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# FLESHY FRUITS IN LILIIFLOROUS MONOCOTS

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## ABSTRACT

Fleshy fruits occur in several monocot orders and families, and it is generally assumed that they have been derived from capsular fruits many times during the evolution of monocot lineages. Huber hypothesized in 1969 that most capsules in Asparagales are derived secondarily from berries and that this transformation was correlated with the evolution of phytomelan-coated seeds, a pivotal character in his circumscription of Asparagales as part of reclassifying Liliaceae s.l. Dahlgren and co-workers suggested several parallel derivations and "reversals" in this character, e.g., the transformation sequence trifollicular fruits → capsules → berries → capsules → berries. Mapping of fleshy fruits on a phylogeny based on molecular characters indicates that Asparagales do not have fleshy fruits as a basal character. Dahlgren's "cyclic character evolution" hypothesis is not supported by the distribution of dry and fleshy fruits, and there is no obvious correlation between baccate fruits and phytomelaniferous seeds in Asparagales. Phytomelaniferous seeds are not an evident synapomorphy of Asparagales as presently circumscribed. The anatomy and development of different capsular and baccate fruits in selected genera are studied in an ongoing project to reveal homologies and establish an adequate fruit typology. Some observations of texture and dehiscence structures in dry and fleshy capsules and in typical berries from hypogynous and epigynous flowers are reported in this paper.

Key words: Asparagales, berries, Dioscoreales, fleshy fruits, Liliales, Liliiflorae, monocotyledons, phylogeny, phytomelan.

## INTRODUCTION

Fruit characters have been given considerable attention in both classic and modern monocot taxonomy. Capsules have generally been considered the "basic" fruit type, from which berries, drupes, and caryopses or nuts have evolved (Dahlgren and Clifford 1982; Dahlgren et al. 1985). Derived fruits may characterize large groups at familial or ordinal level such as Arales (fleshy indehiscent fruits) or Poales (dry indehiscent fruits).

In the liliiflorous monocots (the families that in APG II [Angiosperm Phylogeny Group 2003] constitute Asparagales, Liliales, Dioscoreales, and Pandanales) the "typical" gynoecium is a three-carpellate superior ovary with axile placentation, a single style and several ovules, but degree of fusion and occurrence of nectaries varies, and epigyny occurs in several clades (Rudall 2002). Texture of the pericarp is another highly variable character, ranging from leathery capsules and soft-walled, partially or irregularly dehiscing fruits to typical berries. Presence of fleshy fruits has been an important distinguishing character for some traditional groupings at family rank (e.g., Smilacaceae, Convallariaceae, Luzuriagaceae, Philesiaceae), and several genera have occasionally been raised to family level with special reference to this trait (e.g., *Dianella, Behnia, Petermannia*). The occurrence and evolution of berries in Asparagales was given special attention by Huber and Dahlgren, who pioneered the modern research in monocot phylogeny (see below).

Information on ontogeny, anatomy, and mode of dehiscence or seed release of monocot fruits is, however, very scanty. Even the occurrence and variation of fruit types within some genera are not completely known. In an ongoing study we seek to provide basic information about the nature of fleshy monocot fruits in the broadest sense in order to test hypotheses about homology and evolution of this trait and possible correlation with other traits, e.g., seed characters. Structure and opening mechanisms of capsular fruits in polymorphic families and genera may be included to generate a broader perspective of character evolution.

### Cyclic Evolution of Fruit Types in Asparagales?

Huber (1969) was the first to recognize the asparagoid families as a division at ordinal level of the very broad Liliaceae sensu Engler (1892) and Krause (1930). Huber's rather informal orders were subdivided into "Familiengruppen," arranged in ascending order according to an assessment of evolutionary status (see also Huber 1977). The first "Familiengruppe" out of eight in Asparagales listed Rhipogonaceae, Smilacaceae, Philesiaceae (with *Lapageria*), Luzuriagaceae (including *Behnia*), Petermanniaceae, Ruscaceae, Convallariaceae, Nolinaceae, Asparagaceae, and Herreriaceae. This assemblage, which includes most of the berry-fruited families of Asparagales sensu Huber, was clearly positioned as "basal" in the order in his bubble diagram (Huber 1969: Fig. 35).

Dahlgren accepted Huber's arrangement of Asparagales throughout his classifications (Dahlgren 1975, 1980; G. Dahlgren 1989), although some of Huber's families were eventually transferred to other orders. The "Familiengrup-

pen" were not formalized, but are to some extend reflected in the sequence of families. Dahlgren and Clifford (1982: 219) noted about berries in monocotyledons: "Their distribution is not random but concentrated in certain orders . . . they abound amongst hygrophilous terrestrial plants growing in shady or semi-shady forests, such plants being especially concentrated in the Arales, Cyclanthales, and Taccales and in some genera of the Dioscoreales and in several families in the Asparagales" and, citing personal communication with Huber: "it is possible to interpret the capsules in most Asparagales (but not in the Liliales) as secondarily derived from berries. During the baccaceous stage of the fruit, the seeds lost their ordinary type of testa, which when the fruits became capsular again was substituted by a phytomelan crust." Dahlgren et al. (1985) stated no explicit hypothesis about the basal fruit type in Asparagales, but may have inferred from Huber that berries could be the ancestral fruit type of a monophyletic Asparagales. "A postulated evolutionary sequence of fruit types in the ancestors of Asparagales, in the Liliiflorae, represents an interesting cyclic process. [. . .] The capsules of many Asparagales might be secondary to berries, which are probably, in their turn, derived from capsules with phytomelan-coated seeds. If these surmises are true, the *Haemanthus* berry could have been derived via the sequence trifollicular fruits → capsules→ berries → capsules → berries!" (Dahlgren et al. 1985: 87). They assumed that changes from capsule to berry and from berry to capsule had taken place several times and suggested that a berry-fruited stage could have been an important historical constraint leading to the evolution of phytomelan in seed coats, the most distinctive character (but not synapomorphy!) of Asparagales as originally circumscribed.

## MATERIALS AND METHODS

The phylogeny used in the present investigation is based upon sequences from seven genes, two multicopy nuclear genes (18S and 26S rDNA [ribosomal DNA]), four plastid genes (*atp*B, *mat*K, *ndh*F, and *rbc*L), and a single mitochondrial gene (*atp*1), and is identical to the phylogeny presented by Chase et al. (2006). The analysis includes 141 taxa, 16 of which are dicot outgroups (Qui et al. 1999). The remaining 125 taxa are all monocots and placeholders for nearly all families recognized in the APG II (2003), except a few small families in Alismatales, which were not included. However, due to missing data, three families (Hydatellaceae and the achlorophyllous Corsiaceae and Triuridaceae) were also excluded from the final analysis. Detailed information about primers, accession data, GenBank accession numbers, etc. will be published elsewhere. The analyses were done in PAUP* vers. 4.0b10 (Swofford 2001). To avoid using extensive swapping on suboptimal tree islands, 500 random input replicates were used saving only 20 trees per replicate, using only SPR (subtree-pruning-regrafting) swapping. The trees found in this manner were subjected to TBR (tree-bisection-reconnection) swapping to find all trees. However, this did not yield further trees (length = 62,873; consistency index = 0.54; retention index = 0.48). The tree shown here (Fig. 1) is a simplified strict consensus tree of these trees. Branch support was calculated using bootstrapping, and the

values and a detailed discussion of the topology may be found in Chase et al. (2006).

The occurrence of fleshy fruits, including succulent but dehiscing capsules, as well as typical berries (in the sense of Roth 1977 and Judd 1985) was mapped on this phylogeny (Fig. 1) together with phytomelaniferous seeds, i.e., seeds with a phytomelan crust formed in the outer integument (Huber 1969; Danilova et al. 1995; Graven et al. 1998), and position of the ovary. A formal optimization procedure is not feasible at the family level; as most terminals are polymorphic for the characters mapped, this would leave most of the internal nodes with ambiguous states. Source data for the mapping (Appendix 1) are mainly obtained from Huber (1969), treatments in Kubitzki (1998a), and direct observations of live or conserved material.

The classification follows APG II (2003), but without the optional broad circumscriptions of Alliaceae, Asparagaceae, and Xanthorrhoeaceae in agreement with Pires et al. (2006) in order to facilitate comparison. Hesperocallidaceae are here included in Agavaceae. We have retained the APG II name "Asparagales," although it is antedated by Orchidales and Iridales. The liliiflorous monocots ("lilioid monocots" of Rudall 2002, 2003) are a grade comprising the orders Petrosaviales, Pandanales, Dioscoreales, Liliales, and Asparagales. The commelinid clade, which has been found to be sister to Asparagales (Chase et al. 1995a, b, 2000; APG II 2003), is usually not covered by this term, which largely corresponds to superorder Lilianae in Dahlgren and Clifford (1982) or Liliiflorae in Dahlgren et al. (1985) without most of Pandanales.

