Superorder Liliiflorae

Five Orders: Dioscoreales, Asparagales, Melanthiales, Burmanniales and Liliales.

This superorder is extraordinarily variable and contains some groups which, in our estimation, are likely to have retained many features from the ancestral monocotyledons. The wide range of variation makes a definition difficult and in an evolutionary sense this unit is undoubtedly paraphyletic rather than monophyletic. Some of its orders, on the other hand, we presume to be monophyletic.

The Liliiflorae are annual to perennial plants only rarely aquatic, but ranging from small herbs to shrubs or trees of considerable size and occasionally having a thick, tall trunk. Most families consist of terrestrial plants, but Orchidaceae is rich in epiphytes. This and some other families consist largely of mycorrhizal plants. Achlorophyllous taxa occur in several families, but are otherwise found only in Triuridiflorae.

The roots appear opposite xylem strands only. Except in some orchids the root hair cells are the same size as the other epidermal cells. Several-layered velamen is common in several of the groups, a feature otherwise known, among the monocotyledons, only in Ariflorae. Vessels are probably almost constantly present in the roots, where they often have scalariform perforation plates, although simple or simple as well as scalariform perforation plates occur in a great many families of Asparagales and Liliales.

The underground stem is frequently developed as a rhizome, but in many groups as a corm or tuber, which – except in the Ariflorae – is very rare in monocotyledons. Bulbs, i.e. a short, generally underground stem with fleshy leaves, occur in several families of this superorder but very rarely in others.

The aerial stem varies from slender and herbaceous, often twining, to slender and woody or thick and woody, and this is the only superorder among the monocotyledons where secondary thickening growth occurs (of the Monocotyledonous Type; see p. 9). Rarely the stem is provided with spines or prickles (*Petermannia*, species of *Smilax* and *Herreria*), and the branchlets may be flat and developed as phyllocladia (Ruscaceae, some Asparagaceae), which is never the case in other monocotyledons. Branching is monopodial or sympodial. Laticifers are rarely present (in some Alliaceae). Vessels are often lacking in the underground as well as aerial stem; where present they are nearly always provided with scalariform perforation plates. Hairs of various kinds occur; these and the stomatal complexes are mentioned in connection with the leaves.

The leaves vary much in their position and differentiation. They may be developed as simple cataphylls, they may be linear, with a sheathing base, or they may have a non-sheathing base, a distinct petiole and a broad leaf lamina, the latter type of leaf being more or less reminiscent of that in most dicotyledonous leaves. Rarely, the leaves are opposite or verticillate, which among the monocotyledons is otherwise the case only in some Alismatiflorae. Petiolate leaves in some families have a lobate or truly compound lamina, the latter being otherwise only known in Ariflorae among the monocotyledons. Where the leaves are distichous and linear they may be laterally compressed and ensiform, as in most Iridaceae. In some families the lamina is inverted basally, so that the morphological upper side faces downwards. The ptyxis is highly variable but generally supervolute, conduplicate or flat. Stipules are lacking or atypical. Tendrils from the leaf base occur in most Smilacaceae. Ligules are very rare. The venation in linear leaves is parallel, while in petiolate leaves with a broad lamina the main veins are separate from the base of the lamina and converge at the apex. In several families there is reticulate venation intercalated between the main veins, which in monocotyledons is otherwise the case only in (numerous) Ariflorae and (a few) Alismatiflorae. The stomata are parallel or rarely (Smilacaceae) randomly oriented in relation to the leaf axis. The stomatal complexes are agenous or perigenous (very rarely mesogenous, e.g. in some orchids) in the ontogenetic sense and become anomocytic or more rarely paracytic (very rarely tetracytic) when mature (note that there is *not* strict correlation between ontogenetic type and type of mature stomatal complex). Trichomes are very variable, being unicellular, uniseriate, tufted or otherwise, but often almost lacking. Intravaginal squamules are lacking. Epicuticular wax is unsculptured, irregularly sculptured or sculptured according to the *Convallaria* Type, never of the *Strelitzia* Type. Raphides are commonly present, except in a great part of Liliales and Burmanniales. Silica bodies are re-

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stricted to certain taxa in Apostasiaceae, Cypripediaceae and Orchidaceae. Vessels are generally absent in the leaves.

The inflorescences include both determinate and indeterminate kinds (see further under orders and families). The flowers are mostly trimerous but dimerous in some Dioscoreales, rarely on other numeric bases. It is characteristic of the Liliiflorae that the tepals are largely petaloid, although they are frequently inconspicuous and generally yellowish white or greenish white in Dioscoreales, Melanthiales, many Burmanniales and some primarily baccate Asparagales. In other groups they are generally brightly coloured. Scarious or "bract-like" tepals are rare. Perigonal nectaries occur in certain groups (they occur in very few monocotyledons outside this superorder), and in these groups (mainly Liliales) the tepals are frequently provided with a variegated colour pattern in the form of a checkered pattern, spots or streaks radiating from the centre of the flower, or as coloured sections, all probably important in attracting pollinators, and found in very few taxa outside this superorder. The flowers are hypogynous, hemiepigynous or epigynous. Differentiation in size and shape between the outer and the inner whorl of tepals is common, although the tepals in both whorls are petaloid. Rarely, the outer tepals are shorter, different in colour and tending to be sepaloid, although never typically so.

The stamens are generally 3+3 or 3 in number, but in some families reduced to two or one (e.g. two in Cypripediaceae and one in Orchidaceae). The filaments are free or more or less connate but in Orchidaceae and related families they are fused to the style, forming a gynostemium. The filaments are provided with spreading "food" hairs in some taxa in Asparagales and Melanthiales. In certain families of Asparagales they are flat and extended into a pointed lobe on each side of the anther. They may also be fused into a staminal tube. The anther is basifixed (impeltate) or dorsifixed (peltate) and, especially in some Dioscoreales, the connective extends beyond the microsporangia into a tip or lobe.

When dorsifixed the anthers may be epipeltate or hypopeltate. Sometimes the connective base forms a tube around the filament tip (making it appear basifixed). The anthers are usually introrse but extrorse mainly in some Liliales; they dehisce by longitudinal slits or rarely by apical pores.

The endothecial thickenings are generally of the Spiral Type (the Girdle Type has been reported in some orchids and in *Tacca*). The tapetum is secretory except, perhaps, in Hypoxidaceae, where it approaches the amoeboid type. Microsporogenesis is either successive or simultaneous. The pollen grains are generally dispersed singly or, in most orchids, as tetrads which generally cohere in massulae or pollinia. Their aperture condition is generally sulcate, sulculate or inaperturate (rarely trichotomosulcate, spiraperturate, zonisulculate or foraminate). They are nearly always dispersed in the bicellular state, having quite often a fusiform to crescent-shaped generative cell.

The gynoecium is generally tricarpellary with the three carpels fused at least basally in the ovary region, sometimes in the ovary region only, but in most taxa also in part of the stylar region. The stylar part of the gynoecium is generally long, rarely (as in Asteliaceae) very short or lacking. The placentation is axile or (especially in Orchidaceae of Liliales, most Burmanniales, some other families) parietal (but never laminar-dispersed); in a few genera with one ovule per locule it is basal or apical.

The ovules are generally anatropous, rarely campylotropous and very rarely hemianatropous or orthotropous, crassinucellate or tenuinucellate, and are with or without a parietal cell. Comparatively rarely, as in some Amaryllidaceae, the epidermal cells of the nucellus divide periclinally to form a nucellar cap. Embryo sac formation is generally of the *Polygonum* Type, but the *Allium, Endymion* and *Fritillaria* Types and others occur in scattered families and genera. Endosperm formation is helobial in Melanthiales, many Asparagales, and a few Dioscoreales, but is nuclear in all others and never cellular. In Orchidaceae and Cypripediaceae (and Apostasiaceae?) endosperm formation is soon arrested or (generally) does not take place at all, and endosperm is consequently lacking. In the other groups it becomes copious and stores primarily hemicellulose (in the cell walls), protein and fatty oil but only occasionally starch grains. Embryogeny is generally either of the Asterad or Onagrad Types.

The fruits are capsules or berries, very rarely trifolliculi (some Melanthiaceae) or nutlets. Arils are rare and strophioles or caruncles of different kinds occur in scattered groups. A black phytomelaniferous testal epidermis occurs in nearly all capsule-fruited and some berry-fruited Asparagales. The embryo is generally linear in shape but is sometimes mushroom-shaped (as in *Dioscorea* species) and rarely curved; it is central, varying from very small (*Trillium* Type) to fairly large (*Urginea* Type) and not macropodous. Perisperm occurs only in

Yucca (Agavaceae) and chalazosperm only in Cyanastraceae. The endosperm is ruminate only in some genera of Dioscoreaceae and (the perisperm) in *Yucca* (Agavaceae, Asparagales).

The embryo has a terminal cotyledon except in some Dioscoreales, where the plumule may be subterminal.

The chromosomal conditions are mentioned under the orders and families. The centromere is always localized.

Chemistry: Of chemical characteristics should be mentioned the common accumulation of calcium oxalate in the form of raphides, the very common occurrence of steroidal saponins in most taxa lacking alkaloids, and the common presence of chelidonic acid. Cyanogenesis is evidently not very common, but is known for example in Amaryllidaceae and Alliaceae. Allyl sulphides ("onion oils") occur in some genera of Alliaceae. Alkaloids of different types occur in Amaryllidaceae and Colchicaceae in particular (see under those families), but also in Orchidaceae (several types), Dioscoreaceae (quinuolidine type), Stemonaceae (tuberostemonine type). Of the flavonoids various kinds are known in the Liliiflorae, luteolin/apigenin especially in Alliaceae and Colchicaceae, and sulphated flavonoids in Alliaceae. UV-fluorescent compounds are not known in the cell walls of any Liliiflorae.

Parasites. Some fungal parasites are typical of isolated groups in the Liliiflorae but none are ubiquitous or typical of the superorder.

Distribution. The Liliiflorae do not show a restricted geographical pattern as do some of the other superorders. Many families, especially of Asparagales and Liliales (excluding the orchid group) are concentrated in the Southern Hemisphere and may have differentiated there. Other groups (most Dioscoreales, Burmanniales, orchids) are tropical to subtropical, whereas others again (Convallariaceae, Liliaceae, Melanthiaceae) are largely north-temperate.

Relationships. The Liliiflorae include those extant forms among the monocotyledons that combine the majority of the features here considered to be ancestral. A number of these features are also found in Magnoliiflorae, and we postulate that the monocotyledons and the Magnoliiflorae are sister-groups in the evolutionary sense. Most of the presumably ancestral attributes under this assumption are concentrated in Dioscoreales, in which we include Taccaceae.

In fact, the Ariflorae (e.g. *Pothos* group of Araceae) and the Alismatiflorae (e.g. the Aponogetonaceae), as well as the Asparagales, Liliales and Melanthiales, have obvious connections with members of Dioscoreales, and there are some problems in the delimitation of this order (Smilacaceae could, for example, be referred either to Asparagales or Dioscoreales; *Medeola* and *Scoliopus* connect Trilliaceae with Liliaceae and Uvulariaceae).

Taxa with a concentration of the following features are referred to Dioscoreales: twiners or herbs of forest floor habitats, leaves differentiated into petiole, often with a non-sheathing base, and a broad lamina with reticulate venation, which is often lobate or compound, flowers of moderate size, with inconspicuous perianth, without tepal variegation, microsporangia often below the stamen apex, and thus basifixed-undifferentiated anthers, nuclear endosperm formation, sometimes ruminate endosperm, non-phytomelaniferous, well-differentiated seed coat formed by the inner as well as the outer integument, and sometimes a non-terminal cotyledon. There are some supposedly derived character states in this order, too, e.g. epigynous flowers, non-sulcate pollen grains, nuclear endosperm and simultaneous microsporogenesis, as well as specialization in vegetative respects (tubers, compound leaves, anatomical details) in some taxa.

The Asparagales, we assume, comprise a probable clade, where the seed coat has been specialized, the capsule-fruited taxa having a phytomelan layer. Some family clusters here possibly make up separate clades, such as some shrubby, baccate-fruited families with nuclear endosperm formation and frequently without septal nectaries, others with a bulb and a scapose inflorescence, and yet others with a corm in combination with successive microsporogenesis.

Another probably monophyletic complex is the Liliales, with nuclear endosperm formation, non-phytomelaniferous seed coat, perigonal nectaries and often spotted tepals. In this group we have included Orchidaceae, Cypripediaceae and Apostasiaceae, but not the Burmanniales (Burmanniaceae, Thismiaceae and Corsiaceae); we do not think that these two groups of families are closely related to each other.

The Melanthiales and Burmanniales may each have evolved as a separate clade, but we are uncertain that this is necessarily so. Both have helobial endosperm, and both lack a phytomelaniferous seed coat and perigonal nectaries. A number of genera of Melanthiales share related uredinalean parasites, *Puccinia atropuncta* and *Uromyces vera-*

tri. The Burmanniales in their epigyny, minute seeds, and other features superficially agree with the orchids, but are probably not related with them.

The constellation of orders proposed here is largely based on Huber (1969). It has gained some recent support from the serological results of Chupov and Kutiavina (1978, 1981), which are discussed by Dahlgren (1983a, b). These studies show that there is generally little or no serological reaction between taxa that we refer here to different orders, whereas there is rather strong reaction between at least some families in each order.

We have here excluded from the Liliiflorae the families (orders) with the combination of copious starch in the endosperm, paracytic or tetracytic stomata, *Strelitzia* Type of epicuticular wax, and UV-fluorescent compounds in the cell walls, even where the groups with such attributes may have petaloid and even showy tepals, septal nectaries, raphides, and helobial endosperm, which are all widely distributed in the Liliiflorae.

Order Dioscoreales

Seven Families: Trichopodaceae, Dioscoreaceae (incl. Stenomeridaceae), Taccaceae, Stemonaceae, Trilliaceae, Smilacaceae and Petermanniaceae.

Almost exclusively terrestrial, herbaceous or woody perennial plants with a rhizome or tuber which stores starch. The tuber, at least in *Tacca,* is apparently hypocotylar in character. The tuber in *Dioscorea* may be conspicuously thickened and covered with cork. Secondary thickening growth occurs sometimes in the tuber of *Dioscorea* sect. *Testudinaria*. The roots, as in species of *Dioscorea* (sect. *Testudinaria*) and *Tacca,* may have a single-layered velamen. The aerial stem is often long, twining or trailing, and it usually withers down annually. In Petermanniaceae and some Smilacaceae it is covered with hooks or spines. It has one, two or more rings of vascular bundles. Vessels with scalariform perforations in the end walls are always present in the roots and sometimes in the stems and (in Smilacaceae) also in the leaves. Laticifers are lacking. The leaves are variably arranged on the stem, being dispersed, opposite or verticillate. In most taxa the leaves are differentiated into a petiole and a flat, dorsiventral lamina; there is no petiole in Trilliaceae, however. The leaf base is simple or sometimes sheathing. Stipule-like, often filamentous, appendages are often present on the base, and in Smilacaceae the petiole bears two tendrils. The lamina is usually simple and entire, but may be pinnatisect, pinnatifid or sometimes palmately compound. When simple the lamina usually varies from lanceolate to cordate, with supervolute ptyxis. The primary venation is campylodromous or rarely pinnate and the veinlets, unlike those of most other monocotyledons, generally form a reticulate pattern (Conover, 1983). Ligules are lacking. Oxalate raphides seem to be universally distributed in the order. Trichomes are variable and occur as simple or branched nonglandular hairs, at least in *Dioscorea,* while *Tacca* has characteristic multicellular hairs (see below). The stomata are anomocytic and parallel to the leaf axis, or often, as in Dioscoreaceae, Trichopodaceae and Smilacaceae are randomly oriented.

