemical constituents, differences in details of endosperm formation, etc., the monophyly of the complex can be challenged.

In addition, the occurrence of unitegmic ovules outside these superorders is of particular interest. The Sapotaceae in Ebenales (Primulanae) have unitegmic ovules combined with sympetaly and tenuinucellate ovules, but have nuclear endosperm formation. If this family is correctly placed within Ebenales the unitegmic ovules would have evolved as an autapomorphy. The relationships of Sapotaceae, however, need to be further investigated.

A few other orders and families outside the main Sympetalae complex also have unitegmic ovules throughout, e.g., Myricales, Juglandales, and various taxa of Fagales, viz., Nothofagaceae, Betulaceae, and some Corylaceae. Fagaceae, however, are bitegmic, which is interesting since they differ also in pollen morphology. The unitegmic ovules of the similar Myricales and Juglandales probably represent a synapomorphy, whereas in Fagales the unitegmic ovules have probably evolved more than once.

A transition from the bitegmic to the unitegmic ovules has taken place—in various ways—in a number of families: Ranunculaceae (Bouman and Calis 1977) and Menispermaceae in Ranunculales; Rafflesiaceae in Rafflesiales; Piperaceae in Piperales; Salicaceae in Salicales; Rosaceae and Anisophylleaceae in Rosales; Corylaceae in Fagales; Saxifragaceae in Saxifragales; Tropaeolaceae in Tropaeolales; Balsaminaceae in Balsaminales; Anacardiaceae in Sapindales; and Burseraceae and Meliaceae in Rutales. In each of these families the integument conditions could be of potential interest for evolution at generic or tribal level. Bouman and Schrier (1979) discussed the process of unitegmisation by unitegumentary shifting and they showed that the single integument in the Gentianaceae probably has derived by integumentary shifting.

A transition from bitegmic to ategmic ovules, via unitegmic ovules, can be studied in Olacaceae in Santalales. All other members of Santalales, as circumscribed here, have ategmic ovules. Since the most primitive members of Olacaceae have bitegmic ovules, the unitegmic ovules in some olacaceous genera and the unitegmic ovules of Araliales cannot be referred to as a phylogenetically important similarity, although a close relationship between these orders is supported by chemical evidence (polyacetylenes, sesquiterpene lactones [Dahlgren et al. 1981]).

Ategmic ovules are also typical of Balanophoraceae (Balanophorales), but it is uncertain whether this family is closely related to Santalales. In particular, if

Cynomorium, which has unitegmic ovules, belongs to the same clade as Balanophoraceae the transition from unitegmic to ategmic ovules has occurred *within* Balanophorales, as it has, independently, in Santalales, and consequently one cannot use the shared occurrence of ategmic ovules in the two orders as an indication of close relationship.

More will be mentioned later on the significance of unitegmic ovules in combination with lack of parietal tissue, types of endosperm formation, chemical properties, etc.

Endothelium (Integumentary Tapetum) (Fig. 8)

Endothelium or *integumentary tapetum* is the specially differentiated innermost layer of the seed coat. It is possibly induced by influence from the embryo sac on the inner epidermis (of the single integument in unitegmic ovules and of the innermost integument of the bitegmic ovules). The cells are often polyploid. Endothelium occurs preferably in the dicotyledons (Swamy and Krishnamurthy 1970; Kapil and Tiwari 1978). Presence of endothelium is normally restricted to tenuinucellate and generally unitegmic ovules (tenuinucellate ovules, see the ovules lacking parietal tissue, Fig. 10).

The occurrence of endothelium is not completely known but there are sufficiently many cases of interest in the distribution to allow the following remarks. In the unitegmic Asteranae, Araliae, Solananae, and Ericanae the presence of endothelium and absence of a parietal cell (and tissue) agree fairly well. In Lamianae, however, at least Hippuridales and Hydrostachyales, most Acanthaceae and various Verbenaceae lack endothelium, and in Gentiananae endothelium is absent from most members except Loganiaceae p.p. and Apocynaceae p.p. It is also of note that Ehretiaceae and Boraginaceae–Heliotropoideae in Boraginales (Solananae) have no endothelium.

Endothelium is also combined with bitegmic and tenuinucellate ovules. The combination of these character states is found in Lecythidaceae (Lecythidales), in Marcgraviaceae and Scytotopetalaceae (Theales), in Ebenaceae (Ebenales), and in most Primulales, further in Fouquieriales, and in *Vahlia* in Saxifragaceae, Saxifragales, and some species of *Drosera* of Droseraceae, Droserales. The Balsaminaceae, often placed in Geraniales (but here treated in a separate order, Balsaminales) have a well-developed endothelium in combination with tenuinucellate ovules without a parietal cell.

Some families with bitegmic and weakly to distinctly crassinucellate ovules have an endothelium. This combination is found in Geraniales, viz., at least Balanitaceae, Zygophyllaceae, and of Linales, the families Oxalidaceae, Linaceae (Boesewinkel 1980), and Erythroxylaceae, as well as in members of Celastraceae (Celastrales), and Rhizophorales. This group of families in Geraniales, Linales, and Celastrales also has a number of other character states in common (chlorophyllous embryo, fibrous exotegmen, nuclear endosperm formation, etc.) and are believed to be phylogenetically related (Dahlgren 1988). Endothelium is also present in some members of Fabaceae (Fabales) that have bitegmic and crassinucellate ovules.

Most of these data are taken from Kapil and Tiwari (1978), who do not give

any details of the distribution of endothelium. It is therefore difficult to arrive at any definite conclusions apart from the suggestions given above.

Obturator

The *obturator* is a structure that facilitates the entry of the pollen tube into the ovule (Maheswari 1950). Morphologically it usually originates in the placenta or the funiculus and grows towards the micropyle. The cells forming the obturator can also come from the base of the style, the style canal or even the inner integument, but the function is always the same independent of origin.

An obturator has been recorded from a series of dicotyledon families: Magnoliaceae in Magnoliales; Molluginaceae in Caryophyllales, Ulmaceae in Urticales; Brassicaceae in Capparales (Violanae) (Hill and Lord 1987); Thymelaeaceae in Thymelaeales (both Malvaneae); Anacardiaceae in Sapindales; Linaceae in Linales (Rutanae); Araliaceae in Araliales; Garryaceae in Cornales; Combretaceae in Myrtales; Rubiaceae in Gentianales; and Acanthaceae and Lamiaceae in Lamiales. The list of families is not long and could probably be supplemented, although the distribution pattern of these families in itself shows that an obturator occurs in many scattered orders of dicotyledons. Thus the obturator is not a character state of gross taxonomic importance, as far as can at present be seen.

Parietal Tissue (Fig. 9)

The division of the archesporial cell into a primary parietal cell and a megaspore mother cell is a well-defined character state. The primary parietal cell generally divides further to form a *parietal tissue* consisting of a few to numerous cells located above the embryo sac.

The presence of parietal tissue is not equivalent to a *crassinucellate* condition as such, since the term crassinucellate implies that nucellar tissue surrounds the megaspore tetrad or the embryo sac. However, parietal tissue prevents an ovule from becoming strictly *tenuinucellate* in the sense that the embryo sac is in direct contact with the nucellar epidermis.

The use of the terms crassinucellate and tenuinucellate in the literature is often confusing as has been discussed for instance by Hamann (1966). Emphasis has here therefore been laid on presence or absence of parietal tissue, formation of a nucellus cap, and the total number of layers in the whole nucellus. In some groups a parietal cell is not formed, but epidermal cells of the nucellus divide periclinally to form a "nucellar cap," as in many Ranunculales, for instance.

As a rule no parietal cell is formed in any of the superorders that always have a single integument, viz., Aralianae (Tremandraceae bitegmic), Asteranae, Solananae, Ericanae, Lamianae, Loasanae, Cornanae, and Gentiananae. There are some exceptions within these superorders, however. Thus, a parietal cell is developed in Araliaceae (Aralianae); the Cornanae include some families with a parietal cell: Eucommiaceae in Eucommiales; and Icacinaceae, Alangiaceae, Aucubaceae, and Garryaceae in Cornales. Also most Convolvulaceae (but not Cuscutaceae) in So-

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Fig. 8. Endothelium (integumentary tapetum); in unitegmic ovules: dotted; in bitegmic ovules: hatched.

lanales and most Ehretiaceae (but not Boraginaceae) in Boraginales have parietal tissue.