Observations on selected dry and fleshy liliiflorous fruits were made on material collected in nature or from living specimens in cultivation (Table 1). Standard histological techniques were applied according to Ruzin (1999). Fruits for sectioning in Paraplast® were fixed in FAA and 10 μm thick transverse sections were stained in Johansen's Safranin/Fast Green (S/FG). Fruits for sectioning in glycolmethacrylate were fixed in a mixture of 2% paraformaldehyde and 2.5% glutaraldehyde in 0.1 M phosphate buffer, and 3 μm thick transverse sections were stained in Toluidine Blue O (TB) or with the Periodic Acid Schiff reaction followed by Aniline Blue Black ("Amido Black") (PAS/ABB). Observations were concentrated on the upper part of the fruits. Microscopy images were digitized directly from the Leica DM RXA 2 microscope using a Hamamatsu C-2400 (ORCA II) camera.

## OBSERVATIONS

### Distribution of Fleshy Fruits and Phytomelaniferous Seeds

Fleshy fruits are found in 24 of the 39 liliiflorous (including Pandanales and Petrosaviales) terminals of the phylogeny (Fig. 1). Only five of these (all in Liliales) are not polymorphic. Fleshy fruits are found in all terminals of Liliales except Campynemataceae, and in all of these there are some species with typical berries. In Asparagales, fleshy fruits occur in half of the terminals, and only in seven out of these 12 are true berries recorded. Berries are formed in epigynous flowers in six terminals, scattered in three orders.

Phytomelaniferous seeds are recorded from 19 terminals, all in Asparagales. Records of occurrences outside Aspara-
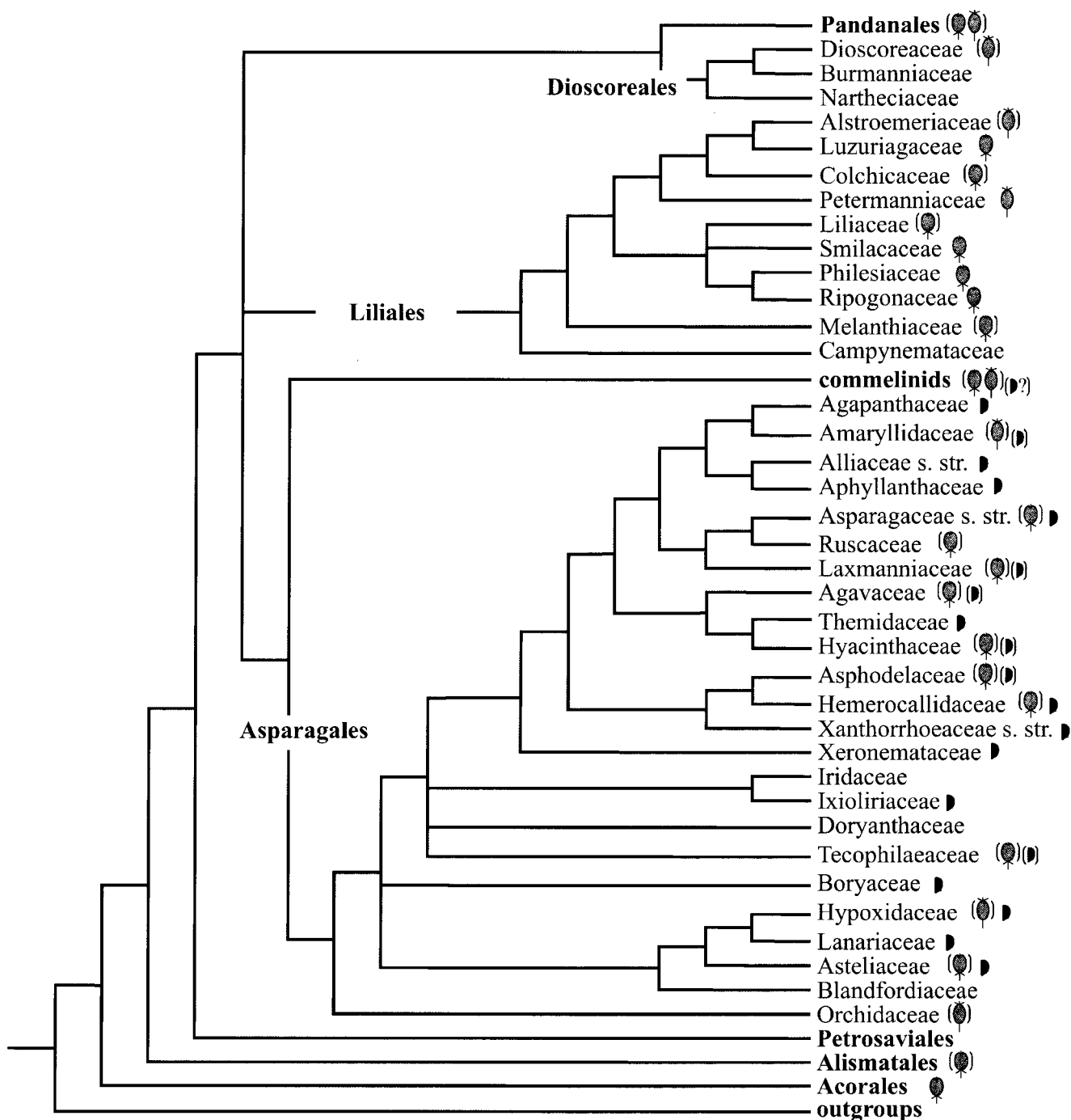
Fig. 1.—Mapping of fleshy fruits (berry symbol) with indication of ovary position (epigynous or hypogynous perianth remnants) and phytomelaniferous seeds (black seed symbol) on a phylogeny of liliiflorous monocots (simplified strict consensus of the trees found by Chase et al. 2006). Brackets indicate that a character is found in some but not all species of a terminal. Absence of fruit symbol indicates that fleshy fruits do not occur in this family. Absence of a seed symbol indicates that phytomelaniferous seeds do not occur or have not been detected in this family. See Appendix 1 for notes on occurrences.

gales, e.g., in Zingiberales, need verification. Six terminals are polymorphic for this character, and polymorphism exists also at the generic level, e.g., in *Leucojum* (Amaryllidaceae). Five of the 24 terminals of Asparagales do not have this trait.

Comparison of character distribution data from different sources is complicated by the fluctuating taxonomy of lili-iflorous monocots. Luzuriagaceae (Liliales) for example, are

always characterized by baccate fruits, but Huber (1969) and Dahlgren et al. (1985) referred this family to Asparagales and included genera here referred to as Agavaceae (*Behnia*), Laxmanniaceae (*Eustrephus*), and Hemerocallidaceae (*Gei-tonoplesium*). Appendix 1 of the present paper contains an annotated list of families with records of fleshy fruits appearing as terminals in Fig. 1, with notes on ovary position and phytomelaniferous seeds.

Table 1.  Material used in anatomical studies. * = Material cultivated in the botanical garden, University of Copenhagen. ** = Material from private gardens. Vouchers are kept at the Botanical Laboratory, University of Copenhagen.

| Species | Family | Collection no. | Origin |
|---|---|---|---|
| *Hyacinthoides non-scripta* (L.) Rothm. | Hyacinthaceae | C0874 | Cultivated ornamental** |
| *Ornithogalum narbonense* L. | Hyacinthaceae | C1432 | France* |
| *O. nutans* L. | Hyacinthaceae | C1415 | Cultivated ornamental* |
| *Maianthemum racemosum* (L.) Link<br>(= *Smilacina racemosa* [L.] Desf.) | Ruscaceae | C0469 | Wisconsin, USA |
| *Galanthus nivalis* L. | Amaryllidaceae | C0774 | Cultivated ornamental** |
| *Haemanthus albiflos* Jacq. | Amaryllidaceae | C0885 | Cultivated ornamental** |
| *Leucojum aestivum* L. | Amaryllidaceae | C1182 | Spain* |
| *Narcissus* cult. | Amaryllidaceae | C1215 | Cultivated ornamental** |

## Fruit Structure

The pericarp of all fruits studied here is composed of an outer (abaxial) epidermis, an inner (adaxial) epidermis, and between them the mesocarp, which consists of ground tissue, mostly parenchyma, and vascular tissue. In most of the species studied so far the outer epidermis has cells with rather thin primary walls having a thin cuticle. In hypogynous flowers the pericarp derives from the carpels only, while in epigynous flowers it may be construed as also including extracarpellary tissues. The fruits are three-carpellate, forming three separate loculi and a central column where the septa meet. Generally, five distinct vascular strands composed of one or more vascular bundles can be identified in each carpel. One single median (dorsal) strand in the middle of the carpel, two marginal (ventral) strands in the septum near or in the central column, and two lateral strands in the pericarp wall where two neighbor carpels fuse, forming the septum. Both the lateral and the marginal strands from neighboring carpels often fuse and form a single strand. Moreover, several more or less prominent vascular bundles can be observed. In epigynous flowers the vascularization is more complex and in *Galanthus nivalis* three vascular bundles are present at the median and lateral positions (Fig. 2). The two outer bundles of the median and the lateral strands continue into the outer tepal and stamen or the inner tepal and stamen, respectively. The inner vascular bundle of the median strand continues into the style while the corresponding bundle of the lateral strand diminishes and ends.

The dehiscing fruits in the taxa studied here are loculicidal and open distally. The carpel walls split through the median vascular bundles and in the central column where the septa meet, resulting in three valves with the placenta on a longitudinal rim in the middle (Fig. 3, 4). Some of the capsular fruits studied deviate from a typical capsule in having a fleshy mesocarp when dehiscing (Fig. 4), while berries are indehiscent with a fleshy mesocarp at maturity.