The inflorescences are very variable in form, and most frequently axillary in position; they are sometimes terminal (and then occasionally one-flowered) on a leafless or leafy branch ("stem") arising directly from the subterranean rhizome or tuber. Flower construction is variable. Generally the flowers are trimerous, but deviations from this condition occur in Stemonaceae and Trilliaceae. The flowers are hypogynous, hemiepigynous or epigynous, actinomorphic, and bisexual or unisexual. The tepals are often inconspicuous, mostly pale yellow, green or dull-coloured (rarely bright white or purple), not spotted, those of the two whorls equal or different from each other, and sometimes fused into a campanulate structure. Nectaries, when present, are perigonal (e.g. species of *Trillium* and *Smilax*) or septal (e.g., in species of *Dioscorea, Trillium* and *Smilax*).

The stamens, like the tepals, occur in two isomerous whorls, one of which is staminodial in some Dioscoreaceae. The filaments may be adnate to or free from the tepals and are often relatively short; in Dioscoreaceae and Smilacaceae they may be fused with each other into a tube. The anthers are basifixed and dehisce introrsely or rarely (some Dioscoreaceae, *Scoliopus* in Trilliaceae) extrorsely. Frequently the stamens project apically beyond the microsporangia. The anthers are tetrasporangiate and anther wall formation proceeds according to the Monocotyledonous or, in *Tacca* (?), according to the Dicotyledonous Type. The endothecial thickenings may be of the Spiral or the Girdle Type. Anther dehiscence is by means of longitudinal slits. The tapetum is glandular and microsporogenesis is simultaneous (e.g. in *Dioscorea* and *Tacca*) or successive (e.g. in *Trichopus, Stemona, Trillium, Smilax*). The pollen grains are single, and may be sulcate, 4-sulcate, 4-foraminate (various Dioscoreaceae), or inaperturate (most Smilacaceae). They are binucleate when dispersed.

The gynoecium is syncarpous and has free stylodia or a single style or (in Stemonaceae) a nearly sessile stigma. The stigma is Dry or Wet. Except in Taccaceae, Stemonaceae and Petermanniaceae the ovary is trilocular with axile placentation. There are several to many ovules in each locule and these are anatropous except in *Stemona* and *Smilax,* where they are orthotropous. Further the ovules are bitegmic, usually crassinucellate and with a parietal cell cut off from the archesporium (except in *Trichopus*). Embryo sac formation is of the *Polygonum* Type or, in most Trilliaceae, of the *Allium* Type. The endosperm is mostly of the Nuclear Type, rarely helobial (*Trillium*). Embryogeny is probably of the Asterad Type although the Solanad Type has been reported for *Trichopus.*

The fruit is either capsular or, rarely, indehiscent and is then baccate (*Tamus, Trichopus*) or dry (*Rajania*). The seeds of capsular fruits frequently have an aril or caruncle, which may function as elaiosome; these are apparently diverse and nonhomologous structures in the different families. The seeds vary in shape, and lack phytomelan, but may possess phlobaphene. The testa consists of both integuments. The endosperm is copious and contains aleurone and fat, while cellulose in variable amounts is deposited in the cell walls. In some genera (*Croomia, Stemona, Paris, Trillium, Ripogonum*) starch grains may also occur in the ripe seeds. Ruminate endosperm is found in *Trichopus* and *Avetra.* The embryo is basically linear and is frequently very small in size; in *Tacca,* however, it is curved. The plumule is often subterminal.

Chemistry. Dioscoreales are rich in steroidal saponins, and chelidonic acid is also common. Cyanogenic compounds are known in *Dioscorea.* Alkaloids occur in at least Stemonaceae and some Dioscoreaceae. Starch is generally deposited in the rhizomes and tubers, and these in *Tacca* contain also ceryl alcohol. The flavonoids are of the commoner types, including proanthocyanins, acylated anthocyanidin glycosides, cyanidin and pelargonidin; myricetin is known in *Tacca.*

Distribution. The Dioscoreales comprise a tropical group of families scattered over all the chief continents with a possible centre in southern Asia and Indonesia. Trilliaceae deviate in having their concentration in regions with a temperate climate in the Northern Hemisphere. The plants of the order are terrestrial and range from shade herbs on the forest floor to climbers in scrubby or rocky habitats. The latter are sometimes strongly adapted to arid conditions (e.g. *Dioscorea* sect. *Testudinaria*). The shade plants are often myrmecochorous.

Relationships. The present circumscription of the order Dioscoreales is unusual in including Taccaceae, as well as Trilliaceae, Smilacaceae and Petermanniaceae. Taccaceae have sometimes, possibly because of their pseudo-umbels, been associated with Amaryllidaceae, with which they have little in common. They have sometimes been treated as a separate order (e.g. by HUBER 1969 and DAHLGREN 1975) or even as a separate superorder, as by HUBER (1977). However, their position in (or at least in the immediate vicinity of) the Dioscoreales (-Stemonales) complex is supported by the whole spectrum of characters, *Trichopus* being perhaps the most apparent connecting link.

The Stemonaceae and Trilliaceae, which comprised a separate order, the Stemonales, in HUBER (1969), approach the Dioscoreaceae and Trichopodaceae, although Trilliaceae with *Scoliopus* has obvious affinities to *Medeola* and other Liliaceae s.str. in the order Liliales.

Smilacaceae and Petermanniaceae, referred previously (DAHLGREN and CLIFFORD 1981; DAHLGREN 1983a) to Asparagales, seem better placed in Dioscoreales on the basis of leaf morphology and floral appearance, but they form a bridge between the two orders.

The most interesting features of the Dioscoreales are certainly those indicating connections with the dicotyledons. These include vegetative features such as the subterminal plumule of the embryo, the few whorls of vascular bundles of the young plants tending to resemble the vascular systems of a dicotyledon seedling, the frequently opposite leaves, the petiolate, well-differentiated leaves with a non-sheathing base and with reticulate veins, and the anomocytic stomata having sometimes a scattered (i.e. not parallel) orientation. The frequently non-terminal microsporangia of the stamens provide a similarity with magnoliifloran families, while the dicotyledonous anther wall formation in *Tacca* may be a casual similarity (if not reported in error). Further, the endosperm is ruminate in *Trichopus* and *Avetra* as it is in numerous magnoliifloran families, and the embryo is generally very small in relation to the endosperm as in these families. Taking account of further considerations, including the frequently unspecialized nature of the perianth and the instability of the type of nectary, Huber (1969) strongly favoured the view that the Dioscorealean-Stemonalean families (he did not include Taccaceae, however) are the ones which most strongly approach the ancestors of the monocotyledons.

In this connection one should consider the variation spectrum and trends present in the Magnoliiflorae, the trends to herbaceous habit (independently) found in Aristolochiaceae and Chloranthaceae, the monocotyledon-like flowers with obvious trimery in several dicotyledonous families, in particular Lactoridaceae, Aristolochiaceae (*Saruma*) and Annonaceae, and the basic, primitive types of ovules and pollen grains.

On the other hand, the Dioscoreales exhibit, in various of their members, a number of advanced vegetative structures and, with their epigynous flower, variable hair types, their often two- or more-aperturate pollen grains and their complex chemistry, are far from primitive. Similarly the Taccaceae, although apparently advanced in their bizarre inflorescences and complicated, epigynous flowers with unilocular ovary and parietal placentae, are probably more nearly primary in the monocotyledons in other character states. One interesting feature met with in several families of Dioscoreales is the common occurrence of both capsular and baccate fruits and sometimes a gradual transition between these fruit types. This flexibility may be considered as rather typical in the order but it also occurs in the Asparagales and Liliales.

Even though there may be most support for considering the basic pattern of the Dioscoreales as quite primitive in monocotyledons, there is not yet substantial fossil evidence for accepting this view, and certain features which are basically considered primitive here, such as the broad, reticulately veined leaf lamina, may in fact represent an adaptation related to the climbing habit in combination with a need for increased assimilating surface (cf. the Smilacaceae).

We claim, however, that the order Dioscoreales shows a number of features ancient for the monocotyledons and several which associate them with dicotyledonous families (even though similarities may have evolved by convergence). Some trends of affinity with primitive Arales (such as Pothoideae), where the flower size is reduced and attraction by a spathe has become general, can be discerned, but the common ancestry of these orders probably lies far back in time.

Taxonomy. The family concepts of the entities of the Dioscoreales are not yet stabilized. Dioscoreaceae are generally acknowledged as a separate family, within which *Stenomeris* could be ranked as a tribe or subfamily or even be elevated to family rank. Trichopodaceae are often included in Dioscoreaceae. Stemonaceae (syn. Roxburghiaceae) are here also treated as a distinct family with Croomiaceae as a synonym. Trilliaceae are often treated as synonymous with Liliaceae s.lat., but in morphology they approach the families mentioned. Taccaceae have generally been regarded as a separate, and isolated, family with other affinities. *Ripogonum* of Smilacaceae is a very distinct genus and is in several respects (sulcate pollen grains, bisexual flowers, lack of tendrils) presumably more primitive than other Smilacaceae. Petermanniaceae, on the contrary, shows some specializations.

Key to the Families

1. Flowers 2-merous (rarely 5-merous)	**Stemonaceae**
1. Flowers 3-merous	2
2. Ovary inferior	3
2. Ovary superior	6
3. Erect, terrestrial herbs, either with a basal leaf rosette (Taccaceae) or with one or several leafy herbaceous stems (Trichopodaceae)	4
3. Twining woody or herbaceous vines	5
4. Flowers solitary or in groups opposite a large cauline leaf; placentation axile	**Trichopodaceae**
4. Flowers in umbel-like inflorescences, inserted between large leafy bracts and subtended by filiform, drooping phyllaries; placentation parietal	**Taccaceae**
5. Placentation central, axile; anthers introrse	**Dioscoreaceae**
5. Placentation parietal; anthers extrorse	**Petermanniaceae**
6. Erect mesophytic herbs, never climbers	**Trilliaceae**
6. Woody or (partly) herbaceous vines	**Smilacaceae**

Trichopodaceae Hutchinson (1934) 1:1 (Figs. 41, 42)

Herbs with erect stems and a short rhizome. The leaves emerge in a rosette from the rhizome. They are simple, entire and petiolate and have three to five main veins, but lack stipule-like appendages (Ayensu 1966). The stomata are anomocytic and randomly directed on the leaf surface. The flowers

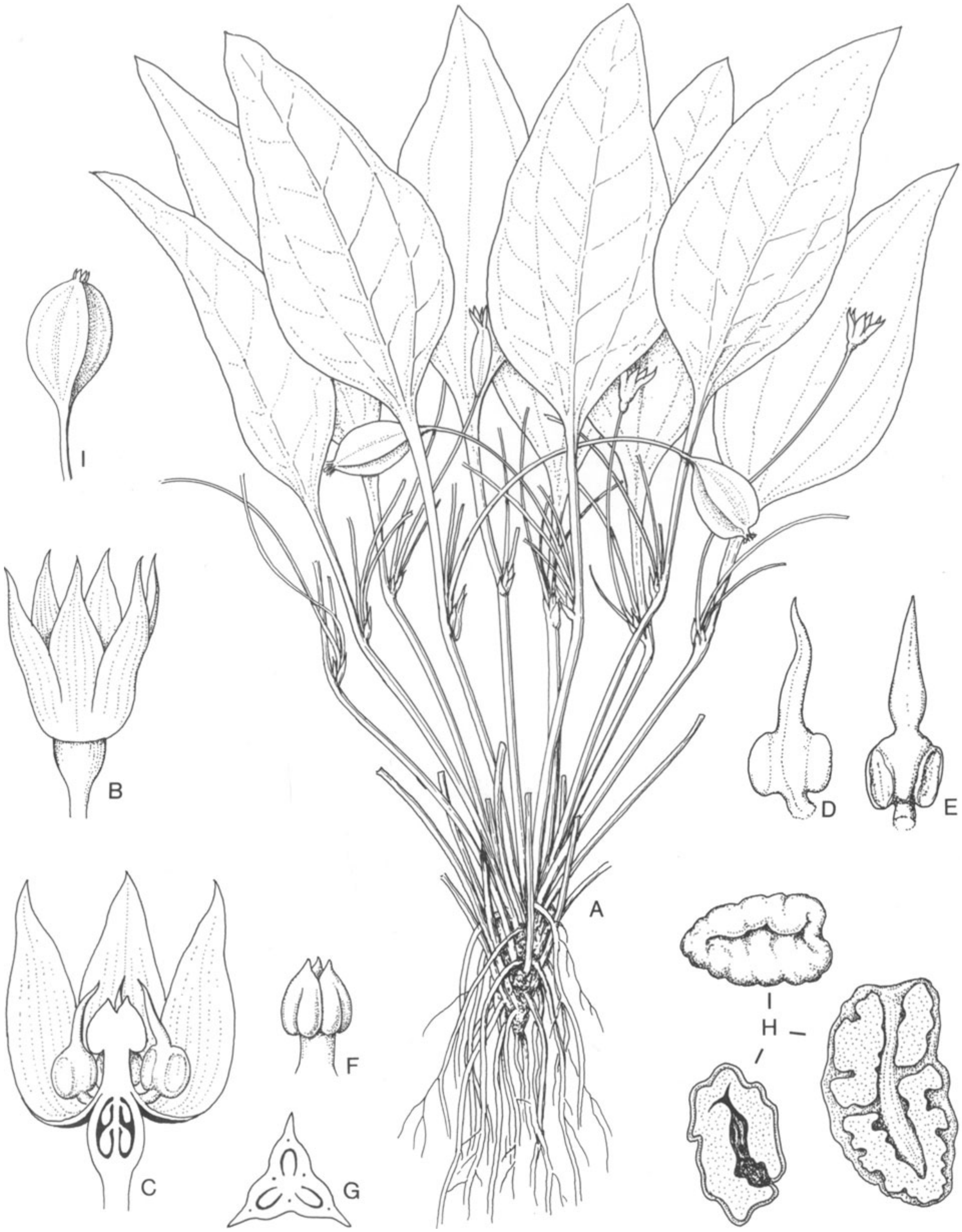


Fig. 41. Trichopodaceae. *Trichopus zeylanicus*. **A** Plant. **B** Flower. **C** Flower, longitudinal section. **D–E** Stamens, introrse, in different views. **F** Style and stigma lobes. **G** Ovary, transverse section. **H** Seed, below in transverse and longitudinal sections, showing the ruminate endosperm. (Redrawn from KNUTH 1924)