In Santalanae and Balanophoranae, superorders in which an integument is generally lacking (exceptions being some Olacaceae and Cynomoriaceae) there is no parietal cell.

Apart from these major, unitegmic and ategmic, complexes where parietal tissue is on the whole lacking, there are various other bitegmic groups, where a parietal cell fails to be formed, and which have tenuinucellate ovules. These include most Theales and all Lecythidales (Theanae) and all Primulanae. It may be noted here that the Chrysobalanaceae have bitegmic and tenuinucellate ovules, this character supporting their place in Theales (Tobe and Raven 1984; Dahlgren and Thorne 1984) rather than in Rosales where they are placed by tradition. But more data are considered. Theales are probably a polyphyletic order; there is also some variation in the presence or absence of parietal tissue, which is found in at least Nepenthaceae and Stachyuraceae.

In Saxifragales all Podostemaceae and at least *Vahlia* of Saxifragaceae lack a parietal cell; this is also the case in *Parnassia* (Parnassiaceae) and some Droseraceae in the order Droserales.

Other groups with bitegmic ovules lacking parietal tissue are many (? or all) Meliaceae (Rutales), the Balsaminaceae (Balsaminales), Tropaeolaceae and Limnanthaceae (Tropaeolales), many Oxalidaceae and Linaceae (Linales), Frankeniaceae and Tamaricaceae p. p. (Tamaricales), Dialypetalaceae (Euphorbiales), most Brassicaceae (Capparales), Calycanthaceae (Laurales), and, in connection with reduction of ovule size, the Rafflesiales. The ovules are not strictly tenuinucellate in all these cases.

A combination of absence of parietal tissue and unitegmic ovules is clearly of phylogenetic significance in the major, chiefly sympetalous superorders mentioned above. The absence of a parietal cell is also characteristic of most Theanae and all Primulanae, for example, and this character should be considered of potential importance in other treatments.

The formation of a parietal cell (or tissue) is normally assumed to be the plesiomorphic state in angiosperms—when a parietal cell is lacking, this is accordingly regarded as being derived. Failure to form a parietal cell has obviously occurred within quite a number of evolutionary lines, as can be seen from the variation in several families and orders. Whether the loss of the parietal cell is an irreversible step in evolution can be argued, and this could be of interest in orders where the parietal tissue is present only in some taxa (Cornales, Solanales, Theales, Droserales).

Embryo Sac Formation

The dominant type of embryo sac formation is the *Polygonum* type, found in more than 80% of the dicotyledonous families. The *Allium* type characterizes the families Theaceae (Theanae), Malpighiaceae (Rutanae), Datisceae (Violanae), and Monimiaceae (Magnolianae), in other words families belonging to different

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Fig. 9. Orders where a parietal cell (parietal tissue) is not formed: dotted.

superorders. Other characteristic types in families are the *Adoxa* type, the *Oenothera* type, the *Penaea* type, and the *Drusa* type. The *Oenothera* type occurs only in the family Onagraceae. The Trapaceae, previously included as a genus in Onagraceae are characterized by the Polygonum type, this character thus supporting to distinguish *Trapa* as a separate family.

The above-mentioned as well as other embryo sac types usually occur together with others in many families, the commonest combination being the Polygonum type and the Allium type (10% of the investigated families). Sometimes three types occur together, and as many as six types of embryo sac formation have been reported in the families Asteraceae, Plumbaginaceae, and Euphorbiaceae.

This short summary is based mainly on Davis (1966). In spite of numerous cases of convergence, the distribution of embryo sac types could be of a certain phylogenetic interest in taxonomy, an example being, e.g., the *Adoxa* type. Besides in the family Adoxaceae (Cornales, Corniflorae) it is hitherto reported from one or few genera/species in Hydnoraceae (Rafflesiales, Magnolianae), Euphorbiaceae (Euphorbiales, Malvaneae), Ulmaceae (Urticales, Malvaneae), Aizoaceae (Caryophyllales, Caryophyllaneae), Plumbaginaceae (Plumbaginales, Plumbaginaneae), *Sambucus* (Caprifoliaceae, Dipsacales, Cornaneae), Solanaceae (Solanales, Solananeae), and Asteraceae (Asterales, Asteraneae) (Palser 1975).

However, many records, both old and new, apparently need to be further investigated according to some embryological reports, for example, by Maheswari. Thus, I see no reason to illustrate different combinations in a diagram at this stage.

Antipodal Cells (Fig. 10)

The antipodal cells of the embryo sac are usually short-lived. There are genera where the three antipodal nuclei of the embryo sac are not even enclosed in cells before they degenerate, e.g., in Sapotaceae and in genera of Lauraceae, Linaceae, Hydrophyllaceae, Illecebraceae, Myrtaceae, and some others. But on the other hand, in many taxa they increase in size or number. The occurrence of large antipodals and of multiple antipodal cells has been mapped here. As seen in Figure 10 large antipodal cells are concentrated in groups on the left-hand side of the system. They are common in Ranunculales as well as Papaverales in Ranunculanae, in Rhamnales in Malvaneae, and various Violanae. In sympetalous groups large antipodal cells are recorded from some Cornales and a few Lamiales but are otherwise rare.

Multiple antipodal cells are scattered throughout the system, although they are commonest in Malvaneae, especially in the orders Urticales-Thymelaeales. They do not seem to be of significance for taxonomic conclusions and will not be enlarged upon here.

Fig. 10. Antipodal cells. Large antipodal cells: hatched; Multiple antipodal cells: dotted.

Fig. 11. Presence of hypostase: dotted.

Fig. 12. Embryogeny: Solanad (S), Caryophyllad (C), Asterad (A), Onagrad (O), Piperad (P) and Chenopodiad (Ch) types.

Hypostase (Fig. 11)

The *hypostase* is the group of often lignified cells with little cytoplasm located below the embryo sac, and where the integuments have their origin according to van Tieghem's (1901) definition. Nowadays hypostase has often been used in a rather loose sense (Singh and Gupta 1967). Its function has been disputed, but morphologically the hypostase is characteristic, and it is recorded from many families (Corner 1976; Bouman 1984). However, it seems to occur throughout the whole system and is thus presumably of no particular phylogenetic importance at higher taxonomic level. It can be noted that, as far as can be seen, the hypostase is lacking in some superorders, e.g., in Ranunculanae, Proteanae, Solananae, and Asteranae.

Embryogeny (Fig. 12)

Embryogeny denotes the mode of cell division of the zygote to the four-celled stage, and the further division of each of these cells to form the different parts of the mature embryo. In the dicotyledons there are six principal types: the *Solanad* (S), *Caryophyllad* (C), *Asterad* (A), *Onagrad* (O), *Piperad* (P), and *Chenopodiad* (Ch) types. A type is often concentrated in families of certain orders and may even be dominant within a superorder. In Figure 12 we find the following tendencies:

The *Solanad* type dominates in Solanales (Solananae), Ericales (Ericanae), Gentianaanae except Oleales, and Araliaanae; it is the only type found in Campanulales (Asteranae). All these groups belong to the mainly sympetalous superorders. The *Solanad* type is also recorded from the orders Rurales, Celastrales, Linales and Polygales (Rutanae), Plumbaginales (Plumbaginanae), and Tropaeolales, which are here placed near Capparales in Violanae (formerly in Rutanae). This position is supported by the results of ovule development studied by Tiwari et al. (1977) and Boeswinkel and Been (1979). In this character state Tropaeolales differ from Capparales, however, and also from all other Violanae except Tamaricales. On the other hand the *Solanad* type occurs in Linaceae in Linales, the neighboring order in its former position. Aristolochiales and Rafflesiales (Magnolianae) and some taxa scattered throughout the whole system are also of the *Solanad* type. The *Solanad* type has not been reported in the monocotyledons, apart from a probable occurrence in the genus *Trichopus* in Dioscoreaceae, the phylogenetic connection between this family and Aristolochiaceae having been discussed (Dahlgren et al. 1985).