*Dry capsules.*—*Hyacinthoides non-scripta, Ornithogalum narbonense, Leucojum aestivum,* and *Narcissus* sp. represent taxa with dry capsules. In *Hyacinthoides* Fabr., the median bundle lies in a narrow zone of the pericarp and the xylem forms a wide V-shaped wedge with protoxylem at the base and two groups of metaxylem separated by parenchyma inside the "V." The phloem outside the metaxylem is also located in two groups separated by parenchyma (Fig. 5). At maturity the cells of the inner epidermis have thick, lignified outer cell walls except for a group of thin-walled, non-lignified cells, small in transection facing the median vascular bundle (Fig. 6). In *Ornithogalum narbonense* the xylem in the median vascular bundle forms a "V" with parenchyma in the wedge (Fig. 7) as in *Hyacinthoides.* Large, thin-walled sclerenchyma cells are present both outside the xylem towards the inner epidermis and outside the phloem towards the outer epidermis. The cells of the inner epidermis have lignified secondary cell walls with U-shaped thickenings (seen transversally, Fig. 7) like the cell walls of the inner epidermis in *Hyacinthoides,* but in *O. narbonense* also the small cells facing the median bundle have U-shaped thickenings. In *Narcissus* as in *O. narbonense* the inner epidermis has lignified and U-shaped secondary cell walls (Fig. 8, 9). In addition, below the inner epidermal cells inside the median vascular bundle is a lignified hypodermal layer in contact with the lignified bundle sheath cells outside the xylem part of the vascular bundle (Fig. 8).

With progressing dehydration at maturity the outer epidermis and the mesocarp shrink while most of the inner epidermal cells maintain their shape due to the thick, lignified cell walls, a fact important for the dehiscence process. In *Hyacinthoides* the small thin-walled cells in the inner epidermis rupture as do the parenchyma cells and the protoxylem, and the median vascular bundle breaks up along a median line with protoxylem and thin-walled parenchyma cells, splitting the phloem and the metaxylem in half (Fig. 6, 10). The final split of the carpels takes place in the outer epidermis where the cells form a slight indentation towards the vascular bundle. In *O. narbonense* the median vascular bundle breaks up as in *Hyacinthoides* and later the thin-walled sclerenchyma cells separate like the small inner epidermal cells with the U-shaped lignified wall (Fig. 11).

The central column in the mature capsule is separated into three parts where the septa meet. In *Leucojum* the inner epidermal cells have prominent U-shaped secondary cell walls, but they are replaced by smaller unlignified cells near the central column. The inner epidermis bursts here and the column splits more or less irregularly through the continuation of the stylar canal in this species (Fig. 12) as in *O. narbonense* and *Narcissus.* Groups of thin-walled sclerenchyma cells occur in the central column of the species studied.

*Fleshy capsules.*—The fruits of *Ornithogalum nutans* and *Galanthus nivalis* are succulent throughout their development and remain so even at dehiscence. The cells of the
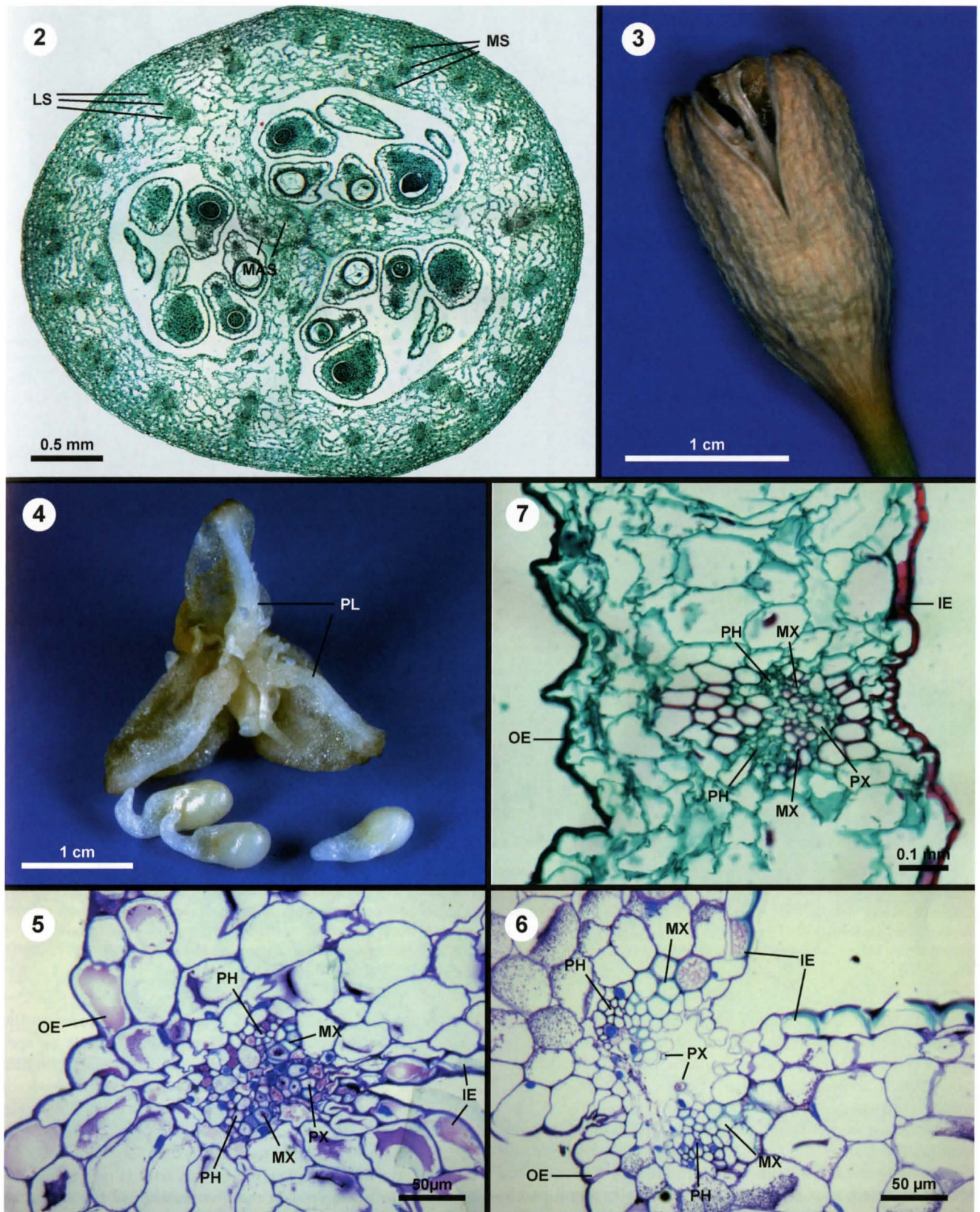
Fig. 2–7.—Dehiscence of fleshy and dry fruits of Amaryllidaceae and Hyacinthaceae.—2. Transverse sections through the upper part of young fruit from *Galanthus nivalis*.—3. Dry capsule from *Narcissus* cult.—4. Fleshy capsule from *Galanthus nivalis* and seeds with an apical hook-like elaiosome.—5–7. Transverse section through median vascular bundles of dry capsules at different ontogenetic stages.—5. Unripe capsule of *Hyacinthoides non-scripta* with thin-walled inner epidermis.—6. Dehiscing capsule of *Hyacinthoides non-scripta* splitting through the protoxylem and parenchyma cells.—7. Unripe capsule of *Ornithogalum narbonense*. (IE = inner epidermis; LS = lateral vascular strand; MAS = marginal vascular strand; MS = median vascular litrand; MX = metaxylem; OE = outer epidermis; PH = phloem; PL = placenta; PX = protoxylem. Staining: Fig. 2, 7 S/FG; Fig. 5–6 TB)
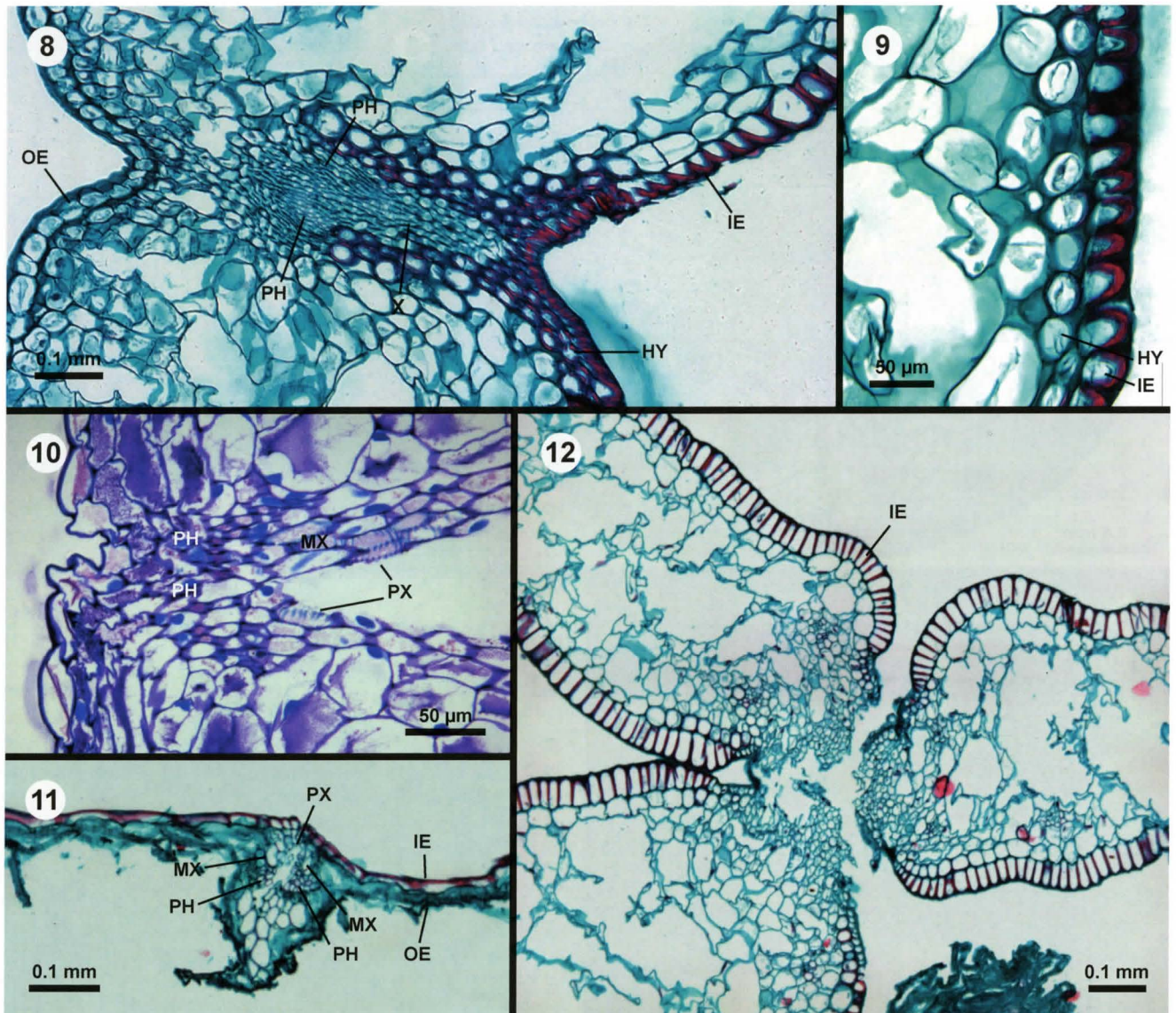
Fig. 8–12.—Transverse section through median vascular bundles and central column of dry capsules showing different stages of dehiscence.—8. *Narcissus* cult., median vascular bundle.—9. Details from *Narcissus* cult.—10. Oblique section of *Hyacinthoides non-scripta* median vascular bundle with schizogenous disruption of protoxylem.—11. Dehiscence in progress along the vascular bundle from *Ornithogalum narbonense.*—12. Division of the central column of a dry capsule from *Leucojum aestivum.* (IE = inner epidermis; HY = hypodermis; MX = metaxylem; OE = outer epidermis; PH = phloem; PX = protoxylem; X = xylem. Staining: Fig. 8–9, 11–12 S/FG; Fig. 10 TB)