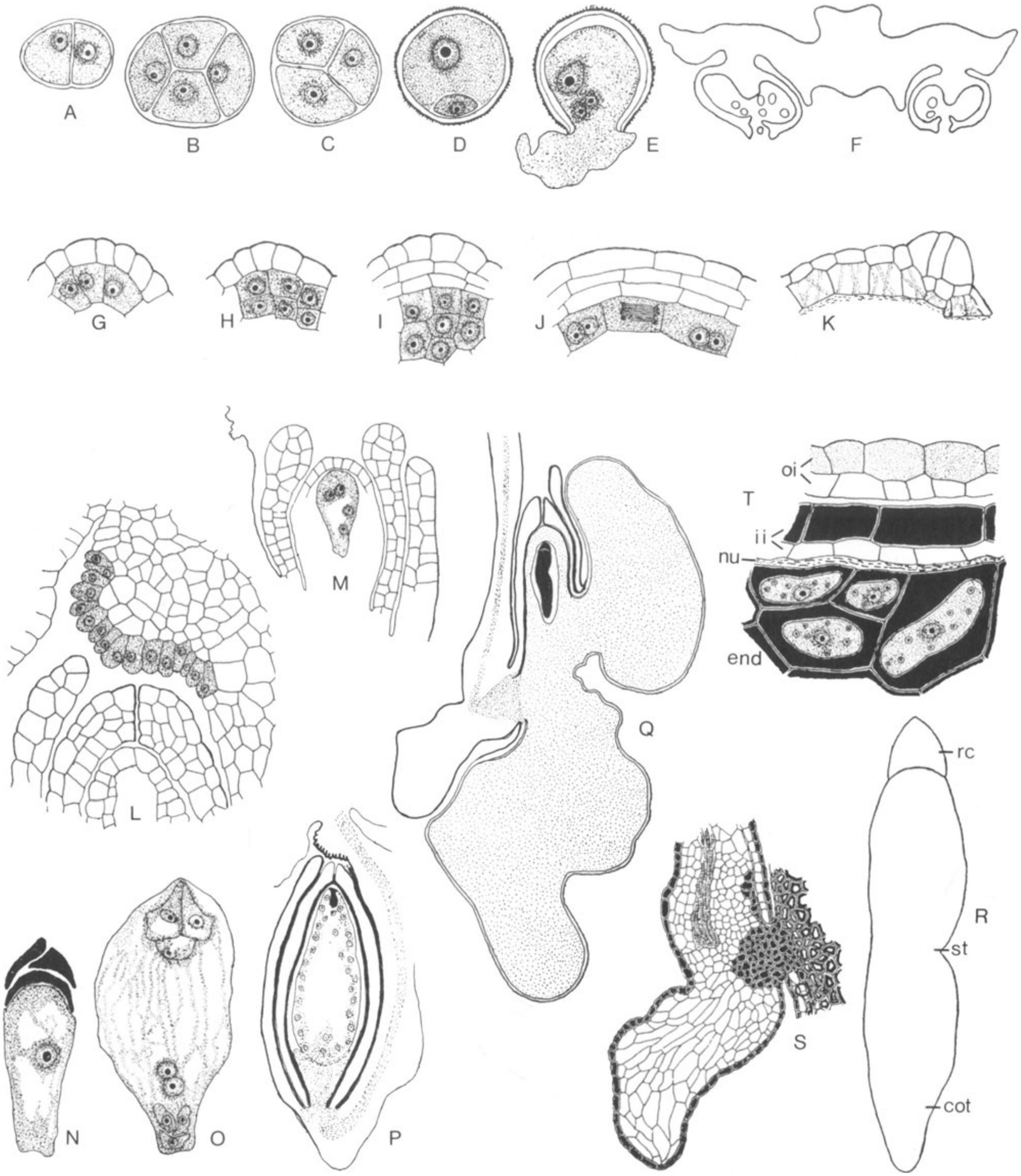


Fig. 42. Trichopodaceae. *Trichopus zeylanicus,* embryological details. **A–E** Successive microsporogenesis, mature pollen and pollen germination. **F** Anther in transverse section, showing the flat, leaf-like structure. **G–K** Pollen wall formation (Monocotyledonous type), tapetum (glandular type) and endothecium with spiral wall thickenings. **L–M** Details of the anatropous ovule. **N–O** Embryo sac mother cell and mature embryo sac (follows the *Polygonum* Type embryo sac formation). **P** Endosperm formation (nuclear type). **Q** Unripe seed showing the small elongate embryo and the extensive endosperm with marked rumination. **R** Embryo (*rc* radicle; *st* stem tip; *cot* cotyledon). **S** Chalazal portion of mature seed. **T** Seed coat and endosperm of mature seed (*oi* testal part; *ii* tegminal part; *nu* nucellar remnants; *end* endosperm cells). (NAGARAJA RAO 1955)

are solitary or paired and have long pedicels. They are bisexual and have 3 + 3 tepals forming a more or less campanulate perigone. There are 3 + 3 stamens which have short filaments and which are apically protracted into a long pointed tip far beyond the introrse thecae. Microsporogenesis (unlike that in the Dioscoreaceae) is successive. The pollen grains are sulcate and dispersed in the binucleate stage (NAGARAJA RAO 1955). The ovary is inferior and trilocular, as in Dioscoreaceae, and is covered with stalked glandular hairs. The three locules each bear one or two ovules. The inner integument becomes three- to four-layered at the micropyle. Unlike in the Dioscoreaceae a parietal cell is *not* cut off. Embryo-sac formation is according to the *Polygonum* Type and endosperm formation is nuclear. The fruit is three-winged, indehiscent and slightly fleshy. The seeds are ovoid and folded and have ruminate, almost starchless endosperm; the outer wall layers are hard and thick owing to heavy deposition of hemicellulose. The embryo in the mature seed is small, linear and straight, with a terminal cotyledon.

The family consists of *Trichopus* (1) *zeylanicus,* which is distributed in South and South-East Asia. It grows on the floor of forests.

Trichopodaceae combines features of Dioscoreaceae (in particular *Stenomeris*), Taccaceae, Stemonaceae and Trilliaceae. In several respects it exhibits supposedly primary character states, such as bisexual flowers, unspecialized rhizome, non-climbing growth, exserted connective tips, sulcate pollen grains and ruminate endosperm, while in other respects it is derived, as in the epigynous, winged fruit which is not readily dehiscent.

Dioscoreaceae R. Brown (1810) 5:625 (Figs. 43, 44)

Herbaceous or rarely shrubby plants, mostly vines with a thick rhizome or tuber, more rarely (as in subfam. Stenomerioideae) with an elongate swollen rhizome. The tubers in subfam. Dioscoreoideae are of different morphological nature: i.e. the hypocotyl, the internode above it, or both. The tuber in some species is covered by a thick coat of cork. The rhizomes and tubers contain starch and sometimes have a continuous secondary growth. The aerial stem is usually long, twining in the vegetation or trailing on the ground. In stem twiners the stems may be rough through the possession of longitudinal ridges or prickles. The vascular strands are generally ordered in one or two rings. At least in *Dioscorea* the stems as well as roots contain vessels with scalariform perforation plates.

The leaves are alternate, with variable phyllotaxis, or rarely opposite. They are petiolate and have a simple lamina (entire or lobate) or are digitately compound with from three to more than six leaflets. Venation is primarily palmate (campylodromous), with 3–13 main converging veins and reticulate veinlets of higher orders. The leaf tips often have a distinct water pore. Some species have stipule-like appendages at the leaf base. Hairs occur in about half of the taxa and are simple and sometimes peg-like, or stellate or bibrachiate, but glandular hairs are lacking. The stomata are anomocytic and often randomly directed on the leaf surface. Glands may occur, for example, on the forerunner tips, and extra-floral nectaries and mucilaginous pits are found in some species. Likewise there may be secretory cells with resinous contents and tanniniferous cells (idioblasts). Bundles of raphides are common.

Bulbils occur in the leaf axils of numerous species of *Dioscorea*; they are of cauline nature and contribute greatly to vegetative propagation.

The inflorescences are axillary panicles, cymes, spikes or racemes, which consist of many or few flowers. The flowers are epigynous, trimerous, and generally unisexual but bisexual in *Avetra* and *Stenomeris;* they are usually fairly small and inconspicuous, but rather conspicuous in *Avetra.* They are subtended by a small to relatively large bract and bear one bracteole or rarely two transverse bracteoles. The 3 + 3 tepals are sometimes fused into a tubular or campanulate structure. At least *Dioscorea* possesses septal nectaries (DAUMANN 1970). In *Tamus* a nectar-secreting tissue is stated to be present on the top of the ovary at the base of the tepal tube. There are 3 + 3 stamens, 3 of which may be staminodial. A disc is said to be present in a Bolivian species of *Dioscorea* (EMBERGER 1960). In *Stenomeris* and *Avetra* the stamens end in a long, subulate or filiform process. Sometimes the filaments may be fused into a tube. The anthers are introrse or extrorse and dehisce longitudinally. The endothecial thickenings are of Spiral Type. Microsporogenesis is simultaneous. The pollen grains are extraordinarily variable in aperture conditions: sulcate in *Stenomeris* and a few species of *Dioscorea,* 2-4-sulculate (*Dioscorea* and other genera) or 4(-5)-foraminate in *Avetra,* where the pollen grains are spinulose.

The inferior ovary is trilocular and the style is apically trilobate or tribrachiate. The stigma is Dry

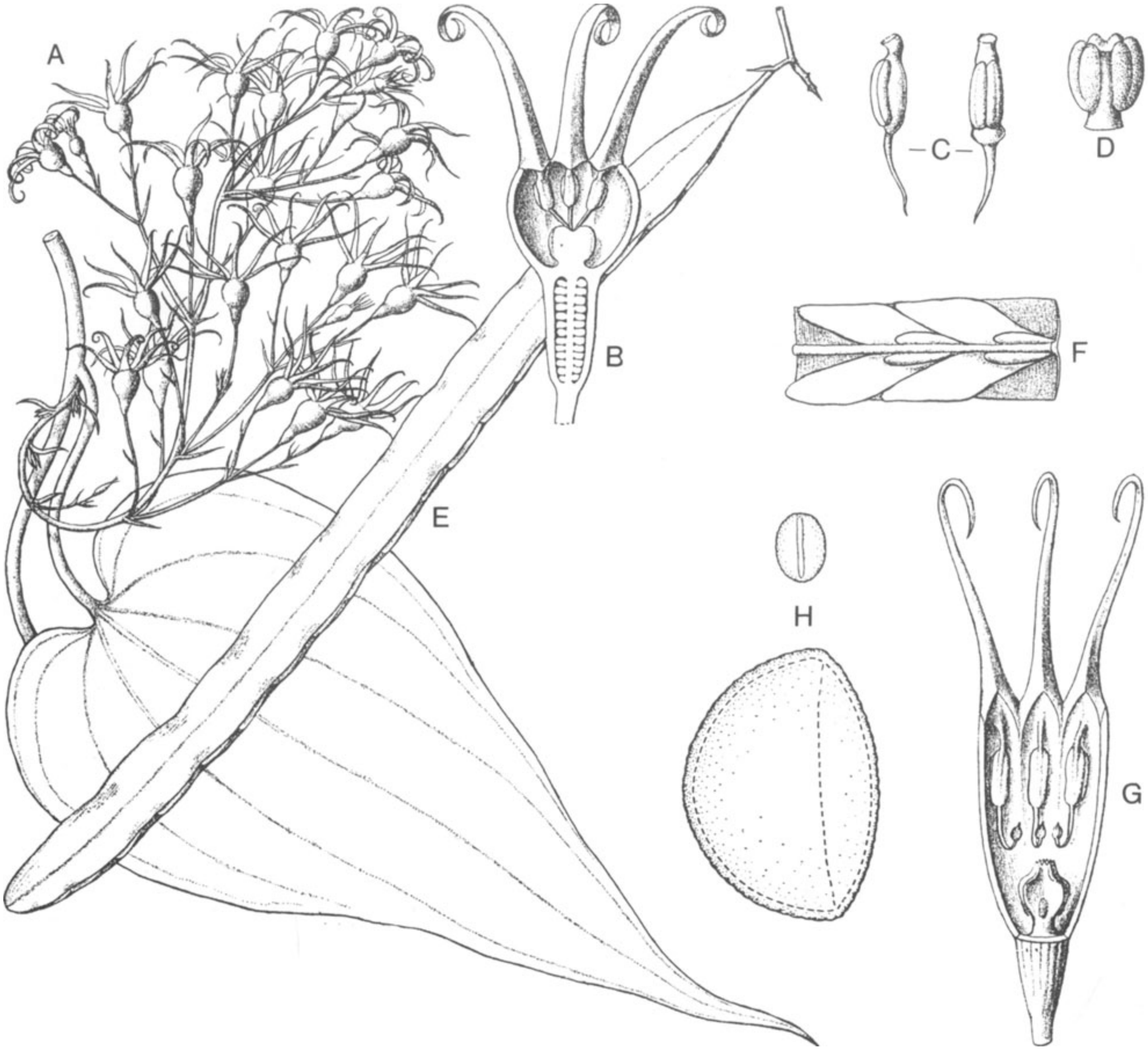


Fig. 43. Dioscoreaceae. *Stenomeris dioscoreifolia*. **A** Part of branch with inflorescence. **B** Flower, longitudinal section. **C** Stamens in the position they have in the flower, filament upwards. **D** Style and stigma lobes. **E** Fruit. **F** Seeds as located in the fruit. (KNUTH 1924) **G–H** *Stenomeris cumingiana*. **G** Flower, longitudinal section. **H** Pollen grains (sulcate). (ERDTMAN 1952)

at least in *Tamus*. Each locule has an axile placenta bearing from two to many ovules. A parietal cell is cut off from the archesporial cell. Embryo sac formation proceeds according to the *Polygonum* Type.

The fruits are usually capsules, which are generally triangular or three-winged, rarely a samara (*Rajania*) or a berry (*Tamus, Avetra*). The seeds, which are solitary to several, are often flattened; they are winged in *Dioscorea* and *Stenomeris,* while *Tamus, Avetra* and *Epipetrum* have globose seeds. The testa of the seed is unusual in having several or sometimes many layers of cells, all with red to yellowish brown pigment (phlobaphene); all cells of the innermost layer of the outer integument in *Dioscorea* contain a crystal of calcium oxalate. The endosperm contains plenty of aleurone and lipids as well as hemicellulose which is deposited in its thick cell walls (pitted in *Epipetrum*). The embryo is small but well differentiated; it has an almost terminal plumule and a more or less lateral, broad, flat cotyledon. $x = 9$, 10, 12, 14.

Chemistry. Chemically the family is characterized by the rich occurrence of steroidal saponins (the aglycone of which is often diosgenin), and in the common occurrence of chelidonic acid. Species of *Dioscorea* contain the alkaloid dioscorrine.