The *Onagrad* type is mainly concentrated in Lamianaes, excluding Hydrostachyales, the position of which is uncertain as regards other features as well. Further, Capparales and Cucurbitales (Violanae), Rurales, Sapindales and Fabales (Rutanae), Magnoliales, Annonales and Laurales (Magnolianae), Ranunculales (Ranunculanae), Myrtales (Myrtanae), and some genera of other orders/superorders have the *Onagrad* type.

The *Asterad* type is found, apart from Asterales, in Proteales, Rosales, Polygonales, Vitales, Cornales, and Dipsacales. It is the dominant type (with only isolated taxa having the *Solanad* and the *Onagrad* types) in Malvales–Rhamnales–Urticales–Thymelaeales (Malvanae), as well as occurring scattered in many orders. The Fouquieriales, by contrast to all other groups of Ericanae, have the *Asterad*

type. The position of Fouquieriales in this superorder can be discussed (see also p. 121).

These three types are the commonest ones. The Caryophyllad type is not concentrated to any particular groups. It is found in Caryophyllaceae (Caryophyllanae), Crassulaceae (Saxifragales, Rosanae), Haloragidales (Myrtanae), Apocynaceae (Gentianales, Gentiananae), in small primitive families in Ericales (Ericanae), some taxa in Boraginales (Solanae), and in Primulaceae (Primulales, Primulanae).

The Chenopodiad type is found mainly in Caryophyllales, except in the family Caryophyllaceae, i.e., it is restricted to those members of the order where betalains occur. Other isolated occurrences of this type are in the families Ehretiaceae, Boraginaceae (Boraginales), Polemoniaceae (Solanales), Lentibulariaceae (Lamiales), and Chloranthaceae (Chloranthales). It can be noted that the first three of these additional families with the Chenopodiad type belong to Solanae.

Finally the Piperad type is rare with some few records from Piperales, Euphorbiales, Violales, Santalales, Balanophorales, and Dipsacales.

Polyembryony (Fig. 13)

Polyembryony can be defined in different ways. Among modern authors Lakshmanan and Ambegaokar (1984) divide polyembryony into two main types, simple and multiple (one vs. several embryo sacs in the same ovule). Further, nucellar, integumentary, zygotic, and synergid polyembryony are described, the first of these being the commonest. However, when polyembryony is recorded in systematic literature it is often noted without regard to origin. In this survey the term is therefore used in the commonest sense found in the literature, i.e., where there is more than one embryo in a seed.

Polyembryony is known from more than 70 families of dicotyledons but, in most of them it has been reported from only one or a few genera (e.g., Rangaswamy 1981; Tiagi 1970; Sachar and Chopra 1957). In five families polyembryony is recorded as common, viz., in Euphorbiaceae (Euphorbiales, Malvanae), Tamaricaceae (Tamaricales, Violanae), Myrsinaceae (Primulales, Primulanae), Rutaceae (Rutales, Rutanae), and Malpighiaceae (Polygalales, Rutanae).

Polyembryonic families are scattered throughout the system but some trends can be seen, e.g., in Caryophyllanae polyembryony occurs in the families Caryophyllaceae, Amaranthaceae, Aizoaceae, Cactaceae, Chenopodiaceae, Portulacaceae, and Nyctaginaceae (Caryophyllales); in Primulanae in Primulaceae and Myrsinaceae (Primulales) and Ebenaceae (Ebenales); in Malvanae in Urticaceae, Ulmaceae and Cannabinaceae (Urticales); Malvaceae, Tiliaceae, and Bombacaceae (Malvales); Rhamnaceae (Rhamnales); and Euphorbiaceae (Euphorbiales). The concentration of polyembryony to these groups can probably be interpreted as additional evidence in support of relationships in these orders and superorders.

Endosperm Formation (Fig. 14)

Endosperm formation in dicotyledons is usually of the *cellular* or *nuclear* type. In a comparatively few dicotyledonous taxa endosperm formation is of intermediate types. The *helobial* type is included here, since it has without doubt arisen

within more than one line and independent of the helobial type in the monocotyledons, as a convergence to this (Hamann 1977).

Cellular endosperm formation shows a clearly "bicentric" distribution in dicotyledons: it is common in Magnolianaes-Nymphaeanaes as well as in most sympetalous orders. Since the former are considered ancestral in many features and the latter advanced, it can be debated as to whether cellular endosperm formation in the two groups of superorders has a common origin. This will be discussed below.

In Magnolianaes, the cellular type occurs in most Annonales that have been studied except Myristicaceae (Bhandari 1971) and Eupomatiaceae; in some Winterales; in all or nearly all Magnoliales, Chloranthales, Illiciales, Nelumbonales, and Aristolochiales; in several families of Laurales, including Monimiaceae but not in most Lauraceae; and in at least some Rafflesiaceae.

Within Nymphaeanaes, the cellular type occurs in many Piperales: Saururaceae and *Heckeria* and *Peperomia* (Piperaceae); and in Nymphaeales: Ceratophyllaceae and most Nymphaeaceae. In Cabombaceae, also Nymphaeales, endosperm formation is of the helobial type.

Thus, the variation in endosperm formation in these two superorders is considerable and if the cellular type is ancestral here, as has been proposed by Wunderlich (1959), transition to the nuclear type has occurred once or several times in each of at least Annonales, Winterales, Laurales, Rafflesiaceae, Piperales, and Nymphaeales, as well as at the family level within Winteraceae, Lauraceae, Rafflesiaceae, Piperaceae, Nymphaeaceae, and possibly others.

In all these groups except Rafflesiaceae and Calycanthaceae cellular endosperm formation is associated with crassinucellate ovules, and there are generally several cell layers between the embryo sac and the nucellar epidermis. The first cell wall of the endosperm is normally transverse (as in helobial endosperm formation), and from this type of endosperm formation it is not a long step to the helobial type as found in Cabombaceae (*Cabomba* and *Brasenia*). It is probable that in the ancestor of the monocotyledons endosperm formation was either cellular or a derivative helobial type, as in the extant family Cabombaceae.

Other dicotyledonous groups with cellular endosperm formation in combination with crassinucellate ovules are, for example, Lardizabalaceae and Circaeasteraceae in Ranunculales (Ranunculanae) and various Rosanae, viz., Trochodendraceae and Tetracentraceae in Trochodendrales; Cercidiphyllaceae and Eupteleaceae in Cercidiphyllales; Platanaceae and certain Hamamelidaceae in Hamamelidales; some Buxaceae (*Buxus* and *Pachysandra*) in Buxales; Gunneraceae in Gunnerales; and various Saxifragales.

In Saxifragales cellular endosperm formation occurs in Crassulaceae and most Saxifragaceae and Grossulariaceae, but helobial endosperm formation is also found in some genera of the last two families. In Greyiaceae, Francoaceae, and Brexiaceae, for example, endosperm formation is nuclear, which supports separating them from Saxifragaceae *sensu stricto*, provided that the nuclear type is plesiomorphic, however; see discussion below. The Podostemaceae, which with their protrusive nucellus resemble some Crassulaceae, form no endosperm at all. The

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Fig. 13. Polyembryony. Reported in a family: one triangle; common occurrence: several triangles.

Cephalotaceae, which are often considered to be closely related to the Crassulaceae, differ from these in having nuclear endosperm formation.

In other Rosanae, including the Cunoniales, Rosales, Droserales, and the amniferous orders, endosperm formation is nuclear. Thus, the Rosanae, like the Magnolianae, vary considerably with respect to endosperm formation.

Other families in which endosperm formation is cellular are some Celastraceae in Celastrales (Rutanae), the Marcgraviaceae in Theales (Theanae), Styracaceae and Ebenaceae in Ebenales (Primulanae), and Fouquieriaceae in Fouquieriales (Ericanae). These are all families that have given rise to problems of relationship with other groups and are in need of reconsideration as regards their position. In nearly all the groups so far mentioned cellular endosperm formation is combined with bitegmic ovules.

Cellular endosperm formation also occurs in all investigated members of Santalales (Santalanae), the ovules of which, if discernible at all lack integuments, except in certain Olacaceae. The Santalales also lack parietal tissue, as do some of the above-mentioned groups. In this combination of character states the Santalales are unique but approach most of the main sympetalous groups. In Balanophorales, which generally have ategmic ovules, endosperm formation is also cellular.