inner epidermis in *O. nutans* have relatively thin and only slightly lignified, U-shaped secondary wall thickenings (Fig. 13), and as in *O. narbonense,* cells facing the median vascular bundle are lignified (Fig. 14). The thick, mature mesocarp consists of large, vacuolated cells except for some thin-walled sclerenchyma cells abutting the median vascular bundle in a narrow region of the pericarp. At dehiscence, the median vascular bundle, which has a very flat and wide V-shaped xylem area (Fig. 14), splits medially along parenchyma cells as in *Hyacinthoides* and *O. narbonense.* The central column has small groups of thin-walled sclerenchyma cells and splits as in *O. narbonense.*

In the median strand of *Galanthus* L. fruits the inner vascular bundle represents the carpel bundle. In this bundle the xylem forms a "V" as the metaxylem is divided by a row

of parenchyma cells (Fig. 15), it is thus very similar to the median vascular bundle seen in dry capsules, while no special structure was observed in the outer vascular bundles. The inner epidermis of the *Galanthus* pericarp consists of cells with primary walls only, the outer epidermis has thin primary cell walls with a distinct cuticle, and towards maturity the shrinking mesocarp cells and large intercellular spaces form the spongy tissue of this fruit (Fig. 16). At dehiscence the septa split in the continuation of the stylar canal.

*Typical berries.*—In the hypogynous *Maianthemum racemosum* and epigynous *Haemanthus albiflos* the inner epidermis has thin primary cell walls, the outer epidermis in both species has thicker cell walls and has a distinct, thin
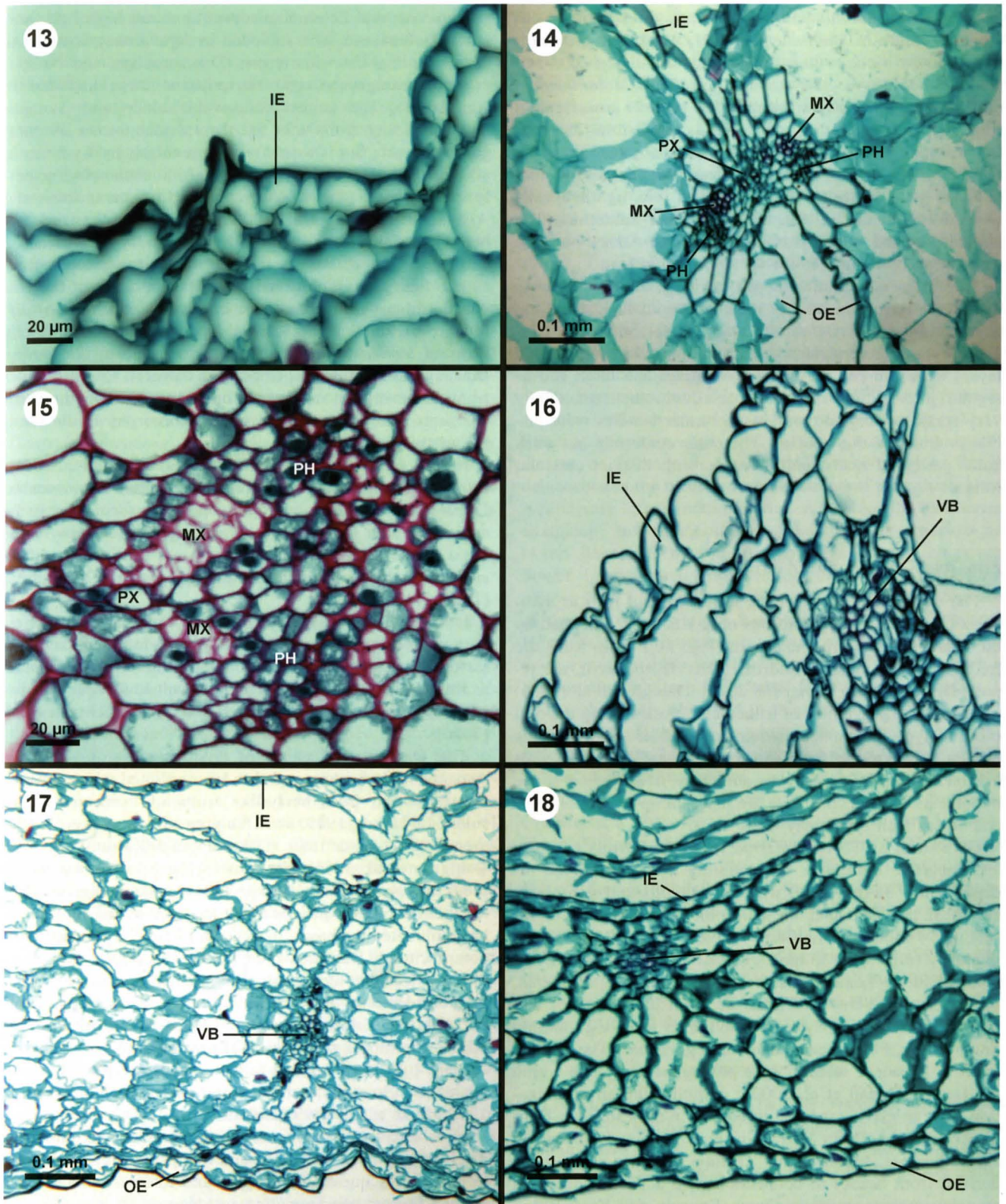
Fig. 13–18.—Transverse sections of fleshy capsules (13–16) and immature berries (17–18).—13. Inner epidermis with rather thin, faintly lignified cell-wall thickenings from mature fruit of *Ornithogalum nutans*.—14. Median vascular bundle of *Ornithogalum nutans*.—15. Carpellary vascular bundle from the median strand of young fruit from *Galanthus nivalis*, inner epidermis to the left.—16. Thin-walled inner epidermis of ripe fruit from *Galanthus nivalis*.—17. *Haemanthus albiflos*, immature berry.—18. *Maianthemum racemosum*, immature berry. (IE = inner epidermis; MX = metaxylem; OE = outer epidermis; PH = phloem; PX = protoxylem; VB = vascular bundle. Staining: Fig. 13–14, 16–18 S/FG; Fig. 15 PAS/ABB)

cuticle in *Haemanthus* and a moderately thick cuticle with cuticular ridges in *Maianthemum* F. H. Wigg. The mesocarp is composed of large thin-walled and vacuolated cells and small, rather few vascular strands (Fig. 17). In *Maianthemum* only the median vascular bundles are seen in cross section (Fig. 18); in *Haemanthus* more strands are visible. The central column consists of homogenous parenchymatous tissue, in *Maianthemum* with small lateral vascular bundles, in *Haemanthus* with relatively larger bundles. No lignified cells were observed in the mesocarp and inner epidermis. The structure of the pericarp of *M. racemosum* resembles the description by Kraus (1949) for *M. bifolium* L.