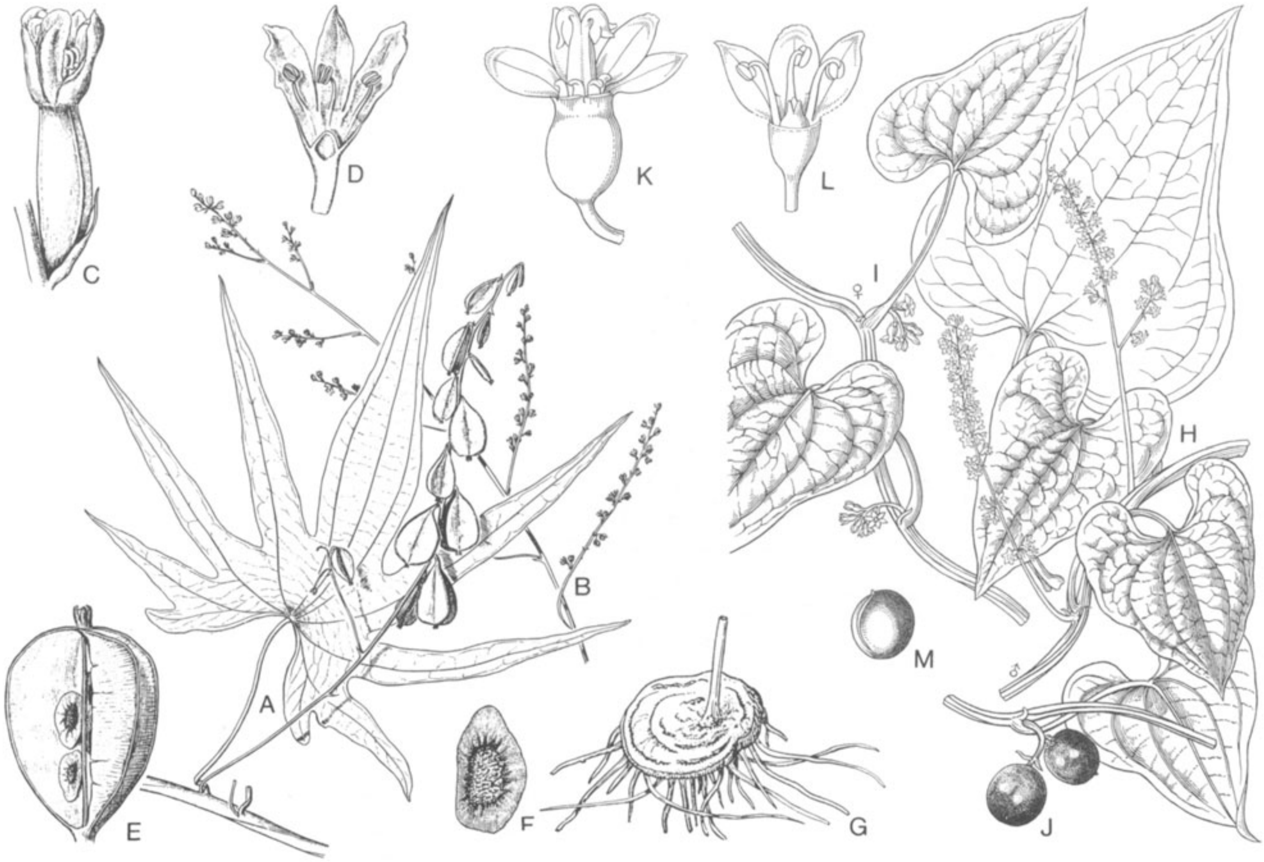


Fig. 44. Dioscoreaceae. **A–F** *Dioscorea brachybotrya.* **A** Branch with leaf and infructescence. **B** Male inflorescence. **C** Female flower. **D** Male flower. **E** Dehiscing capsule. **F** Seed. (Correa 1969) **G** *Dioscorea sinuata,* tuber. (Cabrera 1968) **H–M** *Tamus communis.* **H** Piece of branch with male inflorescences. **I** Piece of branch with female inflorescences. **J** Fruiting branchlet. **K** Female flower, two tepals removed. **L** Male flower, three tepals and three stamens removed. **M** Seed. (Ross-Craig 1973)

Distribution. Dioscoreaceae are widely distributed in the tropics and warm-temperate regions. While *Dioscorea* is widely distributed, *Stenomeris* occurs only in South-East Asia, *Tamus* is confined to Macaronesia and the Mediterranean, *Rajania* and *Epipetrum* occur in the West Indies and *Avetra* occurs on Madagascar.

Subfamily Stenomeridoideae

Subfamily Stenomeridoideae consists of the (perhaps not very closely related) genera *Stenomeris* (5) (Fig. 43) in Indomalesia and the Philippine Islands, and *Avetra,* on Madagascar. They are vines with elongate swollen rhizomes and a twining stem with alternate, cordate or lanceolate leaves. The flowers, solitary or in axillary panicles, are bisexual. *Stenomeris* has an urn-shaped receptacle and six stamens inserted near the top of the tube on short basally directed filaments. The apices of the exserted connectives normally meet above the stigma. The pollen grains in *Stenomeris* are sulcate (a primitive feature in this context) but in *Avetra* four-(to five-)foraminate. The fruit is one-seeded and indehiscent (*Avetra*) or is a many-seeded loculicidal capsule (*Stenomeris*). In *Stenomeris* the fruit is long and linear and has a membranous wing, a similarity to subfamily Dioscoreoideae. This subfamily should perhaps be treated as two, (Stenomeridoideae and Avetroideae) and may deserve family rank.

Subfamily Dioscoreoideae

Subfamily Dioscoreoideae makes up the main part of Dioscoreaceae and consists mainly of vines or trailing plants with an underground tuber which varies in shape and nature, but may be large and woody with a thick cork layer, as in *Dioscorea elephantipes* (sect. *Testudinaria*). The leaves vary from simple to digitately 6-7-foliolate and there is great variation in vegetative features. The flowers are invariably unisexual. In the male flowers the stamens are attached to the base of the perianth; three may be staminodial. The anthers lack apical continuation. The pollen grains are sulcate or bi-(to tri-)sulculate. In the female flowers there are often rudiments of the stamens; the inferior ovary develops into a trivalvular capsule, a berry (*Tamus*) or a samara (*Rajania*).

The subfamily exhibits great variation in various respects, such as tuber morphology, vascular anatomy, leaf morphology, gland morphology, pollen morphology and chemical contents.

Tamus (5) (Fig. 44H–M) is a Macaronesian-Mediterranean genus of vines with red berries, containing globose seeds. The leaves and shoots of *T. communis* may be used as a vegetable. *Dioscorea* (ca. 600) is divisible into numerous sections according to tuber shape, inflorescences, seed wings, etc. *D. cayenensis, D. esculenta* and *D. batatas,* which are all from tropical Asia and Malaysia, and other species cultivated more locally, are used as Yams.

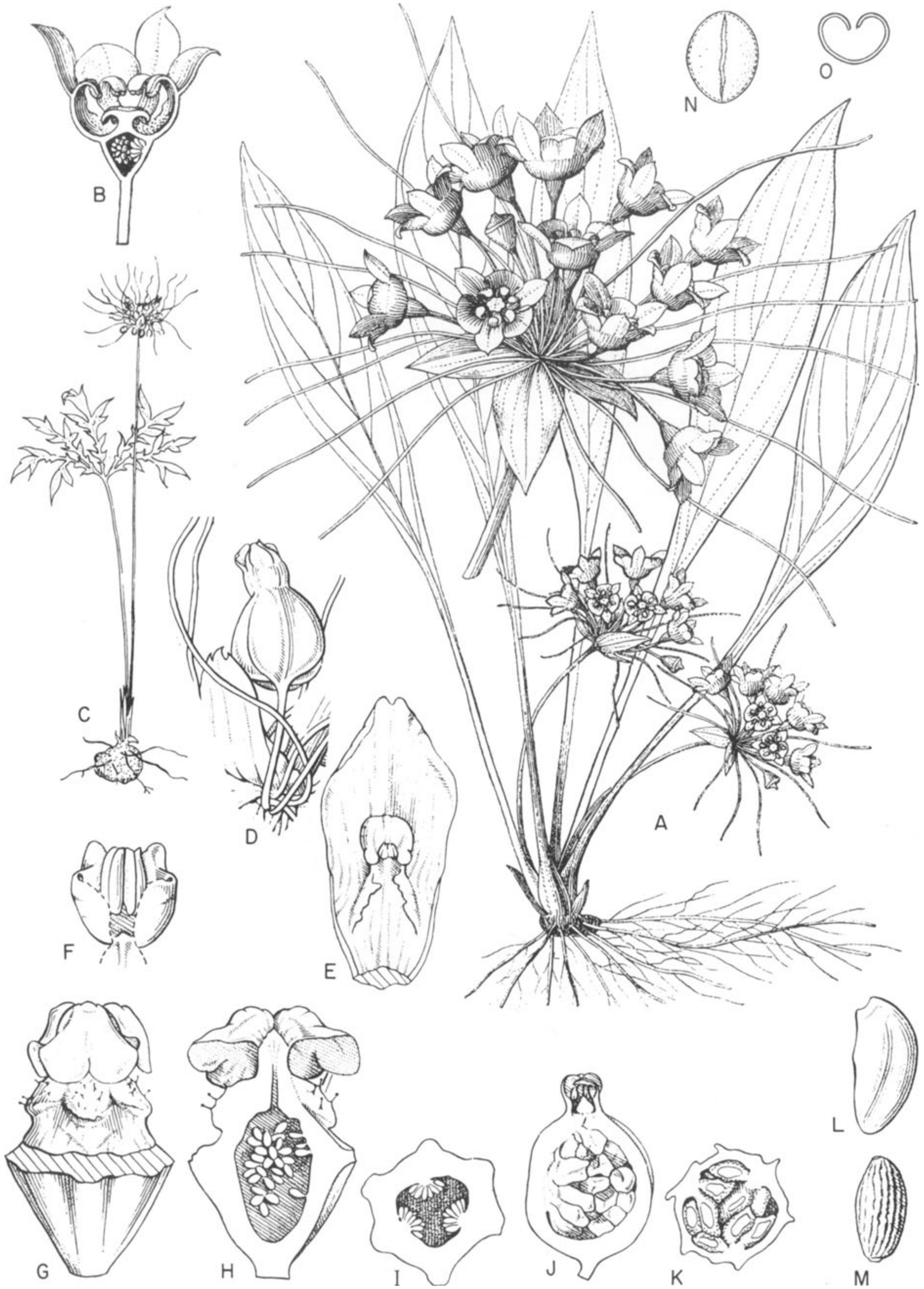
Yams are grown in the wet regions throughout the tropics for the starch-rich tubers and are of great importance as a starchy food. The plants are propagated vegetatively from tubers. The starch cannot be extracted as the grains are held together by mucilage; therefore the use of yams is somewhat restricted. The tubers contain the poisonous alkaloid dioscorine, but the concentration is low in all cultivars and the alkaloid is destroyed by boiling. They also contain steroidal saponins used for producing cortisone. *D. bulbifera,* "Air Potato", likewise from Asia, produces large tubers on the aerial stem as well as underground, and is cultivated in the U.S.A. In some species the tubers are very poisonous; the juice of tubers of *D. hispida* (tropical Asia), when mixed with Antiaria poison, can be used as arrow poison. The tubers of *D. rhipogonoides,* in China, can be used for tanning and dyeing fish nets. *D. villosa* and other species are exploited for the steroidal sapogenins which are used in the production of contraceptive pills and other medical products.

Taccaceae Dumortier (1829) 1:10 (Fig. 45)

Terrestrial acaulescent perennials with a more or less thick rhizome or tuber containing large amounts of starch. The leaves are situated in a basal rosette and are interesting in being more or less long-petiolate and having a lamina varying from entire and lanceolate to broad and pinnatifid, bifid or even deeply palmately partite or palmatisect. The primary venation is pinnate or palmate, the secondary reticulate. The leaf base is more or less widened. From the growth apex of the tuber may be formed runners, which grow downwards and form new tubers. Vessels are confined to the roots and have scalariform perforation plates. Cells containing raphide bundles are concentrated mainly along the veins. Peculiar trichomes, consisting of a short row of cells bearing a multicellular body on which is another cell row at the apex, occur on both sides of the leaf. The stomata are anomocytic or in *Tacca* sensu stricto surrounded by one cell only ("axillocytic") and are randomly distributed on the leaf surface (LING PING-PING 1981).

The inflorescence is borne on a leafless, herbaceous peduncle directly from the rhizome or tuber. It is umbel-like, but apparently cymose, with the flowers inserted between foliose leaves. Long, filiform, drooping bracts subtend the flowers. These are epigynous and bisexual and have 3+3 more or less campanulately fused, dull, dark, brown-purple to greenish perianth members. The stamens, 3+3 in number, are inserted in the perianth tube. The filaments are short, flattened and adnate to the perianth except for the inflexed margins and the helmet-like apical continuation. The thecae are introrse. The anther wall formation is reported to agree with that in most dicotyledons (Dicotyledonous Type), as the outer secondary wall layer forms the endothecium as well as the middle layer, the inner wall layer forming the tapetum only. In all other monocots the middle layer is normally formed from the inner wall layer. The endothecial thickenings are of the Spiral Type. Microsporogenesis is simultaneous and the pollen grains are sulcate, verrucate to striate (ZAVADA 1983) and binucleate when dispersed.

Fig. 45. Taccaceae. **A–B** *Tacca plantaginea.* **A** Plant with inflorescence. **B** Flower, longitudinal section. (LIMPRICHT 1928) **C–M** *Tacca leontopetaloides.* **C** Plant. **D** Flower in centre of inflorescence. **E** Tepal and attached stamen excised from the syntepalous perianth. **F** Stamen from inside the "hood". **G–H** ovary and style, **H** in longitudinal section. **I** Ovary, transverse section. **J–K** Mature fruit, longitudinal and transverse sections. **L** Seed enclosed in aril. **M** Seed with aril removed. (HEPPER 1968) **N–O** *Tacca laevis;* pollen grain, **O** in transverse section. (ERDTMAN 1952)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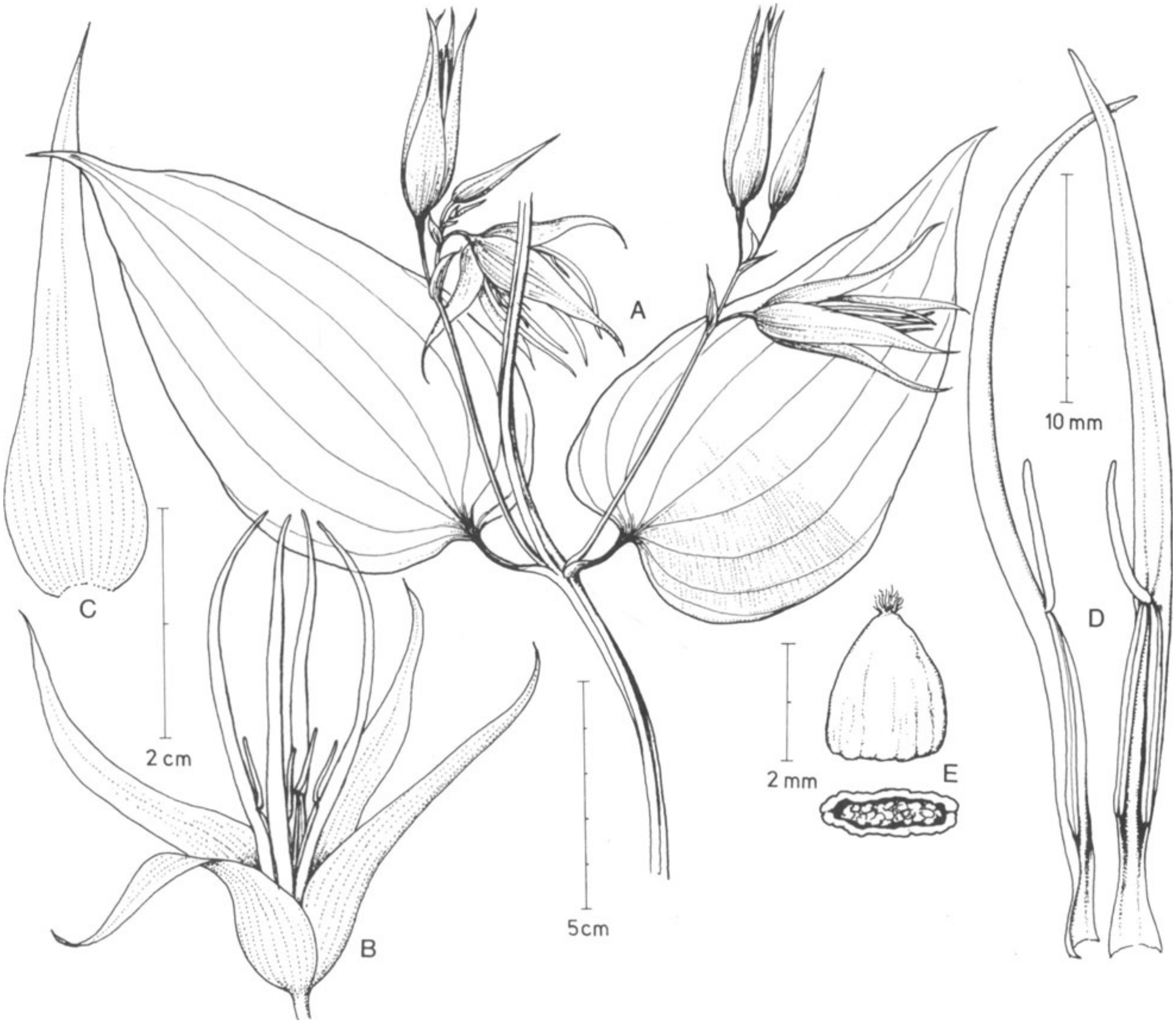
The ovary is tricarpellary but unilocular, with three intrusive parietal placentas, each bearing numerous pendulous, ana- and apotropous ovules. The archesporial cell cuts off a parietal cell. Sometimes glandular cells or a "disc" may surround the stylar base but nectar is not secreted here; septal nectaries have been reported in some species. The style is simple, three-winged, and apically trilobate. The stigma is Dry, with a papillate surface. Embryo sac formation conforms to the *Polygonum* Type and endosperm formation is nuclear.