Among the mainly sympetalous superorders, with unitegmic and tenuinucellate ovules, endosperm formation is generally cellular, although there are a number of exceptions: within Cornales (Cornanae) endosperm formation in the Alangiaceae and Garryaceae is nuclear and both of them also have ovules with parietal tissue, thus deviating from most other Cornales.

In Gentiananae endosperm formation is cellular in Oleales and Goodeniales, but nuclear in nearly all Gentianales. It may be noted that the Menyanthaceae, with cellular endosperm formation, are here placed in Cornales and that Buddlejaceae and Retziaceae, also with cellular endosperm formation, and previously treated as genera in Loganiaceae, have now been transferred to form families of their own in Lamiales (Lamianae). Gentianales, as circumscribed here, seem to make up a homogeneous and well-defined order where nuclear endosperm formation is one of the diagnostic features. In Gentianaceae, however, there are a few exceptions, e.g., the mycotroph genera *Voyria* and *Vouriella* with a cellular type of endosperm. These genera differ from other Gentianaceae also in other embryological characters, e.g., in the ategmic condition (Oehler 1927).

In Asteranae all Campanulales have cellular endosperm formation, whereas Asterales (=Asteraceae) are surprisingly variable—according to Wunderlich (1959) both the cellular and the nuclear types are mingled in most asteraceous tribes, and even in many genera both types are reported, something extremely unusual in dicotyledons.

In Solananae both the cellular and the nuclear types occur in Solanaceae (Solanales) and in addition helobial endosperm formation in *Hyoscyamus*. In other Solanales endosperm formation is nuclear. The Boraginales are also variable, with the cellular type in Ehretiaceae and Boraginaceae subfam. Heliotropioideae, and

Fig. 14. Endosperm formation. Nuclear: unshaded; Cellular: hatched; Intermediate (helobial): dotted; Lacking: cross-hatched.

intermediate or nuclear types in other Boraginaceae, suggesting, in this order, an evolution from cellular to nuclear. In Hydrophyllaceae as well all three types are found.

In nearly all Lamianae endosperm formation is cellular, exceptions with intermediate types being found in Acanthaceae in Lamiales.

In all other dicotyledons not mentioned above endosperm formation is nuclear or occasionally helobial (as in some Linaceae, Linales; and in Balsaminaceae, Balsaminales) or almost entirely lacking (as in Trapaceae, Myrtales; and Podostemaceae, Saxifragales). Nuclear endosperm formation is, accordingly, the most widespread in major complexes of dicotyledons, e.g., Caryophyllanae, Polygonanae, Plumbaginanae, Malvanae, Violanae, Rutanae (rarely helobial), Vitanae, Aralianae, Proteanae, Myrtanae, and with few exceptions in Ranunculanae and Theanae.

The phylogenetic importance of the type of endosperm formation should be viewed according to the above-mentioned patterns of variability; it is obviously of little value in Asteraceae, useful at infrafamilial level in, say, Boraginaceae, at family level in Magnoliales and at ordinal/superordinal level in certain other groups of dicotyledons, e.g., in Gentianales/Gentiananae.

Further conclusions can be drawn for various groups with cellular endosperm formation, if details of cell wall formation in the early endosperm are taken into consideration, and when presence and characters of endosperm haustoria are considered. Di Fulvio (1977, 1981, 1983) has used such evidence for a further classification of cellular endosperm which is phylogenetically useful.

The problem has been raised as to whether the cellular or the nuclear type of endosperm formation is ancestral in dicotyledons (Fig. 15). The commonest view is that the nuclear type is ancestral, as advocated in particular by Sporne (1954), emphasis being laid on the preponderance of cellular endosperm formation in the undoubtedly advanced taxa in the main sympetalous orders (Asteranae, Lamianae, Loasanae, Cornanae, Ericanae, and some Gentiananae).

A different view is taken by Wunderlich (1959), for example. In a survey of endosperm formation in the angiosperms, she emphasizes the fact that apart from most sympetalous groups the cellular type also occurs in a great many Magnolianae and other groups with decidedly archaic features such as Piperaceae, Nymphaeaceae, Lardizabalaceae, Trochodendraceae, Tetracentraceae, Eupteleaceae, and Hamamelidaceae p.p. In these groups cellular endosperm formation is associated with conspicuously crassinucellate bitegmatic ovules and seeds that have copious endosperm and a small embryo, features which are regarded as ancestral in angiosperms. According to Wunderlich (op. cit.) the cellular endosperm formation is therefore the ancestral condition in angiosperms. It is considered to have been retained in certain groups apart from the ancestral groups mentioned, especially in those where the ovules are tenuinucellate. In other dicotyledons the cellular type has been substituted by the nuclear type.

With Wunderlich's interpretation there would be an unbroken evolutionary connection between the clearly primitive and the clearly advanced groups with cellular endosperm formation, and the type of endosperm formation would be of great value in phylogenetic calculations.

However, if we do not take for granted that the transition from cellular to nuclear endosperm formation is irreversible, the following modified view, still largely in accordance with Wunderlich's (1959), could be considered: the cellular

ENDOSPERM FORMATION

Fig. 15. Hypothesis of which type of endosperm formation is the ancestral.

type in the dicotyledon ancestor has been retained in a number of primitive orders, but has been substituted by the nuclear type within a number of evolutionary lines (cf. above comment on the variation within Magnolianaee). In some of the groups where nuclear endosperm formation has arisen, a reversal to cellular endosperm formation may have taken place. Such cases of advanced cellular endosperm formation would be found chiefly in the main sympetalous orders. Whether or not a second transition to nuclear endosperm (from this secondarily cellular type) has occurred in Gentianaales is uncertain, but it is clear that this group is most closely related to groups with cellular endosperm formation.

The fact that cellular endosperm formation in sympetalous groups is fairly variable with regard to the manner in which cell walls are laid down supports this third theory. Hence the cellular type could have appeared independently within different evolutionary lines. For example, the great difference between endosperm formation in Ericaales and Campanulaales can be observed.

One difficulty is the question as to whether cellular endosperm formation in some Rosanae, e.g., Buxaceae, Saxifragaceae, Gunneraceae, is ancestral or derived.

In Boraginales cellular endosperm formation is associated with the least advanced features (see above) but the nuclear type with the more advanced ones, indicating that here the nuclear type is advanced, as in Gentiananae. In Cornales, the situation is different, since Alangiaceae and Garryaceae, for example, are ancestral in that they have parietal tissue while endosperm formation is nuclear.

Future detailed comparative surveys of the early stages of cellular endosperm formation may clarify details in endosperm evolution, which would greatly increase the value of this character state in phylogenetic systematics.

Persistence of Endosperm (Fig. 16)

Although in most angiosperms endosperm is formed after the fusion of the central nuclei and one of the male gametes, certain exceptions should be noted, viz., in the families Podostemaceae (Saxifragales) and Trapaceae (Myrtales). In the former, a so-called pseudoembryo sac is formed in the nucellus and seems to be a substitute for the endosperm as nutritive tissue. In Trapaceae the endosperm nucleus moves to the chalazal part of the embryo sac and there it degenerates.

Even when endosperm is formed there is great variation in the degree of persistence in the ripe seed. In many groups the endosperm is completely consumed during the course of seed development. This is characteristic of the following orders: Laurales, the families Lauraceae and Calycanthaceae in Magnolianaes; Fabales and several families of Sapindales (Sapindaceae, Hippocastanaceae, Aceraceae, Anacardiaceae) in Fabanae; Rosales, Fagales, Casuarinales, Myricales, and Juglandales in Rosanae (possibly a link between "Amentiferae" and the more primitive Hamamelidales, Trochodendrales, etc.); Proteales in Proteanae; Myrtales in Myrtanae; Tropaeolales, Cucurbitales, and Salvadorales in Violanae; finally Asterales in Asteranae.

Most Caryophyllanae and Nymphaeanae belong to the same category, but in these superorders the function of the endosperm has been taken over by the perisperm (p. 145 and Fig. 18).

There is variation in some orders from families or genera where the ripe seeds are completely lacking in endosperm, to taxa where the seeds have a thin layer of endosperm or even copious endosperm. Such variable orders are Malvales and Urticales (Malvanae), Lamiales (Lamianaes), Dipsacales (Cornanae), Boraginales (Solanae), Oleales (Gentiananae), and Capparales (Violanae).