The range of variation in the pericarp of the berries is insufficiently known at this stage of the investigation, but observations on *Paris quadrifolia* L. (Melanthiaceae, Liliales) revealed a very thin pericarp composed of regular cell layers with thin cell walls, large vacuoles and large and irregular intercellular spaces, especially in the septa. Only very small median and marginal vascular bundles were visible in fruits of this species. The outer epidermis has thick outer periclinal walls and a cuticle with distinct cuticular ridges.

## DISCUSSION

### Fruit and Seed Character Phylogeny

The traditional notion of the dry dehiscent fruit as symplesiomorphic in the liliiflorous orders is not manifested by the character map presented here (Fig. 1). Fleshy fruits are frequent in Alismatales, and the fruits of *Acorus* L. are reportedly berry-like (Thompson 2000). Dahlgren et al. (1985) discussed the possibility of trilocular capsules being the oldest fruit type in monocotyledons as a whole. However, the chosen outgroups in phylogenetic analyses of all monocots exhibit a range of fruit types and there is as yet no stable hypothesis of what constitute the sister group to all monocots and which fruit types may occur in it.

Givnish et al. (2006) inferred that fleshy fruits (using a less inclusive definition, not counting *Acorus*) evolved independently 21 times and were lost 11 times in an optimization of this character on a tree of 282 exemplars representing 74 monocot families.

Fleshy fruits seem to have evolved at least twice in Dioscoreales in the family Dioscoreaceae (Caddick et al. 2002a, b). In Liliales, berry-like fruits occur in most families and may be a synapomorphy above the family level, e.g., uniting Smilacaceae, Philesiaceae, and Rhipogonaceae. The baccate fruits of Liliaceae seem to arise phylogenetically late within the family (Rudall et al. 2000b) complicating an optimization with an early transition to berries in the Liliaceae–Smilacaceae clade. Berry-like fruits may be plesiomorphic in Melanthiaceae. In the genus *Trillium* capsules seem to be derived from berries in connection with a shift in dispersal strategy towards myrmecochory (Kawano and Kato 1995). The latter is one of the few possible cases of "secondary capsules" as envisioned by Dahlgren et al. (1985).

It is clear from the phylogeny shown in Fig. 1 that Asparagales as now understood are not derived from a group of plants with baccate fruits. The basic asparagalean families of Huber (1969) and Dahlgren et al. (1985) are now referred to Liliales (Rhipogonaceae, Smilacaceae, Philesiaceae–Lu-

zuriagaceae, and Petermanniaceae) or to the higher Asparagales (Behniaceae, here included in Agavaceae), Ruscaceae s.l. (including Convallariaceae, Dracaenaceae, and Nolinaceae), Asparagaceae, and Herreriaceae (here included in Agavaceae). The largest conceivable clade with synapomorphic fleshy fruits may be the Laxmanniaceae–Asparagaceae branch, but it would require reversals to dry fruits in all three families. In a morphological-molecular phylogenetic analysis of 26 genera of Ruscaceae s.l., Asparagaceae, and Agavaceae (Rudall et al. 2000a) it was hypothesized that berry-like fruits have evolved independently in Ruscaceae and Asparagaceae, the dry fruits of the *Nolina*-group in Ruscaceae being a symplesiomorphy. The topology of the tree with terminals from Ruscaceae in Givnish et al. (2006) differs from Rudall et al. (2000a) and suggests that the dry fruits of *Nolina* Michx. may be apomorphic in the family. Densely sampled phylogenies with several representatives from all genera are needed to form plausible hypotheses of character polarity and levels of synapomorphy in the families of this order.

Berries or berry-like fruits are formed in epigynous flowers in six families scattered in the three orders Dioscoreales, Liliales, and Asparagales. Ovary position seems not to be correlated with fruit texture, which mainly develops in the latest of the three developmental phases (initiation—differential growth—tissue differentiation) recognized by Endress (1994).

It is assumed that fleshy fruits, in particular true berries, may evolve as an adaptation to hygrophilous habitats such as forest understory. Correlation with other characters, such as rhizomatous growth habit and net-veined leaves, was discussed by Patterson and Givnish (2002) and Givnish et al. (2006).

The frequent occurrence of phytomelaniferous seeds in Asparagales was conjectured to be associated with character transformation from berry-like fruits to "secondary capsules" by Huber (1969) and Dahlgren and co-workers (Dahlgren and Clifford 1982; Dahlgren and Rasmussen 1983; Dahlgren et al. 1985), the crust being a protection of the seeds not needed in a berry. The change in the view of monocot evolution generated by analyses of molecular data has eliminated the basal "baccaceous stage" of Huber (pers. comm. cited in Dahlgren and Clifford 1982: 220), which was the basis for this hypothesis. Phytomelaniferous seeds were not considered a synapomorphy of all Asparagales by Huber, but with the exclusion of some of Huber's families from the order it became a possible basal trait in Dahlgren's classifications. It is often implied to be a synapomorphy of Asparagales in systematic textbooks and surveys (Kubitzki et al. 1998; Judd et al. 1999; Bremer et al. 2003). However, a comprehensive reconstruction of the evolution of this character has not been attempted and this paper may be the first to address the question. Dahlgren and Rasmussen (1983) refrained from a diagrammatic consideration of character evolution of the "Asparagales complex" because of uncertainty about the monophyly of the families and the excessive homoplasy that would have to be accepted in any hypothesis.

Phytomelaniferous seeds are not a likely synapomorphy of Asparagales in the present phylogeny if Orchidaceae are included in the order. Even if Orchidaceae are excluded, this character will be highly homoplastic. Meerow et al. (1999)

regarded phytomelan-crusted seeds as an ancestral state of Asparagales and inferred that this trait has been lost five times in Amaryllidaceae. It seems very difficult to estimate the extent of synapomorphy of this trait considering the present uncertainty about the basal branching of Asparagales and the still incomplete knowledge of phylogeny within many families. Phytomelan-crusted seeds are a frequent and distinctive character of Asparagales, but it should not be emphasized as an indisputable synapomorphy of the entire order.

Confirming the occurrence of phytomelaniferous seeds requires anatomical studies of different ontogenetic stages, and the information concerning distribution of this character comes mostly from the comprehensive survey by Huber (1969). Observations of crustose dark seeds in families where phytomelaniferous seeds have not been recorded should be investigated carefully. The only detailed investigation of the formation and chemistry of phytomelan in Asparagales using modern analytical tools are the studies of *Gasteria verrucosa* (Mill.) H. Duval (Asphodelaceae) by Wittich and Graven (1995, 1998) and Graven et al. (1998). A more thorough understanding of this trait and if possible recognition of more states than just presence or absence is highly desirable.

### Evolution of Fruit Structure

Whether dry or fleshy, or evolved from hypogynous or epigynous flowers, the dehiscent fruits examined here are remarkably similar in details of the median vascular bundle in the carpel and the inner epidermis. They possess the V-shaped xylem with a middle strand of parenchyma cells, and the cells of the inner epidermis have lignified, U-shaped secondary cell walls except in *Galanthus*. These traits are supposed to play a role in the regular opening of the dry capsules. The inner epidermal cells facing the median vascular bundle vary slightly in wall thickness and the amount of lignification of the outer wall; a lignified hypodermis was observed in *Narcissus*. The parenchymatous strand through the V-shaped xylem wedge resembles the loculicidal dehiscence line in *Lilium* L. depicted by Roth (1977) and may be homologous.

Von Guttenberg (1971) observed lignification of the inner epidermis in several different lilioid genera and regarded this, in addition to the shape and orientation of the epidermal cells, to be part of the opening mechanism. Also Tilton and Horner (1983) mentioned thickened outer tangential cell walls of the inner epidermis in *Ornithogalum caudatum* Jacq. The rather complex vascularization of carpels and ovules in several liliiflorous fruits, especially in species of Melanthiaceae and Colchicaceae, was described in a series of papers by Sterling (1980 and papers cited therein), Utech and Kawano (1981), and Utech (1986 and papers cited therein), but information about structure of the median vascular strand, the inner epidermis, or other structural traits of relevance for opening mechanisms was not provided.

The fruits of species with fleshy capsules lie on the ground when ripe, the peduncle decays and the fruits are often completely detached at dehiscence. In *Ornithogalum nutans* the inner epidermis of the ripe fleshy capsule has distinct cell wall thickenings, although less pronounced than in species

with dry capsules, indicating an opening mechanism similar to the one in the dry capsules. However, *Galanthus nivalis* lacks cell wall thickenings in the inner epidermis and may dehisce in a different way. *Galanthus* capsules have been observed to open at high humidity (Buxbaum 1934; Frederiksen pers. obs.).