The fruits have a fleshy pericarp and seem to be dehiscent or indehiscent, i.e. capsules or berries. The seeds are prismatic, bean-shaped or almost horseshoe-shaped. They are provided with longitudinal ridges formed by the unusually high inner cell layer of the outer integument. Endosperm is copious and contains aleurone and fatty oils, but no starch. The embryo is small and ovoid. It has a terminal plumule and a lateral cotyledon (Cronquist 1981). $n=15$.

Chemistry. The chemistry is almost unknown. The tubers, which are very rich in starch, contain ceryl alcohol and a bitter principle.

Distribution. The family is pantropical, but is concentrated in Indomalesia, South-East Asia and the Solomons, where nine out of the ten species occur. The species grow on the ground in shady or open habitats: in open forests, forest margins and on savannahs and crop fields.

Tacca (incl. *Schizocapsa;* 10) is the only genus. The flowers are pollinated mostly by flies (*Diptera*). As in species of Aristolochiaceae the flowers exhibit the syndrome of sapromyophily and may function as "traps", so that the flies cannot leave the tubular chamber formed by the perigone without effecting pollination. Species of *Tacca* are used for their tubers, which contain starch; *T. pinnati-*



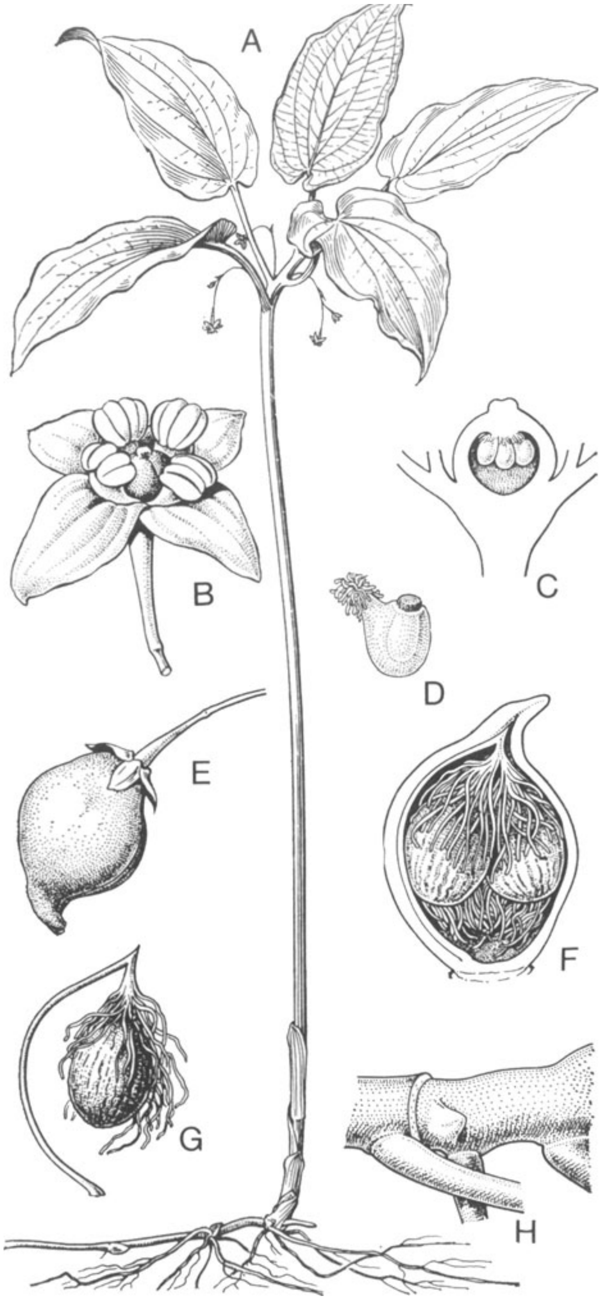


Fig. 47. Stemonaceae. *Croomia pauciflora.* **A** Plant. **B** Flower. **C** Ovary, longitudinal section. **D** Ovule, with funicular aril. **E** Fruit. **F** Same, longitudinal section. **G** Seed; note the aril and the long funicle. **H** Rhizome details. (TAKHTAJAN 1982)

◁ **Fig. 46.** Stemonaceae. *Stemona tuberosa.* **A** Part of flowering branch. **B** Flower. **C** Tepal (outer whorl). **D** Stamens; note the long, exserted stamen, the distinctly separated bisporangiate thecae and the suprathecal, hornlike process. **E** Ovary, lateral view and transverse section; note that the ovary is unilocular and has numerous ovules on a basal placenta (a very rare condition in monocotyledons). (Orig. B. JOHNSEN)

fida is used as "East Indian Arrowroot", but bitter principles must be removed. The tubers can be eaten as a vegetable.

The taxonomic position of Taccaceae has been the subject of much speculation. The family has been considered to be related to, for example, Dioscoreaceae and Amaryllidaceae, and sometimes also to Aristolochiaceae, Velloziaceae, Apostasiaceae and Philydraceae. DRENTH (1972), who revised the group, considered it likely that it had the closest connection with Amaryllidaceae, with which it has the umbel-like inflorescence in common. However, the whole spectrum of characters indicates a rather close relationship to genera like *Stenomeris* (Dioscoreaceae), *Trichopus* (Trichopodaceae) or *Croomia* and *Pentastemona* (Stemonaceae).

Stemonaceae Engler in Engler & Prantl (1887) 4:30 (Figs. 46–48)

Herbs, herbaceous vines or shrublets with subterranean rhizomes or tubers and erect, short or long and climbing stems. The vascular anatomy differs from that in Dioscoreaceae, in that the bundles are borne in one or two rings. The leaves are alternate or frequently opposite or verticillate. Further they are petiolate, non-sheathing at the base, and have an entire, often cordate lamina with 5–15 arching, convergent main veins and numerous secondary transverse cross-veins. Raphides are present or lacking. Vessels with scalariform perforations are known to occur in roots, stems and even leaves (in *Croomia* in roots only). The stomata are transversely oriented on the leaves in *Stemona* and *Stichoneuron,* and are anomocytic. The flowers are solitary and axillary or occur in few-flowered cymes or racemes. They are bisexual or rarely unisexual, hypogynous (*Stemona, Croomia*), half-epigynous (*Stichoneuron*) or epigynous (*Pentastemona*), dimerous, with 2+2 tepals, or pentamerous, with five tepals in one whorl. The tepals are petaloid or sepaloid and may be fused basally. There are 2+2 or five stamens with short filaments, which are free from each other or more often basally connate and sometimes adnate to the perianth. The anthers are introrse, flat, and in *Stemona* produced into long, linear or lanceolate, sometimes flattened connective tips. Their thecae may be distant from each other. Microsporogenesis, as far as is known, is successive. The pollen grains are sulcate and finely reticulate.

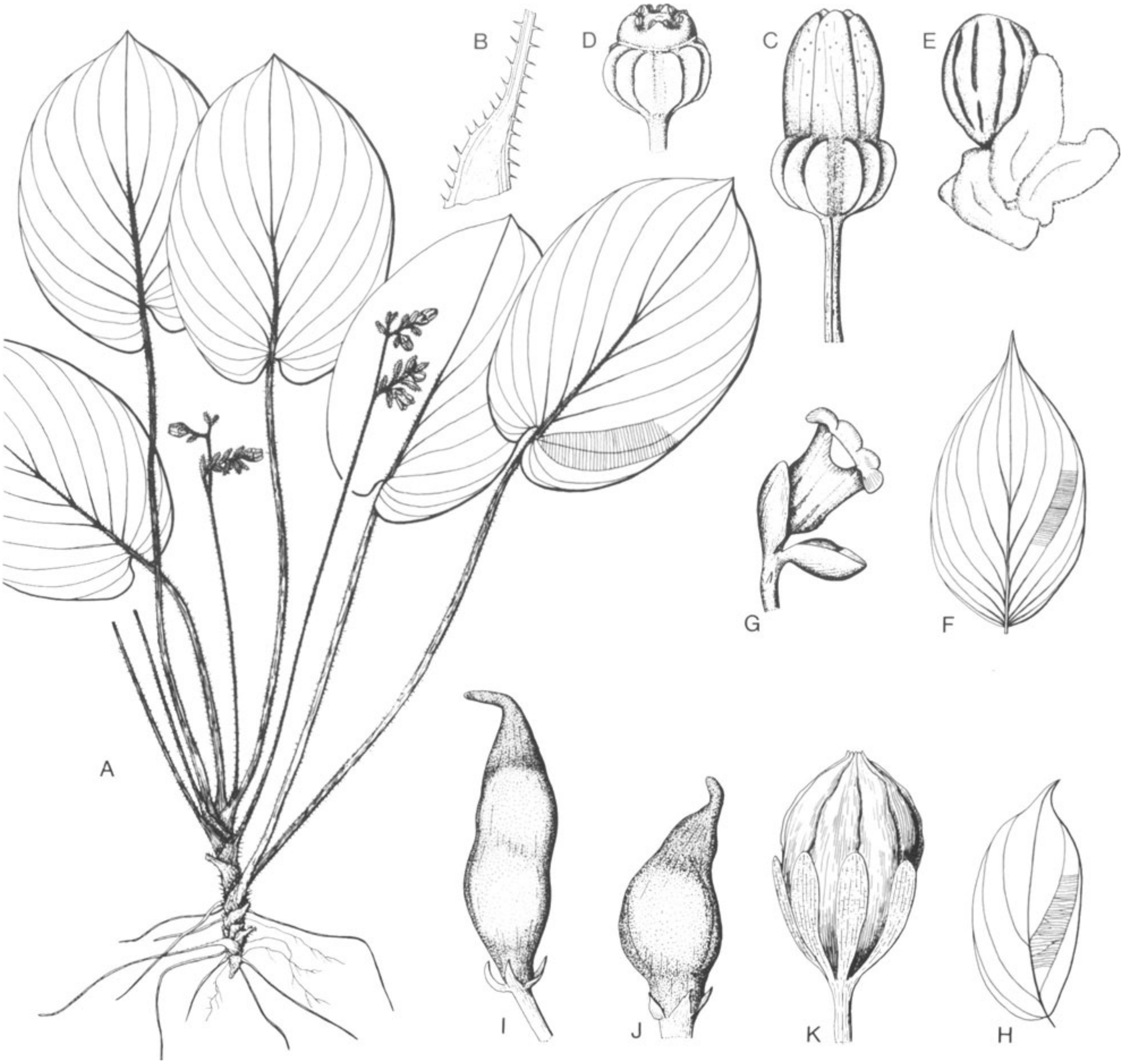


Fig. 48. Stemonaceae. **A–E** *Pentastemona sumatrana*. **A** Habit. **B** Base of leaf sheath. **C** Flower. **D** Flower with tepals removed. **E** Seed with funicular aril. **F–G** *Pentastemona egregia*. **F** Leaf. **G** Flower. **H–K** *Stichoneuron caudatum*. **H** Leaf. **I–J** Fruits. **K** Ribbed seed with lobed aril. (All from VAN STEENIS 1982)

The bicarpellary pistil has a unilocular ovary with sessile or subsessile stigma(s). The ovules are generally few and either basally inserted (*Stemona*) or apical and pendulous (*Croomia, Stichoneuron*). They are anatropous or (in *Stemona*) orthotropous. A parietal cell is cut off from the archesporial cell. Endosperm formation is nuclear. The fruit is a bivalvular, sometimes berry-like capsule with one or few longitudinally ribbed seeds, which bear an elaiosome or caruncle, formed from the hilum and sometimes also from the raphe. The elaiosome is surprisingly variable in the family. It generally contains fat. The endosperm is not ruminate. It contains aleurone, fat and cellulose, but in *Croomia* also copious starch (only a little starch in *Stemona*). $x=7$.

Chemistry. Lactone alkaloids of a characteristic type (tuberostemonin, etc.) occur in at least the underground parts. They represent the effective substances in the insecticides sometimes produced from *Stemona sessilifolia* and *S. tuberosa* in tropical Asia.

Distribution. *Stemona* is distributed in southern Asia and Malaysia to northern Australia, *Croomia* in Japan and Atlantic North America, and *Stichoneuron* in eastern Asia. Some are shade plants and are obviously dispersed by ants.

Within the family, *Stemona* (*Roxburghia*) (25) (Fig. 46) has rather large, often pointed tepals, basal placentation and orthotropous ovules. It has the habit of some *Smilax* species. The outer integument of the seed has three to several cell layers, as in species of *Dioscorea*. The elaiosomes are very variable in the genus.

Croomia (3) (TOMLINSON and AYENSU 1968) and *Stichoneuron* (2) deviate in their smaller rounded tepals and apical, pendulous, and anatropous ovules. In their richness in starch the seeds of *Croomia* resemble those of some species of Trilliaceae.

Pentastemona (2) is a genus described by VAN STEENIS as late as 1982 (see also MEIJER and BOGNER 1983). The two species, *P. sumatrana* and *P. egregia* (Fig. 48), both from Sumatra, are extraordinary in monocotyledons by having actinomorphic pentamerous, tricyclic flowers (T5 A5 G3). They are rather small herbs with long-petiolate leaves with an ovate, mesomorphic leaf blade, cordate or rounded at the base and acute or subacuminate at the apex, pinnately veined with transverse secondary veinlets, tetracytic stomata and raphides as well as crystal styloids. The petioles and the widened sheathing leaf bases are ciliate. The leaves are rosulate, and the peduncles emerge from the ground level and are shorter than the leaves, with small flowers in a thyrse or raceme with one or two lateral components which may represent cincinni. The flowers are bracteate and supplied with a rather large dorsal bracteole, and are bisexual and epigynous with an urceolate-tubular perianth with five rounded lobes. The filaments are fused into a short fleshy tube, on the margin of which the basally widely separated thecae are situated. The pollen grains are inaperturate. The ovary is unilocular, with intrusive, longitudinal placentae, each with numerous ovules. The ovary and fruit are provided with ten longitudinal flanges or ribs. The style is short and thick; five (? nectar-) pouches are present at its base inside the staminal tube. The fruit is a membranous capsule with subglobose seeds which have a transparent sarcotesta, and a vesicular aril. The endosperm is copious and the embryo minute. We find this genus highly distinctive, and although VAN STEENIS (1982) is keen to stress that Stemonaceae should not be divided further, one may consider regarding *Pentastemona* as about as distinct as *Trichopus* or even *Tacca,* and thus worthy of family rank (the Latin description of *Pentastemona* is given in VAN STEENIS 1982, p. 160).