Exceptionally variable is the order Theales. Of the 18 families here distinguished no endosperm is recorded in Quiinaceae, Ochnaceae, Marcgraviaceae, Chrysobalanaceae, Hypericaceae, and Elatinaceae. Copious endosperm occurs in Dioncophyllaceae and Oncothecaceae, rarely copious in Theaceae and "scanty" or "scanty or none" in the remaining families. This character state could perhaps help resolve interfamilial relationships, within Theales.

Finally copious endosperm remains in the ripe seed in many orders, e.g., Magnoliales–Annonales–Aristolochiales and other orders in Magnolianaes; Papaverales–Ranunculales; Polygonales; Violales; Vitales and Araliales.

Fig. 16. Persistence of endosperm. Endosperm lacking or consumed: dotted; Thin, scanty: hatched; Copious: unshaded.

Ruminate Endosperm (Fig. 17)

When the endosperm in the mature seed is irregular in its surface contour, i.e., the margin is folded, it is termed *ruminate* (Periasamy 1962). Morphologically several types can be distinguished.

Rumination has been considered by some workers to be an ancestral feature, occurring in seeds of both primitive and advanced groups (Vijayaraghavan and Prabhakar 1984). It is common in the orders Annonales, Magnoliales, Winterales, and Aristolochiales (Magnolianae); and in Menispermaceae (Ranunculanae). But ruminate endosperm is also reported in derived families and has presumably arisen in parallel. Altogether it occurs in at least 25 dicotyledon families. From Figure 17 we can see that in addition to the above groups it is also found in Bombacaceae and Dipterocarpaceae (Malvales); in Polygonales but not in Plumbaginales, two orders that often share character states, e.g., phytochemical similarities (Bate-Smith 1974) and S-type sieve element plastids (Behnke 1976); in Rubiaceae, Loganiaceae, and Apocynaceae (Gentianales); in Scrophulariaceae and Acanthaceae (Lamiales); etc.

It is also of note that ruminate endosperm seems to be lacking in large superorders such as Caryophyllanae, Rosanae, Myrtanae, Solananae, and Asteranae.

It would appear that ruminate endosperm is of little value as phylogenetic evidence at least at the ordinal level. It can perhaps be used in discussions on family relationships in Magnolianae where it is common, and where many types are represented from those with one or few folds to taxa with a complicated pattern of folds.

Endosperm Haustoria

The occurrence of endosperm haustoria in the dicotyledons has been treated and illustrated in G. Dahlgren (1989). From this presentation it is clear that *chalazal endosperm haustoria*, usually combined with nuclear endosperm formation, have a scattered distribution. They must have arisen many times and are of little importance phylogenetically.

Terminal endosperm haustoria, with few exceptions in combination with cellular endosperm formation, have a very well-defined distribution, occurring in only a few superorders, viz., in Rutanae (Balsaminaceae), Loasanae (Loasaceae), Ericanae (except Sarraceniales, Fouquieriales and Ericales, the families Actinidiaceae and Pyrolaceae), Lamianae (except Hippuridales, but in Hydrostachyales [Rauh and Jäger-Zürn 1966]), and Asteranae (Campanulales). Relationships are discussed in G. Dahlgren (1989). To summarize, Balsaminaceae and Campanulales differ from the other groups and have probably evolved independently. Loasanae, Ericanae, and Lamianae resemble one another embryologically and also chemically, for example in the production of iridoids. Presumably they can be regarded as a monophyletic unit, even if Loasanae are a little doubtful, as they produce seco-iridoids (Dahlgren et al. 1981). Cornanae and Gentiananae, e.g., other seco-iridoid taxa, lack endosperm haustoria.

Fig. 17. Presence of ruminate endosperm: dotted. Presence of endosperm haustoria. Terminal: hatched; Chalazal: dotted; Micropylar: rings.

Perisperm (Fig. 18)

Perisperm is defined as persisting nucellus which by cell division forms a nutritive tissue in the ripe seed. However, the nucellar cells are usually consumed by the developing embryo sac, and perisperm is developed in only a few groups, being restricted to Caryophyllanae, Nymphaeanae, Violanae, and the order Rafflesiales in Magnolianae.

There are two different types of perisperm. In Nymphaeanae the perisperm forms the main part of the seed. The small embryo, enclosed by the endosperm, is confined to the micropylar end. This type is found in the orders Nymphaeales (perisperm occurs in Nymphaeaceae and Cabombaceae but is lacking in Ceratophyllaceae) and Piperales (in both Saururaceae and Piperaceae). Dahlgren and Clifford (1982) base the affinity between these two orders on the similarity in seed structure. The lack of perisperm in Ceratophyllaceae could be an evidence against their assignment in Nymphaeales!

In Caryophyllanae the perisperm occupies the central part of the seed and is surrounded by the embryo. Endosperm is lacking. Perisperm is recorded in 12 of the 16 families distinguished in Caryophyllales and probably exists in all of them (the embryology of the small families Agdestidaceae, Stegnospermataceae, Halophytaceae, and Hectorellaceae has, as far as I know, not been investigated).

In the family Hydnoraceae, Rafflesiales, a thin layer of perisperm surrounds the endosperm which encloses a minute embryo, i.e., the type is here the same as in Nymphaeales and Piperales.

In Violanae perisperm has been reported in the families Capparaceae and Tovariaceae (Capparales), Tamaricaceae (Tamaricales), and Scyphostegiaceae (Violales). The endosperm is scanty or lacking. A persistent perisperm is sometimes present in Capparaceae; in the other families a thin layer of perisperm surrounds the endosperm, if existent. The type of perisperm must be classified as the same as in Nymphaeales and Rafflesiales. By definition the perisperm is a nutritive tissue; it takes over the role of the endosperm, and if this is so in these families with scanty endosperm and a thin perisperm is difficult to say. But at least in Capparaceae there is a true perisperm. Evolution has probably proceeded from the thin perisperm found in the small families considered primitive towards a development of a nutritive perisperm, such as in Capparaceae.

Storage Compounds in the Endosperm (Fig. 19)

Storage compounds in the endosperm that are generally recorded for dicotyledonous families are oil (almost always), starch, protein, hemicellulose, amylose, polysaccharides, and certain acids.

Endosperm containing starch, and endosperm containing hemicellulose, have been mapped to determine their possible phylogenetic importance. The most striking feature of the diagram is that starchy endosperm is distributed in all Polygonanae and Plumbaginanae. However, there is no starch in Primulanae, which are considered to be related to Plumbaginanae (Hutchinson 1973; Thorne

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Fig. 18. Perisperm. Perisperm enclosing endosperm and embryo: dotted; Perisperm surrounded by the embryo: hatched.

1976, 1981). Surprisingly starch occurs in Santalales and it should also be noted that there is starch in both families of Tamaricales. Further it is found in various Malvales (Sterculiaceae, Bixaceae, Sarcolaenaceae, and Cistaceae), Ranunculales (Ranunculaceae, Lardizabalaceae and Sargentodoxaceae), and in some small families of Theales (Ancistrocladaceae, Dioncophyllaceae, and Nepenthaceae) which are often regarded as related.

Some scattered groups are Droseraceae in Droserales, the only "starchy" family recorded in Rosanae, and Aristolochiales, Schisandraceae (Illiciales), and Chloranthales in Magnolianae. Thus, Chloranthales differ in this way from Piperales, two orders that have several character states in common, and also from Laurales, the group in which it seems most likely to be rooted (Endress 1987).

Hemicellulose is less common than starch in the endosperm of Dicotyledonae. Of note is its occurrence in three families of Cornales that are often mentioned as primitive, viz., Alangiaceae, Garryaceae, and Nyssaceae. Other features are also shared by these families. Hemicellulose has also been reported in a few taxa in Gentianales (Loganiaceae, Rubiaceae), Solanales (Convolvulaceae), Saxifragales (Grossulariaceae), and Ranunculales (Berberidaceae and Lardizabalaceae).

Chlorophyllous Embryo (Fig. 20)

A survey of seeds in which the embryo is chlorophyllous (before germination) has been presented by Yakovlev and Zhukova (1973, 1980) and the taxonomic significance of chlorophyllous embryo was discussed in Dahlgren (1980b).