The fleshy, dehiscent fruits of *Ornithogalum nutans* and *Galanthus* are most likely derived from dry capsules similar to the ones found in other species of *Ornithogalum*, or in *Leucojum* and *Narcissus*, respectively. The seeds in *Galanthus* and some species of *Leucojum* have prominent elaiosomes. This and the procumbent nature of the fruits are no doubt adaptations to myrmecochory (Buxbaum 1934). In *Trillium* (Melanthiaceae) capsules are hypothesized to have evolved from typical berries in connection with a change from endozoochory to myrmecochory (Kawano and Kato 1995; Farmer and Schilling 2002).

The berries examined in this study differ mainly from the capsules in the extent of the mesocarp, and they do not have lignified secondary cell wall thickenings of the inner epidermis, or xylem with a preformed parenchymatous line of dehiscence in the median vascular strand of the carpel. There is relatively little structural variation between the two berries examined, and no significant difference was observed between berries formed in the hypogynous and epigynous flower. In preliminary observations of other liliiflorous berries we have found different ways of attaining the succulence of the fruits and various mechanisms for partial opening. However, it is still uncertain to what extent polarity of character evolution between dry or succulent and dehiscent or indehiscent fruits can be inferred from structural studies.

The characters observed in this study must be evaluated in a context of historical ecology. The history of fruits is a reflection of the history of changes in life strategy and invasion of ecological niches and may be expected to show certain correlations to or form patterns with other functional characters, a phenomenon referred to as concerted convergence (Givnish 1997; Givnish and Sytsma 1997; Patterson and Givnish 2002; Givnish et al. 2006) or iterative evolutionary themes (Rudall 2003). The importance of phylogenetic approaches to studies of plant reproductive systems has gained increasing recognition within the last decade (Endress 1994; Silverton et al. 1997; Weller and Sakai 1999), and it is expected that new insight in causes and directions of evolution can be obtained from integrated studies of phylogenetics, structural development, and ecology.

LITERATURE CITED

ANGIOSPERM PHYLOGENY GROUP [APG II]. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* **141**: 399–436.
BREMER, K., B. BREMER, AND M. THULIN. 2003. Introduction to phy-

logeny and systematics of flowering plants. *Symb. Bot. Upsal.* **33**: 1–102.

BUXBAUM, F. 1934. Familie Amaryllidaceae, Vol. 19, pp. 719–819. *In* O. von Kirchner, E. Loew, and C. Schröter [eds.], Lebensgeschichte der Blütenpflanzen Mitteleuropas, Vol. 1, sect. 3. Borntråger, Stuttgart, Germany.

CADDICK, L. R., P. WILKIN, P. J. RUDALL, T. A. J. HEDDERSON, AND M. W. CHASE. 2002a. Phylogenetics of Dioscoreales based on combined analyses of morphological and molecular data. *Bot. J. Linn. Soc.* **138**: 123–144.

———, ———, ———, AND ———. 2002b. Yams reclassified: a recircumscription of Dioscoreaceae and Dioscoreales. *Taxon* **51**: 103–114.

CAMERON, K. M., AND M. W. CHASE. 1998. Seed morphology of vanillioid orchids (Vanilloideae: Orchidaceae). *Lindleyana* **13**: 148–169.

CHASE, M. W., M. R. DUVALL, AND H. G. HILLS. 1995a. Molecular phylogenetics of Lilianae, pp. 109–137. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

———, M. F. FAY, D. S. DEVEY, O. MAURIN, N. RØNSTED, T. J. DAVIES, Y. PILLON, G. PETERSEN, O. SEBERG, M. N. TAMURA, C. B. ASMUSSEN, K. HILU, T. BORSCH, J. I DAVIS, D. W. STEVENSON, J. C. PIRES, T. J. GIVNISH, K. J. SYTSMA, M. A. MCPHERSON, S. W. GRAHAM, AND H. S. RAI. 2006. Multigene analysis of monocot relationships: a summary, pp. 63–75. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution (excluding Poales). Rancho Santa Ana Botanic Garden, Claremont, California, USA.

———, R. W. SPJUT, D. E. SOLTIS, P. S. SOLTIS, P. J. RUDALL, M. F. FAY, W. J. HAHN, S. SULLIVAN, W. S. JUDD, M. MOLVRAY, P. J. KORES, T. J. GIVNISH, K. J. SYTSMA, AND J. C. PIRES. 2000. Higher level systematics of the monocotyledons: an assessment of current knowledge and a new classification, pp. 3–16. *In* K. L. Wilson, and D. A. Morrison [eds.], Monocots: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

———, D. W. STEVENSON, P. WILKIN, AND P. J. RUDALL. 1995b. Monocot systematics: a combined analysis, pp. 685–730. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

CLIFFORD, H. T., R. F. J. HENDERSON, AND J. G. CONRAN. 1998. Hemerocallidaceae, pp. 245–251. *In* K. Kubitzki [ed.], The families and genera of vascular plants, Vol. 3. Monocotyledons: Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany.

CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York, USA. 1262 p.

DAHLGREN, G. 1989. An updated angiosperm classification. *Bot. J. Linn. Soc.* **100**: 197–203.

DAHLGREN, R. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. *Bot. Not.* **128**: 119–147.

———. 1980. A revised system of classification of the angiosperms. *Bot. J. Linn. Soc.* **82**: 91–124.

———, AND H. T. CLIFFORD. 1982. The monocotyledons: a comparative study. Academic Press, London, UK. 378 p.

———, ———, AND P. F. YEO. 1985. The families of the monocotyledons. Springer-Verlag, Berlin, Germany. 520 p.

———, AND F. N. RASMUSSEN. 1983. Monocotyledon evolution, characters and phylogenetic estimation. *Evol. Biol.* **16**: 255–395.

DANILOVA, M. F., E. N. NEMIROVICH-DANCHENKO, G. A. KOMAR, AND M. M. LODKINA. 1995. The seed structure of monocotyledons, pp. 461–472. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Humphries [eds.], Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

DRESSLER, R. L. 1993. Phylogeny and classification of the orchid family. Cambridge University Press, Cambridge, UK. 314 p.

DUYFJES, B. E. E. 1991. Stemonaceae and Pentastemonaceae; with miscellaneous notes on members of both families. *Blumea* **36**: 481–499.

ENDRESS, P. K. 1994. Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge, UK. 511 p.

ENGLER, A. 1892. Syllabus der Vorlesungen über spezielle und medizinisch-pharmaceutische Botanik. Borntråger, Berlin, Germany. 184 p.

FARMER, S. B., AND E. S. SCHILLING. 2002. Phylogenetic analyses of Trilliaceae based on morphological and molecular data. *Syst. Bot.* **27**: 674–692.

GIVNISH, T. J. 1997. Adaptive radiation and molecular systematics: issue and approaches, pp. 1–54. *In* T. J. Givnish and K. J. Sytsma [eds.], Molecular evolution and adaptive radiation. Cambridge University Press, New York, USA.

———, J. C. PIRES, S. W. GRAHAM, M. A. MCPHERSON, L. M. PRINCE, T. B. PATTERSON, H. S. RAI, E. H. ROALSON, T. M. EVANS, W. J. HAHN, K. C. MILLAM, A. W. MEEROW, M. MOLVRAY, P. J. KORES, H. E. O'BRIEN, J. C. HALL, W. J. KRESS, AND K. J. SYTSMA. 2006. Phylogenetic relationships of monocots based on the highly informative plastid gene *ndh*F: evidence for widespread concerted convergence, pp. 28–51. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution (excluding Poales). Rancho Santa Ana Botanic Garden, Claremont, California, USA.

———, AND K. J. SYTSMA. 1997. Consistency, characters, and the likelihood of correct phylogenetic inference. *Molec. Phylogen. Evol.* **7**: 320–330.

GRAVEN, P., P. E. WITTICH, F. BOUMAN, G. NACHTEGAL, AND A. P. M. KENTGENS. 1998. Characterization of phytomelan in the seed coat of *Gasteria verrucosa* (Mill.) H. Duval, pp. 121–147. *In* P. E. Wittich [ed.], Seed development and carbohydrates. Landbouniversiteit Wageningen, Wageningen, The Netherlands.

HUBER, H. 1969. Die Samenmerkmale und Verwandschaftsverhältnisse der Liliifloren. *Mitt. Bot. Staatssamml. München* **8**: 219–538.

———. 1977. The treatment of the monocotyledons in an evolutionary system of classification. *Pl. Syst. Evol.* **1**: 285–298.

JUDD, W. S. 1985. A revised traditional/descriptive classification of fruits for use in floristics and teaching. *Phytologia* **58**: 233–242.

———, C. S. CAMPBELL, E. A. KELLOG, AND P. F. STEVENS. 1999. Plant systematics: a phylogenetic approach. Sinauer Associates, Inc., Sunderland, Massachusetts, USA. 464 p.

KAWANO, S., AND H. KATO. 1995. Evolutionary biology of *Trillium* and related genera (Trilliaceae) II. Cladistic analyses on gross morphological characters, and phylogeny and evolution of the genus *Trillium*. *Pl. Spec. Biol.* **10**: 169–183.

KRAUS, G. 1949. Morphologisch-anatomische Untersuchung der entwicklungsbedingten Veränderungen an Achse, Blatt und Fruchtknoten bei einigen Beerenfrüchten. *Oesterr. Bot. Z.* **96**: 325–360.