Trilliaceae Lindley (1846) 5:50 (Figs. 49, 50)

Rhizomatous herbs, generally with an erect aerial stem. The rhizome varies from long to short, thick and tuber-like. The stem is unbranched and generally bears a verticil of 3–6 or more leaves (generally the same number as each of the floral whorls) in its upper parts, except in *Scoliopus,* where the two leaves are basal. In the vascular strands, which are frequently disposed in three circles, vessels seem to be lacking; they are confined to the roots and have scalariform perforation plates. The leaf blades are entire, sessile and ovate to lanceolate in outline, and parallel-veined with pinnate secondary venation. Oxalate raphides are found in stems and leaves. The stomata are not always parallel to the main veins.

The flowers are solitary and terminal on the erect stem or (in *Scoliopus*) emerge from the rhizome. They are hypogynous, bisexual and usually 3–8-(-10)-merous. Tepals and stamens are persistent and remain withered around the fruit. The tepals occur in two whorls; the outer (especially in *Trillium*) are sometimes sepaloid, and are purplish or greenish; the inner are often petaloid and white, yellow, purple or of some other colour; they are either broader or, frequently, much narrower than the outer, sometimes even rudimentary (*Paris tetraphylla*). Aestivation is imbricate or contorted. The shape of the tepals varies from narrowly linear or filiform to ovate. Nectar is secreted from the tepal bases in at least some species of *Trillium,* in which genus septal nectaries have also been reported.

The stamens are isomerous with the tepals. They have a distinct filament and an elongate, basifixed, longitudinally dehiscing, introrse or (in *Scoliopus*) extrorse anther. In some genera, as in Stemonaceae, the connective may continue as a narrow apical process. Microsporogenesis is successive. The pollen grains are sulcate or inaperturate (*Trillium* s. lat.).

The ovary is usually 3-6(-8)-carpellary. It is roundish or angular, and sometimes depressed at the top and either has separate locules or is partly unilocular, and then with strongly intrusive placentae. The style is branched low down or there are free stylodia, which are slender or thick

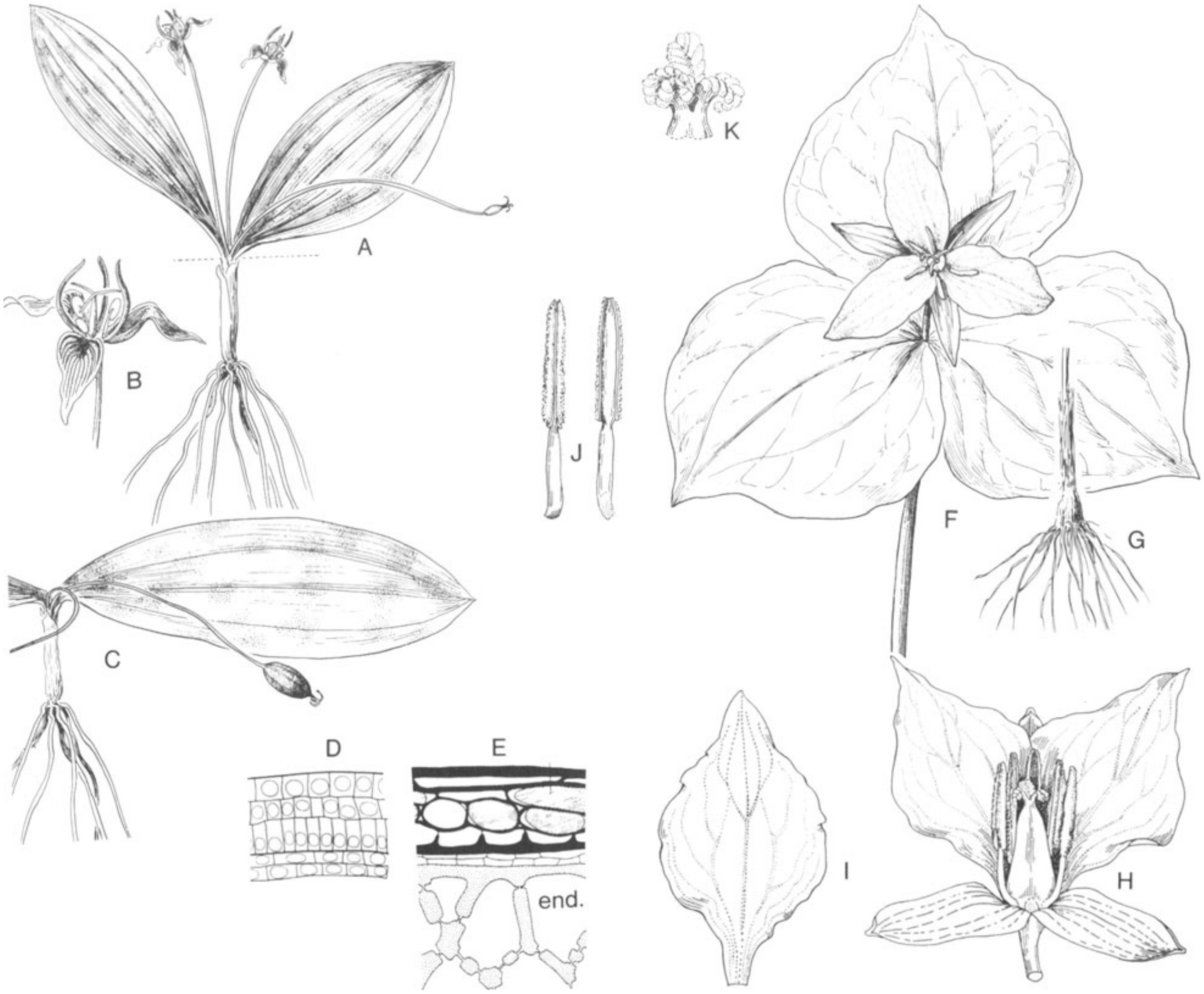


Fig. 49. Trilliaceae. **A–C** *Scoliopus hallii.* **A** whole, flowering plant. **B** Flower. **C** Fruiting plant. (Hitchcock et al. 1969) **D–E** *Scoliopus bigelovii,* seed coat in unripe and ripe seed, respectively. The seed coat does not have phytomelan. (Berg 1959) **F–G** *Trillium ovatum.* (Hitchcock et al. 1969) **H–K** *Trillium rivale.* **H** Flower with one of the inner petaloid tepals and the opposite stamen removed. **I** Tepal of inner whorl. **J** Stamen, the left seen from centre of flower (the anthers are introrse). **K** stylodial branches. (Sealy 1964)

(*Daiswa*), and then separated from the ovary by a transverse rim; the stigmas are Dry. The ovules are anatropous and a parietal cell is normally cut off from the archesporial cell. The embryo sac is generally of the *Allium* Type, or rarely (in *Scoliopus*) of the *Polygonum* Type. Endosperm formation is helobial in *Trillium* but nuclear in at least *Paris* and *Scoliopus*.

The fruit is a berry (*Paris, Kinugasa,* species of *Trillium*) or a fleshy capsule (*Daiswa,* species of *Trillium*). According to Berg (1958) the capsular fruits, which are the most common in *Trillium* (and also occur in *Daiswa*), seem to be derived from berries – a supposedly unusual evolutionary course. Seeds in *Trillium* may bear an oil-rich elaiosome developed from the raphe and hilum. The seeds have a testa formed mainly by the outer integument, which is 3–5 cell layers thick; in *Trillium* the innermost layer is strongly pigmented. A scarlet and juicy sarcotesta is present in *Daiswa* (Takhtajan 1983). The copious endosperm contains aleurone, lipids and also plenty of starch grains. The embryo is small, undifferentiated, and globose to ovoid.

Chemistry. Chelidonic acid and steroidal saponins occur in Trilliaceae; in *Paris,* at least the latter are strongly poisonous. It is noteworthy that

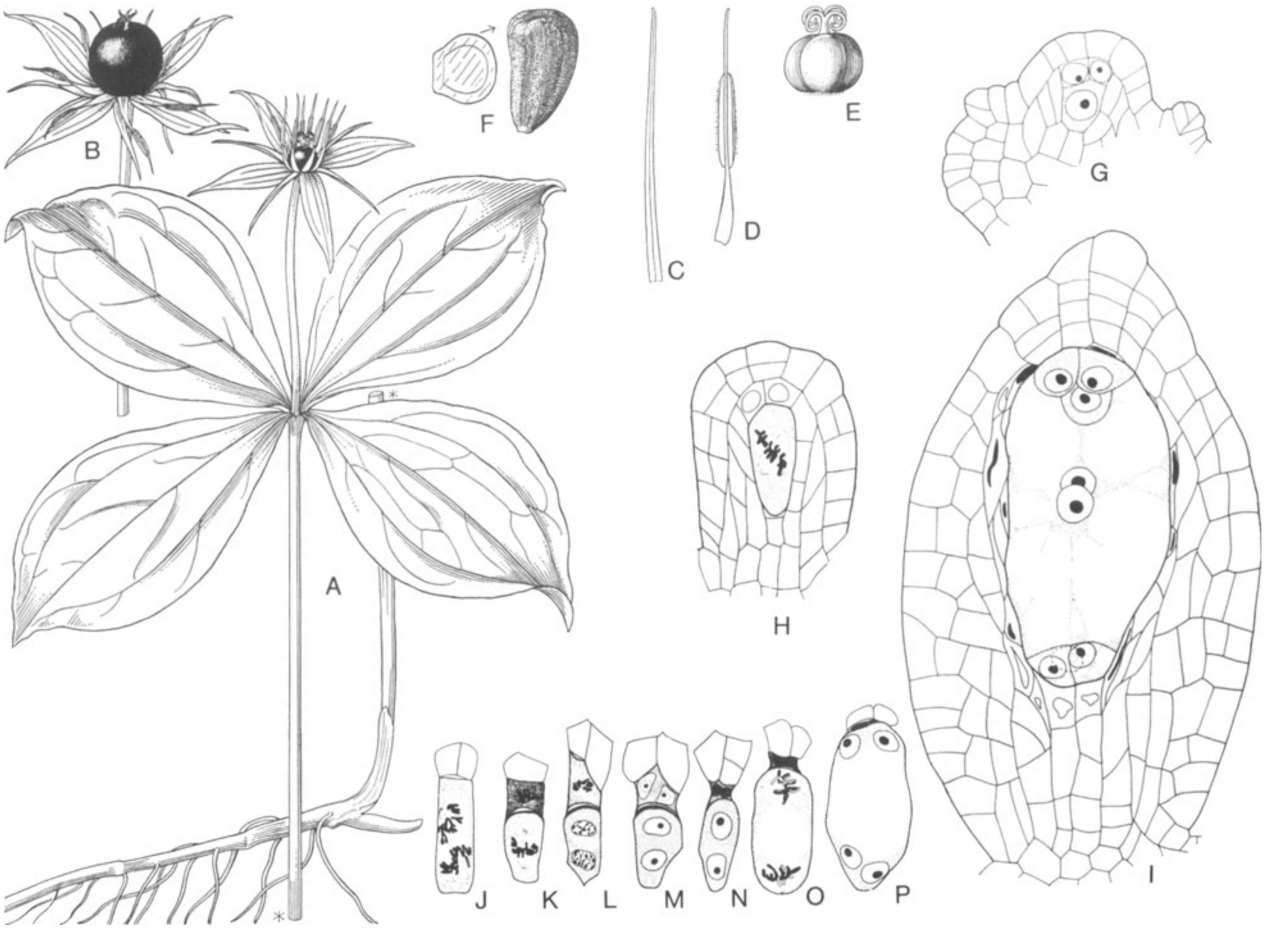


Fig. 50. Trilliaceae. **A–F** *Paris quadrifolia.* **A** Plant. **B** Fruit. **C** Tepal of inner whorl. **D** Stamen. **E** Ovary. **F** Seed, to the *left* in transverse section. (ROSS-CRAIG 1972) **G–I** *Paris quadrifolia,* embryology. **G–H** Early stage of ovule; parietal cells cut off. **I** Mature embryo sac. **J–P** Ontogeny of embryo sac; note that the four nuclei at the stage in **M** are the megaspore nuclei, and that the embryo sac is bisporic, of the *Allium* Type. (BERG 1962b)

Paris has poisonous, but *Kinugasa* non-poisonous and edible berries (TAKHTAJAN 1983). Several types of sapogenin are known in the family.

Distribution. Trilliaceae is mainly a Northern Hemisphere family with its widest distribution in temperate regions of Asia and North America. Most species are herbs growing in shady woods.

Trillium (30) (BERG 1958; 1962b) has trimerous flowers and three cauline leaves. The tepals are broad and often conspicuous; the inner are petaloid and white to reddish. The fruit is generally a three-valvular capsule, rarely a berry. Its seeds are provided with an elaiosome. The leaves of *T. grandiflorum* may be eaten as a vegetable, while the rhizomes of *T. erectum* have medicinal use. Some species are used in ornamental horticulture.

In *Paris* (4), *Kinugasa* (1) and *Daiswa* (15) the tepals are narrow and linear, sometimes rudimentary. The connectives may be prolonged apically. *Paris* and *Kinugasa* have a berry, black and poisonous in *Paris*, but dark purple and edible in *Kinugasa*. The two genera also differ in that *Paris* has a slender and *Kinugasa* a thick rhizome. *P. quadrifolia* is common in European woods. Its leaves have medical use. The species of *Daiswa,* which have a thick rhizome, are characterized by having a fleshy loculicidal capsule and seeds with a sarcotesta. The flowers in this genus vary from being 4- to 8- (or even 10-)merous. These genera have a palaeotemperate distribution. The above division of *Paris* s.lat. was proposed by Takhtajan as recently as 1983.