In dicotyledons a chlorophyllous embryo is found in nearly all taxa of the following orders: Capparales, Fabales, Geraniales, Linales, Rhizophorales, Celastrales, Balanopales (Cronquist 1981), Malvales, Salicales, Plumbaginales, and Nylumbonales, and in various families in Rutales, Polygalales, Sapindales, Santalales, and Rhamnales. Furthermore, chlorophyllous embryos occur in some families of Nymphaeales (Ceratophyllaceae), Cornales (e.g., Alangiaceae, Cornaceae, and Icacinaceae), Gentianales (Asclepiadaceae, Gentianaceae p.p.), Caryophyllales (taxa of Chenopodiaceae, Nyctaginaceae, and Basellaceae), Solanales (Convolvulaceae, Cuscutaceae, and certain Polemoniaceae), Boraginales (Hydrophyllaceae p.p.), Dipsacales (Dipsacaceae, Morinaceae, and Valerianaceae), Euphorbiales (some Euphorbiaceae), Theales (Hypericaceae), Scrophulariales (Lentibulariaceae, and a few Scrophulariaceae), Myrtales (Memecylaceae, some Myrtaceae, and *Sonneratia* of Lythraceae), and Violales (Violaceae).

Dahlgren (1980b) points to a certain degree of correlation between chlorophyllous embryo and the lack of endosperm. Lack of endosperm or endosperm that is consumed in the ripe seed has been discussed here on p. 141 and is illustrated in Figure 16. The diagram for this character can be compared with that for chlorophyllous embryos.

There are, however, some orders that have a chlorophyllous embryo in spite of having copious endosperm, e.g., Plumbaginales and Santalales. Plumbaginales differ in this character from Primulales, Ebenales, and Polygonales, taxa being discussed as related to each other (e.g., Thorne 1981). Moreover a nonchloro-

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Fig. 19. Storage compounds in endosperm. Starch: dotted; Hemicellulose: triangles.

phyllous embryo in combination with lack of endosperm occurs in orders such as Asterales and Rosales.

Since this character accordingly is fairly scattered throughout the dicotyledons its value in phylogenetic discussions is restricted. However, as it is commonly present in certain orders such as Malvales–Rhamnales, Geraniales–Polygalales, and Fabales this suggests relationship.

The presence of chlorophyll in the embryo has also been used as additional evidence when discussing certain relationships, such as between Sapindaceae and Fabaceae–Caesalpiniaceae–Mimosaceae (Dickison 1981), among Rhizophoraceae, Elaeocarpaceae, and Celastraceae; and in families of Linales (Dahlgren 1988). It can be used in support of placing Cistaceae in Malvales, and as an argument for regarding Plumbaginales as distantly related to both Polygonales and Primulales.

Some surprising anomalies in the distribution of this character also occur. Thus by contrast with other families in Solanales, the Solanaceae lack chlorophyll in the embryo, and the Asclepiadaceae differ from the Apocynaceae in the presence of a chlorophyllous embryo. Furthermore, the Caprifoliaceae differ from other Dipsacales in that they lack chlorophyll in the embryo.

In monocotyledons presence of chlorophyll in the embryo is generally associated with lack of endosperm in the ripe seed. This seems to be true of only some of the above-mentioned dicotyledonous groups with green embryos, even though this combination is typical of groups such as Fabales and many Capparales.

Embryo Size (Fig. 21)

In dicotyledons the embryo varies widely in size and shape, from very small and undifferentiated embryos to large well-developed embryos that are straight, curved or coiled, the cotyledons being thin or thick and sometimes folded. In this survey I have chosen to map the character state “large embryo.”

This can be considered a controversial choice as being too broad a character state to use, but the detailed information on embryo characters has not been consistently reported in the literature and they thus cannot be used separately. On the other hand I have tried to deduct from the information supplied whether the embryo is small or large. A small embryo is considered the plesiomorphic state, a large embryo being derived.

The correlation between chlorophyllous embryo and lack of endosperm has been discussed on p. 147 and there is an even stronger correspondence between a large embryo and lack of endosperm.

Large embryos occur more or less consistently in Caryophyllales, Fabales, and Asterales (but not in Campanulales) and are dominant in Capparales and Tro-paeolales. The sympetalous groups are heterogeneous with regard to embryo size by contrast to the distribution of many other characters. Thus, in Gentianales only Apocynaceae have a large embryo; in Ericales, Actinidiaceae; a few families in Cornales–Dipsacales and Solanales–Boraginales; in Lamiales, Lamiaceae, Ver-benaceae, Acanthaceae, and Bignoniaceae.

The distribution is also scattered in Rosanae with a large embryo in the “woody”

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Fig. 20. Chlorophyllous embryo in ripe seed. Dominant: hatched; Scattered: dotted.

orders Fagales–Juglandales–Trochodendrales, in most orders of Rutanae, and in Malvanae. In Primulanae, Ebenales have a large embryo, Primulales (except Theophrastaceae) have not, thus agreeing with Polygonales and Plumbaginales, cf. “Chlorophyllous embryo,” p. 147.

Within the superorders placed near the monocotyledons only Ceratophyllaceae in Nymphaeanae; Nelumbonales and Lauraceae in Magnolianae have a large embryo. Neither Ranunculales (except for Menispermaceae) nor Papaverales, (both in Ranunculanae) have a large embryo.

SEED COAT CHARACTERS

Seed coat characters have been monographed by Corner (1976), who introduced the following terminology: seed coats with a thick-walled layer(s) in the outer integument were termed “testal,” and those with a thick-walled layer(s) in the inner integument “tegminal.” Each of these types were classified as exo-, meso-, and endotestal and exo-, meso-, and endotegminal respectively, according to whether the outer, middle, or inner cell layer(s) of the integuments form the thick-walled layer.

On the basis of the type of seed coat Corner (1976) came to a number of phylogenetic conclusions, some of which run contrary to the views of other investigators. For instance, in his “Summary of positive contributions” he suggested that Brassicaceae should be removed from the Capparales; that Burseraceae (here Rutales) and possibly also Combretaceae (here Myrtales) could belong to Laurales; that Myrtales should be divided into Myrtales *sensu stricto* and Lythrales; that Geraniaceae should be placed together with Hypericaceae (Theales) rather than with the other families normally placed in Geraniales; and that Piperales were perhaps derived from the papaveraceous stock.

Although these and other of his taxonomic conclusions gain little support from other sources, some of Corner’s conclusions are of interest, e.g., the following: that Calycanthaceae belong to Laurales; Podophyllaceae to Berberidales (=Ranunculales); Cactaceae and Nyctaginaceae to Centrospermae (=Caryophyllales); Punicaceae in the vicinity of Lythraceae and Combretaceae; Buxaceae in the vicinity of Hamamelidaceae, not in Euphorbiales; that Vitaceae should be removed from Rhamnales (cf. Behnke 1974); that Chloranthaceae should not be included in Piperales (see also Endress 1987); that the Salicaceae are related to Tamaricales; that Bombacaceae, Malvaceae, Sterculiaceae, Tiliaceae, Dipterocarpaceae, and Thymelaeaceae, and Euphorbiaceae subfam. Crotonoideae are all related; and that Elaeocarpaceae should be excluded from Malvales.

Most of the above has been taken into account in the classification presented here. Thus, the families mentioned above belong to the orders where Corner has placed them. Buxaceae and Hamamelidaceae have been accorded the rank of order and placed next to each other in Rosanae; Vitaceae are a separate order (and superorder); Chloranthaceae are an order in Magnolianae; Salicales are placed next to Tamaricales in Malvanae, and from Malvales in this superorder Elaeocarpaceae have been moved to Rhizophorales (Rutanae).

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Fig. 21. Large embryo: dotted.

Of the seed coat features presented by Corner I have selected three conditions, which seem to be of particular phylogenetic significance.

Seeds with Exotegminal Fibers (Fig. 22)

Exotegminal fibers (Corner 1976; Boesewinkel and Venturelli 1987) occur in the following families: Aristolochiaceae (Aristolochiales); Myristicaceae (Annonales); Chloranthaceae (Chloranthales), Papaveraceae and Fumariaceae (Papaverales); Pandaceae and Euphorbiaceae subfam. Crotonoideae (Euphorbiales); Flacourtiaceae, Scyphostegiaceae, Violaceae, and Caricaceae (Violales); Resedaceae and Capparaceae (Capparales); Meliaceae (Rutales); Malpighiaceae (Polygalales); Tremandraceae (Pittosporales); Sapindaceae, Connaraceae, and Staphyleaceae p.p. (Sapindales); Oxalidaceae, Linaceae, and Erythroxylaceae (Linales); Rhizophoraceae p.p. ("Legnotidaceae"), and Elaeocarpaceae (Rhizophorales); Celastraceae (Celastrales); Droseraceae (Droserales); Proteaceae (Proteales); and some families of Myrtales.