KRAUSE, K. 1930. Liliaceae, pp. 227–386. *In* A. Engler [ed.], Die natürlichen Pflanzenfamilien, Vol. 15a. W. Engelmann, Leipzig, Germany.

KUBITZKI, K. 1998a. The families and genera of vascular plants, Vol. 3. Monocotyledons: Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany. 478 p.

———. 1998b. Pentastemonaceae, pp. 404–406. *In* K. Kubitzki [ed.], The families and genera of vascular plants, Vol. 3. Monocotyledons: Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany.

———, AND P. J. RUDALL. 1998. Asparagaceae, pp. 125–126. *In* K. Kubitzki [ed.], The families and genera of vascular plants, Vol. 3. Monocotyledons: Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany.

———, ———, AND M. C. CHASE. 1998. Systematics and evolution, pp. 23–33. *In* K. Kubitzki [ed.], The families and genera of

vascular plants, Vol. 3. Monocotyledons: Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany.

MEEROW, A. W., AND J. R. CLAYTON. 2004. Generic relationships among the baccate-fruited Amaryllidaceae (tribe Haemantheae) inferred from plastid and nuclear non-coding DNA sequences. *Pl. Syst. Evol.* **244**: 141–155.

————, M. F. FAY, L. G. CHARLES, L. QIN-BAO, F. QAMARUZ-ZAMAN, AND M. W. CHASE. 1999. Systematics of Amaryllidaceae based on cladistic analysis of plastid *rbc*L and *trn*L–F sequence data. *Amer. J. Bot.* **86**: 1325–1345.

NISHIMURA, G., AND M. TAMURA. 1993. Seed coat formation in *Apostasia nipponica. J. Jap. Bot.* **68**: 219–223.

NORDAL, I. 1998. Hypoxidaceae, pp. 286–295. *In* K. Kubitzki [ed.], The families and genera of vascular plants, Vol. 3. Monocotyledons: Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany.

PATTERSON, T. B., AND T. J. GIVNISH. 2002. Phylogeny, concerted convergence, and phylogenetic niche conservatism in the core Liliales: insights from *rbc*L and *ndh*F sequence data. *Evolution* **56**: 233–252.

PIRES, J. C., I. J. MAUREIRA, T. J. GIVNISH, K. J. SYTSMA, O. SEBERG, G. PETERSEN, J. I DAVIS, D. W. STEVENSON, P. J. RUDALL, M. F. FAY, AND M. W. CHASE. 2006. Phylogeny, genome size, and chromosome evolution of Asparagales, pp. 287–304. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution (excluding Poales). Rancho Santa Ana Botanic Garden, Claremont, California, USA.

QIU, Y.-L., J. LEE, F. BERNASCONI-QUADRONI, D. E. SOLTIS, M. ZANIS, Z. CHEN, V. SAVOLAINEN, AND M. CHASE. 1999. The earliest angiosperms: evidence from mitochondrial, plastid and nuclear genomes. *Nature* **402**: 404–407.

ROTH, I. 1977. Fruits of angiosperms. Bornträger, Berlin, Germany. 675 p.

RÜBSAMEN, T. 1986. Morphologische, embryologische und systematische Untersuchungen an Burmanniaceae und Corsiaceae (Mit Ausblick auf die Orchidaceae–Apostasioideae). Cramer, Berlin, Germany. 512 p.

RUDALL, P. J. 2002. Homologies of inferior ovaries and septal nectaries in monocotyledons. *Int. J. Pl. Sci.* **163**: 261–276.

————. 2003. Unique floral structures and iterative evolutionary themes in Asparagales: insights from a morphological cladistic analysis. *Bot. Rev. (Lancaster)* **68**: 488–509.

————, M. W. CHASE, D. F. CUTLER, J. RUSBY, AND A. DE BRUIJN. 1998. Anatomical and molecular systematics of Asteliaeae and Hypoxidaceae. *Bot. J. Linn. Soc.* **127**: 1–42.

————, J. G. CONRAN, AND M. W. CHASE. 2000a. Systematics of Ruscaceae/Convallariaceae: a combined morphological and molecular investigation. *Bot. J. Linn. Soc.* **134**: 73–92.

————, AND D. F. CUTLER. 1995. Asparagales: a reappraisal, pp. 157–168. *In* P. J. Rudall, P. J. Cribb, D. F. Cutler, and C. J. Hum-

phries [eds.], Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.

————, K. L. STOBART, W.-P. HONG, J. G. CONRAN, C. A. FURNESS, G. C. KITE, AND M. W. CHASE. 2000b. Consider the lilies: systematics of Liliales, pp. 347–359. *In* K. L. Wilson, and D. A. Morrison [eds.], Monocots: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

RUZIN, S. E. 1999. Plant microtechnique and microscopy. Oxford University Press, New York, USA. 322 p.

SILVERTON, J., M. FRANCO, AND J. L. HARPER (editors). 1997. Plant life histories: ecology, phylogeny and evolution. Cambridge University Press, Cambridge, UK. 313 p.

SIMPSON, M. G., AND P. J. RUDALL. 1998. Tecophileacae, pp. 429–436. *In* K. Kubitzki [ed.], The families and genera of vascular plants, Vol. 3. Monocotyledons: Lilianae (except Orchidaceae). Springer-Verlag, Berlin, Germany.

STERLING, C. 1980. Comparative morphology of the carpel in the Liliaceae: Helonieae. *Bot. J. Linn. Soc.* **80**: 341–356.

STEVENS, P. F. 2001 onwards. Angiosperm Phylogeny Website, vers. 3. *http://www.mobot.org/MOBOT/research/APweb/* (Mar 2005).

SWAMY, B. G. L. 1947. On the life history of *Vanilla planifolia. Bot. Gaz.* **108**: 449–455.

SWOFFORD, D. 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods), vers. 4.0b10. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

THOMPSON, S. A. 2000. Acoraceae, pp. 124–127. *In* Flora of North America Editorial Committee [eds.], Flora of North America north of Mexico, Vol. 22. Magnoliophyta: Alismatidae, Arecidae, Commelinidae (in part), and Zingiberidae. Oxford Press, New York, USA.

TILTON, V. R., AND H. T. HORNER. 1983. Carpel development, anatomy, and function in the reproductive process in *Ornithogalum caudatum* (Liliaceae). *Flora Morphol. Geobot. Oekophys.* **173**: 1–31.

UTECH, F. H. 1986. Floral morphology and vascular anatomy of *Amianthium muscaetoxicum* (Walter) A. Gray (Liliaceae, Veratreae) with notes on distribution and taxonomy. *Ann. Carnegie Mus.* **55**: 481–504.

————, AND S. KAWANO. 1981. Vascular floral anatomy of the East Asian *Heloniopsis orientalis* (Thunb.) C. Tanaka (Liliaceae–Helonieae). *Bot. Mag. (Tokyo)* **94**: 295–311.

VON GUTTENBERG, H. 1971. Bewegungsorgane und Perzeptionsorgane. Bornträger, Stuttgart, Germany. 332 p.

WELLER, S. G., AND A. K. SAKAI. 1999. Using phylogenetic approaches for the analysis of plant breeding system evolution. *Ann. Rev. Ecol. Syst.* **30**: 167–199.

WITTICH, P. E., AND P. GRAVEN. 1995. Histochemical study of the development of the phyotomelan layer in the seed coat of *Gasteria verrucosa* (Mill.) H. Duval. *Protoplasma* **187**: 72–78.

————, AND ————. 1998. Callose deposition and breakdown, followed by phytomelan synthesis in the seed coat of *Gasteria verrucosa* (Mill.) H. Duval. *Protoplasma* **201**: 221–230.

Appendix 1.   Annotated list of families with records of fleshy fruits appearing as terminals in Fig. 1. Ovary position and occurrence of phytomelaniferous seeds are noted. The estimated number of species in the genera is shown in parentheses.

## PANDANALES

PANDANACEAE and CYCLANTHACEAE (epigynous, hypogynous, or pistillate flowers without perianth): not "liliiflorous" in traditional classifications, but associated with palms. However, floral similarities with Dioscoreales, especially Stemonaceae, were pointed out already by Dahlgren et al. (1985), and they have been placed basally in Liliiflorae in analyses of molecular data (Chase et al. 1995a, b, 2005; Caddick et al. 2002a). The fruits of Pandanaceae and Cyclanthaceae are generally fleshy drupes or berries.

STEMONACEAE (hypogynous or semi-epigynous): Stemona Lour. (25) have thin-walled capsules, sometimes described as berry-like, but this may be caused by juicy seed hairs. The fruits of Pentastemona Steenis (2) are described as berries (Kubitzki 1998b; Duyfjes 1991).

## DIOSCOREALES

DIOSCOREACEAE (epigynous): fruits with varying degrees of fleshiness occur in some species of Dioscorea L. (600) according to Caddick et al. (2002a). One or two species traditionally classified as Tamus L. have indisputable berries. Trichopus Gaertn. (2, including Avetra H. Perrier) have irregularly dehiscing fleshy fruits. Tacca J. R. Forst. & G. Forst. (10) has fruits ranging from dry to fleshy capsules and true indehiscent berries.

## LILIALES

ALSTROEMERIACEAE (epigynous): some species of Bomarea Mirb. (100) have berries; other are reported to have fleshy capsules. Some species of Alstroemeria L. have dry indehiscent capsule-like fruits.