The differences between *Scoliopus* (2) (Fig. 49) in North America, and other Trilliaceae in the embryo sac and other characters (BERG 1962b) sug-

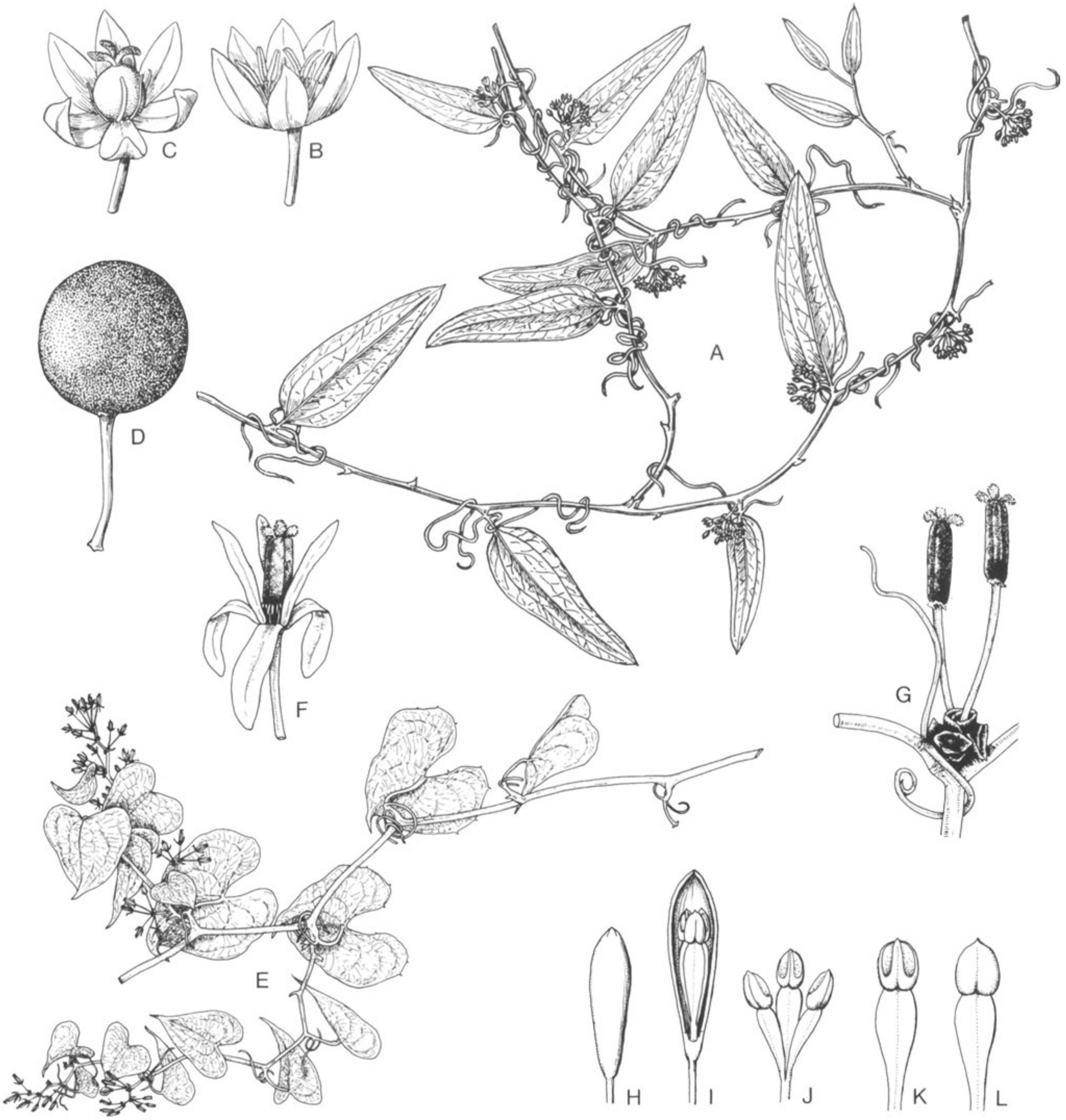


Fig. 51. Smilacaceae. **A–D** *Smilax campestris*. **A** Flowering branch. **B** Male flower. **C** Female flower. **D** Fruit. (CABRERA 1968). **E–G** *Smilax aspera*. **E** Flowering branch. **F** Flower. **G** Young fruits. (JAFRA and EL-GADI 1978) **H–L** *Heterosmilax japonica*. **H** Male flower bud. **I** The same in longitudinal section. **J** Androecium. **K–L** Stamen, front and back. (Redrawn from KOYAMA 1978)

gest that this genus might be better placed in Uvulariaceae. *Medeola,* which has also been referred to Trilliaceae, may have a similar affinity.

In its largely boreal-temperate distribution Trilliaceae deviates from the other families in Dioscoreales and joins up with Liliales (Melanthiaceae, Liliaceae) and Asparagales (Convallariaceae).

Smilacaceae Ventenat (1799) 4:310 (Fig. 51)

Herbs, shrubs or partially woody vines or twiners arising from thick, starch-rich rhizomes or tubers. The roots are mycorrhizal and lack root hairs. Secondary thickening growth is lacking. The branches climb or straggle with the help of tendrillar appendages from the base of the petiole (see below). In many species the stems are provided with prickly thorns (trichome homologues). The leaves are alternate or (in *Ripogonum*) opposite and are petiolate or subsessile. The lamina is lanceolate, broadly cordate or hastate, and is usually stiff and coriaceous; it has campylodromous primary venation, pinnate and marginally brochidodromous secondary venation, and a reticulate pattern of finer venation between the main veins. In all taxa except *Ripogonum* the petiole, at its junction with the only rarely broad and sheathing base, is provided with a pair of tendrils (which have sometimes been considered homologous with midveins of two lateral leaflets).

Laticifers are lacking. The vascular strands of the roots and stems, and at least sometimes also the leaves, contain vessels with simple or scalariform perforation plates. The stomata are anomocytic and often randomly oriented or transverse. The stomata in *Ripogonum* are mesoperigenous (Conover, 1983). Oxalate raphides contained in mucilage cells occur frequently, for example in the saponin-rich rhizomes or tubers.

The inflorescences are axillary or situated on the tips of branchlets. They often consist of one or more (superimposed) verticils of flowers (appearing like umbels or racemes). The flowers are actinomorphic, hypogynous and mostly unisexual (the plants dioecious) or rarely (*Ripogonum*) bisexual, and possess 3 + 3 more or less equal tepals, inconspicuous but petaloid, and sometimes fused into a short or (in *Heterosmilax*) long tube. The male (or bisexual) flowers have 3 + 3 (rarely 3 or 3 + 3 + 3 or up to 18) stamens. Their filaments are free from each other or sometimes more or less fused into a tube or column. The anthers are basifixed, introrse or latrorse, lack apical appendages, and dehisce longitudinally; they are tetrasporangiate and dithecous, but the thecae may become confluent (Cronquist 1981). The tapetum is glandular and microsporogenesis successive. The pollen grains are globose, inaperturate (or indistinctly aperturate) and spinulose in most genera, but sulcate and reticulate in *Ripogonum*. They are free and dispersed in the two-celled stage. Nectaries are often present at the base of the tepals or stamens. The functional pistil is syncarpous and trilocular (rarely, in *Smilax pumila,* monocarpellary); it has three stylodia which are free or rarely fused basally for a short distance. Septal nectaries are present. The stigmas are papillate and Dry. The locules generally contain one or two pendulous ovules. These are incompletely anatropous, hemianatropous, campylotropous or (as a rule) orthotropous. A parietal cell is cut off from the archesporial cell. Embryo sac formation proceeds according to the *Polygonum* Type and endosperm formation is nuclear. The fruits are globose berries with one or three seeds. These are globose or ovoid and very hard; when ripe the outer epidermis is obliterated, and loosens from the inner shiny part of the seed, and the inner integument is comparatively well developed. Phytomelan is lacking. The hardness of the seeds depends on the endosperm which consists of radially elongated thick-walled cells (with scalariform-pitted walls). In addition to the cellulose, the endosperm contains aleurone and fatty oils (except *Ripogonum* where these products partly seem to be substituted by starch grains). The embryo is straight, linear and very small.

Distribution. Smilacaceae with its few genera is rich in species, the largest genus, *Smilax,* being pantropical-subtropical with the centre in America; in Europe, Eastern Asia and North America it reaches into temperate regions. The other genera have smaller East-Asiatic distributions, except *Ripogonum,* which occurs from Australia to New Guinea and New Zealand.

Subfamily Ripogonoideae

Ripogonum (7) (MacMillan 1972), deviates from the other genera in several characters. These include opposite leaves, lack of tendrils, bisexual flowers in spike-like inflorescences, non-confluent thecae, sulcate, reticulate pollen grains, anatropous ovules and starch-rich endosperm. It is arguable whether this genus belongs in Smilacaceae at all; Huber is also inclined to treat it as a separate, closely related family.

Subfamily Smilacoideae

Smilax (300) and the smaller genera, *Heterosmilax* (6–15) in India–Japan with three stamens fused into a column, and *Pseudosmilax* (2), on Formosa with nine or more stamens, are all more or less similar in having leaves with variably long paired tendrils on the petiole and in having unisexual flowers (the plants are dioecious). *Smilax* is exceedingly variable in habit, leaf shape, number of seeds per berry and curvature of the tepals. A few species occur in Europe: *S. aspera* in a great part of the Mediterranean area and *S. excelsa* in the Balkan Peninsula. *S. canariensis* occurs in the Azores. The tubers of *S. china,* in Eastern Asia, are used in a decoction against gout. The roots of the Mexican *S. aristolochiifolia* and other species are important in yielding various types of "radix sarsaparillae" used in medicine as a tonic against digestive disturbances. The active substances are steroidal saponins, such as parillin, smilasaponin, and the poisonous sarsasaponin. The starch-rich tuber-like rhizomes of some species are used as potatoes, and the leaves of some species are used for tea. The berries of *S. megacarpa* in South-Eastern Asia (mostly Java) are eaten, mainly as preserves.

Petermanniaceae Hutchinson (1934) 1:1 (Fig. 52)

Fig. 52. Petermanniaceae. *Petermannia cirrosa.* **A** Flowering branch; branching is sympodial. **B** Tendril, which represents a transformed inflorescence. **C** Flower. **D** Flower bud. **E** Stamens (the anthers are extrorse). **F** Style apex and stigma. **G** Ovary, transverse section; note that it is unilocular and has parietal placentae. (Knuth 1924)

A woody vine with more or less prickly stem (cf. *Smilax*) arising from a swollen, woody subterranean rhizome with irregularly distributed adventitious roots (Tomlinson and Ayensu 1969). The leaves are spirally set, subsessile, broadly lanceolate and acuminate. Stipules, leaf tendrils and similar structures are lacking, and the primary venation is pinnate-campylodromous with reticulate finer venation. Vessels are restricted to the roots (cf. Smilacaceae), and have oblique end-walls with scalariform perforations. Raphides are present in all parts of the plant, and the stomata are anomocytic (Tomlinson and Ayensu 1969). Branching is sympodial and some of the raceme-like paniculate inflorescences, principally terminal in position (but "leaf-opposed"), are transformed into tendrils. The flowers are bisexual, actinomorphic and epigynous. The 3+3 tepals are subequal and spreading to deflexed. There are 3+3 stamens with free, erect filaments and extrorse, tetrasporangiate anthers with contiguous loculi. The connective is not produced beyond the thecae, and the pollen grains are sulcate. The pistil has a unilocular, tricarpellary ovary. Its style is simple and stigma capitate. The parietal placentae bear fairly numerous ovules. The fruit is a berry with several seeds.

Petermannia (1) *cirrosa* is restricted to New South Wales and Queensland in Australia.

This genus, like *Ripogonum* and other Smilacaceae, combines features of Dioscoreales and Asparagales (e.g. the Philesiaceae). With some uncertainty, it seems to merit family rank separate from Smilacaceae.

Order Asparagales

The Order includes 31 families: Philesiaceae, Luzuriagaceae, Convallariaceae, Asparagaceae, Ruscaceae, Herreriaceae, Dracaenaceae, Nolinaceae, Asteliaceae, Hanguanaceae, Dasypogonaceae, Calectasiaceae, Blandfordiaceae, Xanthorrhoeaceae, Agavaceae, Hypoxidaceae, Tecophilaeaceae, Cyanastraceae, Eriospermaceae, Ixioliriaceae, Phormiaceae (incl. Dianellaceae), Doryanthaceae, Asphodelaceae, Anthericaceae, Aphyllanthaceae, Hemerocallidaceae, Funkiaceae, Hyacinthaceae, Alliaceae (incl. Gilliesiaceae), Amaryllidaceae.

Perennial herbs as well as subshrubs, shrubs and sparingly branched trees usually with terminal leaf rosettes. In some families the stems are woody and in certain of these there is secondary thickening growth which is dissimilar to that in dicotyledons. The roots in rare instances are fusiform and nutrient-storing; one- to several-layered velamen is reported in several taxa. Most members have rhizomes or bulbs, bulbs being in particular characteristic of Amaryllidaceae, Alliaceae and Hyacinthaceae; corms occur in, for example, Tecophilaeaceae and some Alliaceae and Hypoxidaceae, and tubers in Eriospermaceae.

Vessels are present in the roots, where they have simple or scalariform perforation plates or both types; vessels with scalariform perforation plates also occur in the stems of several families, such as Philesiaceae and Luzuriagaceae and, in tree-like taxa, e.g. Agavaceae. Laticifers are restricted to some Alliaceae.

The leaves are alternate and distichous or more often with other phyllotaxies; rarely they are opposite or verticillate. They are always simple and generally narrow, with filiform or linear to lanceolate or oblong laminae; further they are mostly sessile and sheathing at the base with parallel or arching veins, but in some groups the leaves are differentiated into a petiole, which is not sheathing at the base, and a broad lamina which in a few families has reticulate venation. Succulent leaves occur in some families, sometimes in association with the presence of tough fibres. Ligules occur in at least some species of *Sowerbaea* and *Allium*. Peculiar appendages to the leaves occur in species of *Eriospermum,* Eriospermaceae.

The stomata are generally parallel to the leaf axis. They are agenous or perigenous in ontogenetic terms, and most often of the anomocytic type (lacking subsidiary cells) when mature, but paracytic stomata occur, for example in Hypoxidaceae, Xanthorrhoeaceae, Doryanthaceae and *Astelia* of Asteliaceae, and tetracytic stomata are frequent in Asphodelaceae subfam. Alooideae. Hairs are frequently lacking and when present are mostly simple and unicellular or uniseriate. Oxalate raphides contained in mucilage-filled cells or sacs are common throughout the order, while silica bodies are lacking.

The inflorescences are borne terminally or laterally and are often long-pedunculate (scapose), especially in groups with bulbs. Determinate as well as indeterminate inflorescences occur in the order, in the former case sometimes assuming an umbel-like appearance.

The flowers are actinomorphic or more rarely zygomorphic, hypogynous or epigynous, and generally pentacyclic, with two, mostly trimerous whorls of more or less petaloid tepals, two whorls of stamens and a pistil consisting of one whorl of carpels. In most cases the outer and inner tepals are similar to each other. They may be free or fused into a campanulate or tubular structure. The tepals are generally neither spotted nor variegated; they are provided with basal nectaries only in Philesiaceae and some Luzuriagaceae.