Boesewinkel and Venturelli (1987) reported exotegminal fibers in seeds of the families Krameriaceae, Trigonaceae, and Vochysiaceae (here Polygalales). They discuss embryological attributes in addition to other seed characters and according to them these families seem to be more closely related to Linales than to Polygalales.

Corner divided his "exotegminal" families into three groups according to the manner in which taxa with exotegminal fibers were combined with two testal character states. Thus, one group consists of taxa with multiple exotegminal fibers combined with a thick-walled exotestal layer and with crystals in the endotestal layers. Here belong Violaceae and Passifloraceae (Violales), Oxalidaceae (Linales), Elaeocarpaceae (Rhizophorales), as well as Trapaceae, Lythraceae, and Onagraceae (Myrtales). These character states are also combined in Papaveraceae and Fumariaceae (Papaverales), in Aristolochiaceae (Aristolochiales), and in Chloranthaceae (Chloranthales). This unusual combination of three microcharacters has obviously evolved within at least six evolutionary lines.

In a second group nonmultiple exotegminal fibers are combined with a thick-walled exotestal layer and crystals in the endotestal layer. This group consists of Meliaceae (Rutales), Connaraceae (Sapindales), Proteaceae (Proteales), and Droserales, taxa that are more or less closely related.

In a third group, nonmultiple exotegminal fibers are combined with a thick-walled exotestal layer but there are no crystals in the endotestal layer. Here belong members of Celastraceae (Celastrales) and Sapindaceae (Sapindales).

The common occurrence of exotegminal fibers in some families of Linales, and in some families here placed in Rhizophorales (Rhizophoraceae and Elaeocarpaceae) and Celastrales (Celastraceae), should be regarded as significant since these families have quite a number of characters in common. However, they differ in the structure of the exotestal layer and in the occurrence of endotestal crystals.

Exotegminal fibers, either multiple or nonmultiple, are also characteristic of

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Fig. 22. Seed coat characters. Seeds with exotegminal fibers: horizontally hatched; thickwalled exotestal layer: dotted; crystals in the endotestal layer: vertically hatched.

some families in Violales (Flacourtiaceae, Scyphostegiaceae, Violaceae, and Caricaceae), and likewise of several families in Myrtales (Dahlgren and Thorne 1984). In both orders the fibrous exotegmen is combined with a thick-walled exotesta, and in the myrtalean families in particular often with crystals in the endotestal layer.

Although these features are also combined in Papaveraceae and Fumariaceae (Papaverales), the general characteristics do not support a connection with the previous orders; it is also dubious as to whether Violales and Myrtales are closely related phylogenetically.

Seeds with Exotegminal Palisade (Fig. 23)

In these seeds the outer layer of the inner integument comprises the mechanical tissue. Corner (1976) describes these cells as a prismatic palisade with angular, isodiametric or shortly oblong facets. Exotegminal palisade occurs in the following families: Bombacaceae, Sterculiaceae, Tiliaceae, Bixaceae, Cistaceae, Dipterocarpaceae, and Malvaceae (Malvales); Gonystylaceae and Thymelaeaceae (Thymelaeales); Euphorbiaceae p.p. (Euphorbiales); Passifloraceae and Turneraceae (Violales); *Perrotetia* in Celastraceae (Celastrales); Piperaceae (Piperales); Rafflesiaceae p.p. (Rafflesiales); Bonnetiaceae, Hypericaceae, and Elatinaceae (Theales); Geraniaceae (Geraniales); and Podostemaceae (Saxifragales).

The agreement in seed coat characters between most families of Malvales is of considerable significance. Furthermore, Turneraceae and Passifloraceae agree in this respect, as also do some families of the probably heterogeneous order Theales. Isolated groups with exotegminal palisade are Piperales, Rafflesiales, and Podostemaceae (Saxifragales), all of which have cuboid rather than palisadelike cells.

Seeds with a Sclerotic Mesotestal Layer (Fig. 24)

This type of seed coat occurs in the following families: Illiciaceae and Schisandraceae (Illiciales); Lardizabalaceae (Ranunculales); Lecythidaceae (Lecythidales); Melastomataceae, Myrtaceae, Penaeaceae, Combretaceae, Lythraceae (incl. Punicaceae and Sonneratiaceae), Onagraceae, and Trapaceae (Myrtales) (of which the last three families also have a fibrous exotegminal layer, see above); Balanitaceae (Geraniales); *Sarcococca* in Buxaceae (Buxales); Hamamelidaceae (Hamamelidales); Marcgraviaceae, Stachyuraceae, Theaceae, and Hypericaceae tribus Calophylleae (Theales); Rosaceae (Rosales); Staphyleaceae p.p. and Sapindaceae p.p. (Sapindales); Moringaceae (Capparales); Ebenaceae p.p. (Ebenales); Myrsinaceae (Primulales).

Of these the myrtalean families are undoubtedly closely related. This type of seed coat is obviously also an apomorphy of the order Illiciales, and possibly in the enumerated families of Theales, which in this respect agree with the Lecythidales. Corner considers that this type of seed coat also provides evidence that the Moringaceae are not capparalean; the resemblance to some Sapindaceae may be of phylogenetic significance since *Moringa* is strongly reminiscent of some members of this family.

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Fig. 23. Seed coat characters. Seeds with exotegminal palisade: hatched.

ARILS

Arils (Fig. 25) are appendages on seeds, usually fleshy, and sometimes brightly colored. Morphologically they have been subdivided (e.g., by van der Pijl 1982) into (1) true arils, which are outgrowths on the funiculus or hilum, (2) caruncles or arillodes, which are outgrowths on the exostome, and (3) strophioles, which are swellings on the raphe. However, there are also intermediate types, all in all there being a great diversity of aril, and many authors prefer to use the term "aril" in a broad sense (Corner 1976; Kapil et al. 1980).

In this survey of arillate taxa the term aril has been used in the broad sense, and moreover includes elaiosomes, a term introduced by Sernander (1906) for seeds with fleshy parts dispersed by ants, the structure studied, e.g., by Bresinsky (1963). Arils formed from the placenta, as in Apocynaceae and Cucurbitaceae, and also arils formed from the carpels, have been excluded.

It is striking that arils are practically lacking in the sympetalous groups: Araliaeae, Santalanae, Asteranae, Solananae, Ericanae, Cornanae, Gentiananae, and Lamianae. Exceptions are the family Apocynaceae (Gentiananae), where the genus *Voacanga* has been reported to have a funicular aril, and Tremandraceae in Pittosporales (Aralianae). Rudimentary arils have also been recorded in Rubiaceae (Gentiananae).

In Rosanae, Myrtanae, and Proteanae as well, arils are rare, having only been reported for the families Crossomataceae in Rosales, Grossulariaceae in Saxifragales, and Melastomataceae (the genus *Vestigia*) Myrtales.

In Magnolianae-Nymphaeanae, the superorders of dicotyledons closest to the monocotyledons in the diagram, there are arillate genera of Aristolochiaceae (Aristolochiales), Myristicaceae and Annonaceae (Annonales), Monimiaceae (Laurales), and Nymphaeaceae (Nymphaeales). Dahlgren and Clifford (1982) discussed the distribution of arils in monocotyledons. Arils were there concentrated in Zingiberales, but were rare or lacking in orders placed near the dicotyledons.

In the remaining superorders arils are found scattered in a considerable number of families in Malvanae, Violanae, Rutanae, and also Caryophyllanae.

The distribution of arils, classified as here in a single category, yields no detailed phylogenetic information. If the different morphological types of arils had been used, would this have given rise to a different pattern? To test this I distinguished exostomal arils from the other types (Fig. 25). However, the distribution of these arils proved to be roughly the same as for arils taken in a broad sense.

The combination of the morphological diversity in arils and their widespread distribution points to the fact that arils are of polyphyletic origin and are thus not homologous in the different groups. They have probably arisen to facilitate dispersal by animals, as is often the case with seed structures.