LUZURIAGACEAE (hypogynous): both genera (Drymophila R. Br. [2] and Luzuriaga Ruiz & Pav. [3]) have typical berries. The indication of phytomelan in the seeds of Luzuriaga by Rudall and Cutler (1995) has not been confirmed.

COLCHICACEAE (hypogynous): Disporum Salisb. ex D. Don (10) has berries. Fleshy, dehiscent fruits are observed in Schelhammera R. Br. (2), Tripladenia D. Don (1), and Kuntheria J. G. Conran & H. T. Clifford (1).

PETTERMANNIACEAE (epigynous): this family has been associated with or included in bacciferous families of the Liliaceae clade, and has also been included in Colchicaceae (Stevens 2001). The fruit of Petermannia Klotzsch (1) is a typical berry.

LILIACEAE (hypogynous): Medeola L. (1) and Clintonia Dougl. ex Lindl. (5) have berries, their subfamily Medeoloideae is embedded within the family (Rudall et al. 2000b). The bacciferous genera Streptopus Michx. (2) and Prosartes D. Don (6) have been included in Disporum of Colchicaceae, and may be referred to Calochortaceae, if that family is distinguished from Liliaceae.

SMILACACEAE (hypogynous): this family has earlier been used to accommodate a number of bacciferous genera (Cronquist 1981), but has been much narrowed in recent classifications, although it often includes the following two families. In accordance with APG II (2003) it is here reduced to just Smilax L. s.l. (310). All species have berries.

PHILESIACEAE (hypogynous): both genera, Philesia Comm. ex Juss. (1) and Lapageria Ruiz & Pav. (1) have typical berries.

RHIPOGONACEAE (hypogynous): all species in Rhipogonum J. R. Forst & G. Forst. (6) have berries.

MELANTHIACEAE (hypogynous): the circumscription and contents of this family have varied considerably: Trilliaceae were included by Chase et al. (2000) and in APG II (2003). Fleshy or berry-like fruits are found in Paris L. (5), Kinugasa Tatewaki & Suto (1), and Trillium L. (50) subgen. Trillium (Kawano and Kato 1995).

## ASPARAGALES

AMARYLLIDACEAE (epigynous): analyses by Meerow et al. (1999) and Meerow and Clayton (2004) indicated berries as a synapomorphy of the branch Haemantheae–Calostemmateae. Indehiscent fleshy fruits are found in Apodolirion Baker (6), Gethyllis Plum. ex L. (32), Haemanthus L. (22), Scadoxus Raf. (9), Cryptostephanus Welw. ex Baker (5), and Clivia Lindl. (4). The berries of Gethyllis and Apodolirion deviate in being oblong with numerous small, hard seeds. Species of Calostemma R. Br. (2) have capsule-like fruits that may be secondary. More or less fleshy, but eventually dehiscent fruits are found in several genera, e.g., Sternbergia Waldst. & Kit. (8), Galanthus L. (17), and Leucojum L. (10). At least some species of Crinum L. (60) of tribe Amaryllideae have fleshy fruits. However, based on the phylogeny by Meerow and co-workers, dry and dehiscent fruits are most likely the plesiomorphic condition of the family.

Phytomelaniferous seeds are found in several genera and were considered plesiomorphic by Meerow et al. (1999). However, in the bacciferous tribe Haemantheae, the only occurrence is in terminal genus Cryptostephanus (Meerow and Clayton 2004). Huber (1969) reported a thin phytomelan crust in the outer integument of Leucojum and Galanthus and regarded this as a step towards complete loss. We have not seen this layer in material of Galanthus nivalis L.

ASPARAGACEAE (hypogynous): all species of Asparagus L. (ca. 200) have typical berries, but the much deviating North American genus Hemiphylacus S. Watson (5) has capsular fruits. Phytomelan seems to be present in the seeds of all species, but the position and amount vary (Kubitzki and Rudall 1998).

RUSCACEAE (hypogynous): in the broad sense adopted by Rudall et al. (2000a) and APG II (2003) this family includes former Ruscaceae s.s., Convallariaceae, and Dracaenaceae, which contains ca. 450 species. They all have more or less fleshy fruits, most of them typical berries, but drupes and dehiscent fleshy fruits are reported from some genera. Comospermum S. Rauschert (2, earlier in Anthericaceae), and Eriospermum Jacq. (100, earlier in Eriospermaceae), and "nolinoids" (ca. 50, earlier Nolinaceae) have generally dry dehiscing fruits, but detailed information on fruits of these plants is sparse. Phytomelan-crusted seeds are not found in any genus of Ruscaceae s.l.

LAXMANNIACEAE (hypogynous): this family is very diverse in all aspects, and its position in phylogenies, where it is represented by one or two genera, should be interpreted with much caution. In Givnish et al. (2006) this family is circumscribed differently and indicated as clearly polyphyletic. Fleshy capsules and berries may occur in Cordyline Comm. ex R. Br (20), but data on fruit details are inadequate. Eustrephus R. Br. (1) has reportedly berry-like capsules. The seeds in this family are also very variable. Several genera have seeds with a phytomelan crust; the genera with non-phytomelaniferous seeds all have capsular fruits.

AGAVACEAE (hypogynous [all fleshy-fruited genera], epigynous): Behnia F. Didrichs. (1), with typical berries and non-phytomelaniferous seeds, is included here in APG II (2003). Fleshy berry-like fruits are found in some spp. of Yucca L. (40). The seeds of most Agavaceae have a phytomelan crust.

Appendix 1.   Continued.

HYACINTHACEAE (hypogynous, semi-epigynous [*Bowiea* Haw.]): the fruits are generally capsular. Some capsules have a very fleshy pericarp, e.g., in *Fessia* Speta (10) and *Pfosseria* Speta (1). Both dry and fleshy capsules occur in *Ornithogalum* L. (ca. 50). The seeds often have a thin phytomelan crust, but some have no phytomelan. Seed data are missing for many genera.

ASPHODELACEAE (hypogynous): the fruits of several genera are leathery, in *Lomatophyllum* Willd. (14) they are described as dehiscent berries. The seeds are variously colored, some are distinctly phytomelaniferous (e.g., *Gasteria* Willd.)

HEMEROCALLIDACEAE (hypogynous, semi-epigynous): *Geitonoplesium* A. Cunn. (1), *Dianella* Lam. (20), *Rhuacophila* Blume (1) have true berries. The fruit of *Simethis* Kunth (1) is capsular according to Clifford et al. (1998) but scored as berry by Rudall (2003). The seeds have a phytomelaniferous coat.

TECOPHILAEACEAE (hypogynous, semi-epigynous): fruits of *Walleria* J. Kirk (3) and *Conanthera* Ruiz & Pav. (5) may be berry-like; the seeds are not phytomelaniferous (Simpson and Rudall 1998; Rudall et al. 1998). The seed structure is highly variable. *Kabuyea* Brummitt (1) and *Cyanastrum* Cass. (3) are scored as non-phytomelaniferous by Rudall (2003); *Cyanella* L. (3) contains a thin phytomelan crust according to Simpson and Rudall (1998), but Huber (1969) does not mention phytomelan explicitly in his description. More observations are needed.

ASTELIACEAE (hypogynous): *Astelia* Banks & Sol. ex R. Br. (25), *Neoastelia* J. B. Williams (1), and *Collospermum* Skottsb. (4) have typical berries, while *Milligania* Hook. f. (5) has capsular fruits. The seeds of all genera seem to have a thick phytomelan crust. The bacciferous genus *Cordyline* was placed in Asteliaceae by Dahlgren et al. (1985), but is now referred to Laxmanniaceae.

HYPOXIDACEAE (epigynous): the fruits in *Hypoxis* L. (50) are septicidal capsules or pyxides. Species in some of the smaller genera have irregularly dehiscing thin-walled fruits, which may be berry-like and some of these are subterranean. *Empodium* Salisb. (10), *Curculigo* Gaertn. (10), *Molineria* Colla (7), and *Hypoxidia* F. Friedmann (2) are reported to have more or less typical berries (Nordal 1998; Rudall et al. 1998; Rudall 2003). The seeds have a thick phytomelan crust.

ORCHIDACEAE (epigynous): the vast majority of orchids have capsular fruits, but true berries, as well as typical orchidaceous three-valved capsules, are found in the basal genus *Neuwiedia* Blume (8). Subfamily Vanilloideae shows several examples of more or less baccate fruits, most notably *Vanilla* Miller (107) and *Cyrtosia* Blume (7), which have large red berries. *Palmorchis* Barb. Rodr. (12) of the basal tribe Neottieae, in the higher subfamily Epidendroideae, have berry-like fruits thought to be eaten by birds (Dressler 1993).

A phytomelan crust has not been found in orchid seeds. The black-crusted seeds found in *Apostasia* Blume and *Neuwiedia* were examined in detail by Rübsamen (1986) who found that the crust is formed from the innermost cell layer of the outer integument, confirmed by Nishimura and Tamura (1993). They are thus not directly comparable to phytomelanous seeds as used by Huber (1969). The thick dark-brown crust in seeds of *Vanilla* is derived from the outer layer of outer integument (Swamy 1947) or both integuments (Cameron and Chase 1998), but the dark deposits are not phytomelan (Graven pers. comm.). The dark seeds observed in some species of *Selenipedium* Rchb. f. and *Palmorchis* seem not to have been studied anatomically.