It has also been a matter of conjecture as to whether arils are primitive or derived structures. Corner (1976) is of the opinion that the aril is a primitive structure, whereas van der Pijl (1982) holds that arils are derived. Figure 25 shows that arils are found in both primitive and derived groups, but are lacking in all those superorders normally considered the most advanced. Possibly could this be

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Fig. 24. Seed coat characters. Seeds with sclerotic mesotestal layer: hatched.

interpreted in support of primitiveness? Even if some are primitive, others must be secondarily derived, however, according to the distribution.

DRY AND WET STIGMA TYPES

Dry and wet stigma types (Fig. 26) have been described by Heslop-Harrison and Shivanna (1977). Briefly, stigmas can be defined as "dry" when there is little or no surface secretion at maturity and "wet" when there is a visible surface secretion, with a free fluid surface. These two types can be further subdivided according to the appearance and shape of the epidermis cells, whether the surface is papillate, etc.

The stigma type is comparatively consistent at generic level and mostly also at family level and thus, it can be of some taxonomic significance, at least together with other characters, in phylogenetic and evolutionary studies.

Dry and wet stigma types sensu Heslop-Harrison and Shivanna (1977) are presented in Figure 26. The commonest type is dry and this is probably the plesiomorphic state. Constellations with only dry stigmas or where dry stigmas dominate are Nymphaeanae, Malvanae (except Sterculiaceae), Violanae, Primulanae, Vitanae, Plumbaginanae, Polygonanae, Caryophyllanae (except Cactaceae), Proteanae, and Loasanae. Even if these groups belong to the category "consistency of stigma type" according to Heslop-Harrison and Shivanna (1977), there is variation between families or orders. Thus, in Brassicaceae, the stigma is always dry with unicellular papillae, whereas in Malvaceae it is dry but different types of papillae occur within the family.

Heterogeneous superorders are Gentiananae, Rosanae, Rutanae, Magnolianae, and others. In Gentiananae, Gentianales are heterogeneous with both dry and wet stigmas in Rubiaceae, Asclepiadaceae, and Apocynaceae, while Oleales and Goo-deniales all have dry stigmas only.

Dry stigmas occur in Fagales, Myricales, Juglandales, Cunoniales, Droserales, and Gunnerales in Rosanae; also in Rosaceae, but not in Amygdalaceae and Malaceae; and in Saxifragaceae, but not in the other families in Saxifragales. The genus *Saxifraga* is heterogeneous as to shape of papillae. In Rutanae the dry type dominates in Celastrales, Geraniales, Linales, Polygalales, and Rutales p.p., i.e., Fabales-Sapindales are excluded. In Magnolianae dry stigmas are noted in Magnoliales, Laurales, and Chloranthales. Most of the species have the same papilla type, but within *Magnolia* a simpler type of papilla also exists.

Wet stigmas dominate in Fabales and Sapindales. However, it is necessary to investigate whether the type of stigma is the same in both orders. Other groups with wet stigmas are most Ericales; nearly all Solanaceae but not other Solanales; all Pittosporales; Apiaceae and Araliaceae p.p. in Aralianae, Dilleniales; Paeoniales, Lecythidales; various Theales in Theanae; and further orders where it is necessary to determine whether the wet stigmas are all of the same kind. Finally, only wet stigmas have been reported from Annonales and Winterales in Magnolianae.

Strikingly, the following pairs differ from each other: Illiciaceae from Schisan-

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Fig. 25. Occurrence of arils: dots; Exostomal arils: stars.

draceae; Solanaceae from Convolvulaceae; Cactaceae from other Caryophyllales; Sterculiaceae from all other Malvales; Caprifoliaceae from other Dipsacales; and Verbenaceae from Lamiaceae. It can also be noted that Balsaminales have wet stigmas, in contrast to Geraniales, Linales, and Celastrales, together with which they were formerly placed, but have here been moved to the vicinity of Sapindales-Fabales.

Relationships between the stigma type and the self-incompatibility (SI) system in the plant have been treated by Heslop-Harrison (1975), and Brewbaker (1967) discussed the correlation between pollen characteristics and the SI-system. If the pattern of dry-wet stigma (Fig. 26) is compared with the distribution of 2-celled and 3-celled pollen grains in the dispersal state (Fig. 4), we find a certain agreement between 3-celled pollen and a dry stigma. This could possibly be explained by the fact that families with SSI (sporophyte self-incompatibility, i.e., how the pollen reacts is determined by the genotype of the plant that delivers the pollen) have dry stigmas, and usually 3-celled pollen grains. The growth of the pollen tube ceases on or immediately below the stigma. Families with GSI (gametophyte self-incompatibility) have wet stigmas. The pollen grains are 2-celled and the inhibition of the pollen tube occurs in the style or in the ovule.

There are some exceptions from this coincidence of dry stigma and 3-celled pollen, viz., Cactaceae in Caryophyllales, Lecythidales, Araliales (mainly Apiaceae), and Dipsacaceae-Valerianaceae in Dipsacales.

To summarize, even if most groups where the pollen is dispersed at the 3-cell stage have dry stigmas there are also groups with wet stigmas; on the other hand 2-celled pollen occur combined with both wet and dry stigmas. There is a trend among the dicotyledons, though not as strong as in the monocotyledons, towards the combinations dry stigma-3-celled pollen grains and wet stigma-2-celled pollen grains.

CONCLUSIONS

Some of the characters presented show distinct patterns of distribution and contribute useful information on phylogenetic relationships. This category includes unitegmic ovules, absence of a parietal cell and presence of endothelium, all of which have similar patterns; pollen grain dispersal and endosperm formation also belong here.

Sometimes with a certain combination of character states the exceptions are of greater interest phylogenetically. Distinct exceptions in at least five characters are found in Ceratophyllaceae when these are compared with other Nymphaeales, and they should perhaps be placed in Nelumbonales. For instance Hippuridales and Hydrostachyales in Lamianae have no endothelium in contrast to Lamiaceae. Hydrostachyales also differ from other Lamianae as regards embryogeny and Hippuridales differ as regards terminal endosperm haustoria (G. Dahlgren 1989). The position of these orders is still somewhat uncertain. Judged on these characters they seem to fit better in Cornanae; in others they agree well with Lamianae, for example in their chemical pattern (Jensen et al. 1975).

←

Fig. 26. Dry (dotted) and wet (hatched) stigma types.

For characters such as embryogeny, haustoria, storage compounds, chlorophyllous embryo, embryo size, seed coat, and stigma type the distribution pattern is less distinct. However, they can be of some help in clarifying relationships, often together with the results from morphological, anatomical and/or chemical investigations.

Only slight trends can be seen, e.g., in the pattern of polyembryony, persistence of endosperm, and rumination. Further studies are often necessary to reveal whether trends will be borne out. The occurrence of an obturator, a hypostase, antipodal cells, and arils is scattered in orders throughout the system and at first sight scarcely contributes any support as regards phylogenetic conclusions at higher taxonomic levels. However, there are orders or superorders in which some character states that are otherwise variable can nevertheless be used taxonomically. This importance can also be ascribed to characters classified in this category, e.g., antipodal cells and an obturator.

Finally, the position of the previously doubtful constellations of taxa in Geraniales-Linales-Rhizophorales-Celastrales receives support from the combination of embryological and other characters. Apart from the above examples of Ceratophyllaceae and Hippuridales-Hydrostachyales, there are some other taxa, whose position is still uncertain, for instance, Fouquieriales in Ericanae. Dahlgren et al. (1976) and Dahlgren (1983) point out that Fouquieriaceae resemble Ericales—and Cornales—in a number of respects, but in embryological features the family often differs from other Ericales and also from all other sympetalous groups. There still needs more study before Fouquieriales can be definitely placed. Thorne (1976) has treated Fouquieriaceae as a family in the order Solanales of his Malviflorae and Cronquist (1988) treats them as a family in Violales.

Further, Marcgraviaceae differ in some characters from other Theales. The delimitation of Cornales can perhaps be queried. It is a large paraphyletic order, in which the position of the Icacinaceae, Escalloniaceae, Alangiaceae, Garryaceae, and possibly other families is still uncertain.

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FOOTNOTE

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