The stamens generally have basifixed or dorsifixed-hypopeltate anthers (see Fig. 3) and narrow or broad filaments, sometimes (as in many genera of Hyacinthaceae, Alliaceae and Amaryllidaceae) with lateral processes on each side of the attachment point of the anther; rarely, they are fused basally or high up into a staminal ring or tube. Hairy filaments occur in some genera of Asphodelaceae and Anthericaceae and in *Yucca* of Agavaceae. The anthers are tetrasporangiate and generally introrse but extrorse in, for example, Ruscaceae. They dehisce by lateral slits or, rarely, by pores, as in Tecophilaeaceae, Cyanastraceae, Calectasiaceae, some Phormiaceae and a few genera in other families. The endothecial thickenings are of the Spiral Type (except in *Lomandra* of Dasypogonaceae where they are of the Girdle Type). The tapetum is mostly secretory, but stated to be amoeboid at least in some Hypoxidaceae. Microsporogenesis is successive in most families but simultaneous in, for example, most or all Asphodelaceae, Tecophilaeaceae, Cyanastraceae, Phormiaceae, Doryanthaceae and Hemerocallidaceae. The pollen grains are mostly sulcate, but bisulculate in some genera of Dasypogonaceae and Amaryllidaceae, spiraperturate in Aphyllanthaceae and *Lomandra* of Dasypogonaceae, trichotomosulcate in some Luzuriagaceae and Anthericaceae and in

Phormiaceae and inaperturate in, for example, Philesiaceae. They are dispersed in the two-celled or rarely in the three-celled state (see WUNDERLICH 1936). The pistil is syncarpous and generally trilocular but rarely unilocular, as for example Philesiaceae and Calectasiaceae and in some Asparagaceae. Inferior ovaries (epigynous flowers) occur in several groups, the most important being the Amaryllidaceae, Hypoxidaceae and part of the Agavaceae, although single genera with epigyny occur in other families. Semi-inferior ovaries occur in particular in Tecophilaeaceae and Cyanastraceae. Septal nectaries occur in most members of the order but are absent at least from some Luzuriagaceae and Philesiaceae (with perigonal nectaries) and from Hypoxidaceae and Tecophilaeaceae. The septal nectaries are of external or internal types and quite variable; in groups with inferior ovaries they discharge at the style base. The style is simple or apically three-armed or three-lobed, free stylodia being absent from the order. In the Ruscaceae and Hanguanaceae and in some Asteliaceae the style is obsolete and the stigma(s) sessile or subsessile. The stigma is Dry or more rarely Wet. The placentation is mostly axile in trilocular ovaries with several to numerous ovules, and rarely basal or apical. A single ovule or two ovules per carpel are found in Ruscaceae, Dracaenaceae, Dasypogonaceae and a few genera of other families.

The ovules are mostly anatropous or, less often, hemitropous, campylotropous (frequent, for example, in Anthericaceae and Alliaceae) or orthotropous (occurring in several families). A parietal cell is usually cut off, forming a variably extensive parietal tissue, but is lacking in several groups, including some genera of Nolinaceae, Hypoxidaceae, Phormiaceae and Alliaceae, and also, for example, in Dracaenaceae and certain Amaryllidaceae, where the nucellar epidermis may divide periclinally to form a "cap". Embryo-sac formation generally conforms to the *Polygonum* Type, less often to the *Allium* Type, and very rarely to the *Scilla, Clintonia* or *Drusa* Types. Endosperm formation proceeds almost equally often according to the Nuclear and the Helobial Types (see under the separate families), and embryo formation according to the Asterad or Onagrad (rarely the Solanad) Types.

The fruit is generally a loculicidal capsule but in several families it is baccate (these families being treated first below); rarely it is dry and indehiscent. Other fruit types are the septicidal capsule (*Herreria, Blandfordia, Yucca, Excremis*) and capsules opening with a circumcissile slit (some Hypoxidaceae) or irregularly (*Ophiopogon*), the schizocarp (*Tricoryne, Cyanastrum*), and nutlets (genera of Nolinaceae and Dasypogonaceae).

The seeds are variable in size and shape, but are often ovoid or angular. The outer epidermis is obliterated in the seeds of most taxa with baccate fruits. In most taxa with capsules and a few of those with berries the outer integument is encrusted with phytomelan, an opaque, brittle charcoal-like substance which is chemically very inert. Rarely, the seeds have a brightly coloured testa (*Ophiopogon*). The inner integument in the seed coat is usually compressed into a colourless or red-brown membrane. Endosperm is usually present, but rarely substituted by chalazosperm (Cyanastraceae) or perisperm (*Yucca,* Agavaceae). The endosperm contains fatty oils, aleurone and cellulose, while starch grains are only occasionally present (then mostly in genera of Amaryllidaceae). The embryo is linear and usually straight, but is sometimes curved, e.g. in some Anthericaceae and Alliaceae. The plumule is lateral.

Chemistry. Chemically the order is characterized by the common presence of steroidal saponins, but these are lacking or rare in certain families, in particular in Amaryllidaceae, where there is instead a richness of particular alkaloids. Anthraquinone derivatives occur at least in Asphodelaceae and Xanthorrhoeaceae, bufodienolide in Hyacinthaceae and cardenolide in Asparagaceae. Fructan and glucomannan are frequently deposited in subterranean storage organs (rhizomes, corms, etc.). Chelidonic acid is widespread in the order, while cyanogenic compounds are rarer (certain Amaryllidaceae, Alliaceae, etc.).

Distribution. The order Asparagales is widely distributed and various groups of families show different patterns of distribution. RAVEN and AXELROD (1974) consider the group to be most likely of West Gondwanaland origin from which it could have invaded the Northern Hemisphere before the close of the Cretaceous. The rich representation of families such as Asparagaceae, Tecophilaeaceae, Asphodelaceae, Hypoxidaceae and Amaryllidaceae in Southern Africa suggests that their ancestors occurred on the Southern Hemisphere continents while these were still adjacent; the distributions of Xanthorrhoeaceae, Dasypogonaceae and Anthericaceae suggest a differentiation in continents derived from eastern Gondwanaland.

Relationships. The present circumscription of the Asparagales agrees largely with that proposed by HUBER (1969), who reinstated many of the families recognized earlier (e.g. by LOTSY 1911) but more recently submerged in a widely circumscribed Liliaceae s. lat. These families fall mainly under the Asparagales, the remainder into Liliales and Dioscoreales.

The differences between Asparagales and Liliales, can be summarized in Table 1 extracted largely from HUBER (1969:510–512).

It is obvious that taken singly none of the above characters is sufficient for distinguishing the families into different orders, but in conjunction they seem to be of great significance. Among the families which bridge the orders are Philesiaceae, with perigonal nectaries and tepals with variegated pattern. Philesiaceae could alternatively be placed in Liliales (as in DAHLGREN and RASMUSSEN 1983). Some families of Dioscoreales, especially Smilacaceae and Petermanniaceae, also show similarities to Asparagales, with which they could perhaps be treated with some justification.

A great problem is the circumscription of the families in Asparagales. While most taxonomists seem to be inclined to use a broad family circumscription, others restrict the circumscription and recognize many families. We have preferred not to give them a broader circumscription than is compatible with a probability that they are monophyletic. Exceptions are probably the Anthericaceae and perhaps the Alliaceae, which may turn out to be heterogeneous.

From an evolutionary point of view the Asparagales form a large fairly homogeneous complex of families which seem to have evolved parallel to the Liliales and Dioscoreales. Of primary importance for their recognition are the seed coat characters, especially the strongly deteriorated inner integument and, in most capsule-fruited taxa, *the phytomelan crust* of the outer epidermis. Phytomelan-encrusted seeds in the monocotyledons are probably restricted to Asparagales. Most berry-

Table 1. Comparison between the orders Asparagales and Liliales

	Asparagales	Liliales
Raphides	Common	Often lacking
Roots	Often fusiform, thickened	Rarely fusiform
Habit	Variable, rosette trees, shrubs, etc. rather common, many bulb plants.	No rosette trees, rarely shrubs, most often herbs with thick corms
Succulence	In several families	None
Inflorescence	If delimited from the vegetative region, terminal or axillary, often scapose	If delimited from the vegetative region, usually terminal, rarely scapose
Tepals	Generally not variegated or with drop-like colour pattern	Quite often variegated with drop-like colour pattern
Nectaries	Usually in the septa of the ovary	Mostly on the base of the tepals or filaments (except in the Ixioideae in Iridaceae)
Anthers	Basifixed or dorsifixed-hypopeltate	Basifixed, dorsifixed-epipeltate or tubularly arched over the filament tips ("pseudo-basifixed")
Anther dehiscence	Introrse (except in Ruscaceae)	Introrse, latrorse or often extrorse
Style (stylodia)	Usually simple style	Simple style or three stylodia
Ovules per locule	Numerous to two or one	Numerous
Fruit	Berries or mostly loculicidal capsules	Septicidal or loculicidal capsules (or separate follicles)
Unripe testa	Free from starch (except, for example, in some Asparagaceae and Convallariaceae)	Probably always with starch, disappearing at maturity
Testa	Never sarcotesta	Occasionally sarcotesta
Outer epidermis of testa	Obliterated in most baccate fruits; present and encrusted with phytomelan in capsular fruits	Always present and well developed, free from phytomelan
Tegminal part of seed coat	Usually completely collapsed to form a reddish brown or colourless membrane	The cellular structure usually retained

fruited taxa (exceptions occur in at least *Dianella, Asparagus* and *Geitonoplesium*) lack the phytomelan crust. The seeds are also devoid of phytomelan in a few genera with capsules, such as all Doryanthaceae, Dasypogonaceae, Calectasiaceae and Cyanastraceae and a few species of Hyacinthaceae and Amaryllidaceae. In *Eriospermum* and *Blandfordia* the testa is hairy and in *Walleria* it has wart-like epidermal projections (bearing small hairs); phytomelan is lacking also here, but the taxonomic position of these genera is still uncertain.

Other characteristics mentioned in Table 1 are less consistent and can only be used to support the seed characters. For a few taxa there is great doubt as to their correct position, for superficial gross-morphological characters are opposed, for example, to embryological characters. Thus BJÖRNSTAD (1970) points out that *Disporum* and *Clintonia,* previously referred to Convallariaceae, show better agreement with Uvulariaceae, Colchicaceae and Liliaceae, and the genera are here transferred to Uvulariaceae of Liliales. As they have berries with phytomelanless seeds and are also neutral in most floral characters distinguishing Asparagales from Liliales, their previous position is understandable.

A similar case is Philesiaceae-Luzuriagaceae of Asparagales: the asparagalean affinity of the Luzuriagaceae being supported, for example, by their phytomelan-encrusted seeds. This family group is dubiously homogeneous; several members show affinity in various details with the Alstroemeriaceae, placed in Liliales with some hesitation. The most obvious similarity between the three families is perhaps provided by the inverted leaf blades, for which convergent evolution is a possible explanation, but in view of the similar geographical distribution of the families not indisputable. Philesiaceae (*Philesia, Lapageria*) show some further lilialean attributes, such as spotted tepal pattern and presence of perigonal nectaries.

CONOVER (1983) notes that the Philesiaceae (in our circumscription) show great similarity in venation and other leaf attributes with the Smilacaceae. Thus the Philesiaceae seem to form a link between the liliifloran orders Dioscoreales, Asparagales and Liliales, although this may well be due to derived states. In DAHLGREN and RASMUSSEN (1983) they are treated in Liliales near Alstroemeriaceae.

These cases provide insufficient reason, however, for lumping together indiscriminately the families here placed in Asparagales and Liliales, although if we were utilizing the category of suborder, these orders might appropriately be reduced to that rank and combined in a single order.

The specialized seed coat in the capsule-fruited Asparagales could, according to HUBER (personal communication), be explained by the theory that the common ancestors of the order, like many extant families, had baccate fruits and that in these the seed coat evolved to the point where it lost its protective ability. In a reversion to a second capsular stage the innovation of a phytomelan-encrusted outer epidermis has compensated for the degeneration of cell layers in the testa. This theory of HUBER's receives some support from the findings by BERG (1958), that the capsular fruit in *Trillium,* within the otherwise baccate-fruited Trilliaceae, most likely represents a secondarily capsular stage. Such a reversion represents a case parallel to that proposed for the Asparagales.

The following key has been prepared as a guide to the kinds of character that may be useful for distinguishing between families. It is meant to reflect the structure of the order rather than to be reliable key to identifying the families.

Key to Families of Asparagales

1.	Ovary inferior or semi-inferior	2
1.	Ovary superior	8
2.	Underground parts a (sometimes bulb-like) corm	3
2.	Underground part a rhizome or bulb	5
3.	Ovary semi-inferior	4
3.	Ovary wholly inferior	**Ixioliriaceae**
4.	Seeds with chalazosperm, lacking phytomelan, leaves pseudopetiolate	**Cyanastraceae**
4.	Seeds lacking chalazosperm, with phytomelan, leaves not constricted into a pseudopetiole	**Tecophilaeaceae**
5.	Inflorescence scapose, umbel-like, plants bulbous (seeds generally with phytomelan)	**Amaryllidaceae**
5.	Inflorescence paniculate or racemose, plants rhizomatous	6
6.	Seeds lacking phytomelan (huge rosette plants with bright red bird-pollinated flowers)	**Doryanthaceae**
6.	Seeds with phytomelan (plants variable, incl. huge rosette plants, but flowers then not bright red)	7
7.	Massive, often fleshy rosette plants.	**Agavaceae** (subfam. **Agavoideae**)
7.	Herbaceous non-fleshy plants of small or medium size (hairs often branched)	**Hypoxidaceae**
8.	Fruit a fleshy berry or drupe	9
8.	Fruit hard or leathery, generally capsular, rarely a nutlet	17
9.	Placentation parietal; ovary unilocular	**Philesiaceae**
9.	Placentation not parietal; ovary trilocular	10

10\. Seeds with phytomelan 11
10\. Seeds without phytomelan 13
11\. Leaves small or rudimentary (not inverted), stems often green, sometimes cladodial . . . . **Asparagaceae**
11\. Leaves large and well-developed; no phylloclades 12
12\. Leaf blades non-sheathing, usually with inverted blades . . . . **Luzuriagaceae**
12\. Leaf blades sheathing, usually basally compressed . . . . **Phormiaceae**
13\. Branchlets developed into phylloclades, anthers extrorse . . . . . . **Ruscaceae**
13\. Branchlets not phyllocladial, anthers introrse 14
14\. Flowers small, unisexual, pistil ovate-globose with sessile stigma . . . . **Hanguanaceae**
14\. Flowers variable in size, bisexual, pistil with distinct style 15
15\. Leaves non-sheathing, blades usually inverted . . . . **Luzuriagaceae**
15\. Leaves sheathing, blades not inverted 16
16\. Plants with a thick aerial stem (with secondary growth), or short, basal, but leaves then very thick and fleshy . . . . **Dracaenaceae**
16\. Plants lacking a thick aerial stem, leaves not particularly fleshy . . . . **Convallariaceae**
17\. Seeds without phytomelan 18
17\. Seeds with phytomelan 23
18\. Seeds invested with long hairs 19
18\. Seeds glabrous 20
19\. Perianth syntepalous, campanulate, flowers yellow, orange and red; plant rhizomatous (Australia) . . . . **Blandfordiaceae**
19\. Perianth members free or almost free to the base, flowers more or less open; generally whitish; plants with a tuber (Southern Africa) . . . . **Eriospermaceae**
20\. Seeds with chalazosperm . . . . **Cyanastraceae**
20\. Seeds without chalazosperm 21
21\. Dwarf shrubs, flowers with papery blue tepals, anthers poricidal . . . . **Calectasiaceae**
21\. Herbs, dwarf shrubs or large rosette plants, tepals not blue, anthers longitudinally dehiscent 22
22\. Guard cells rich in oil (New World) . . . . **Nolinaceae**
22\. Guard cells lacking oil (Australia) . . . . **Dasypogonaceae**
23\. Pollen grains spiraperturate (small blue-flowered herbs with reduced leaf blades) . . . . . . **Aphyllanthaceae**
23\. Pollen grains otherwise 24
24\. Pollen grains trichotomosulcate (medium-sized to large herbs with distichous, basally compressed leaves) . . . . **Phormiaceae**
24\. Pollen grains not trichotomosulcate 25
25\. Twiner, leaves in clusters, sometimes opposite (seeds winged) . . . . **Herreriaceae**
25\. Non-twiners, or if twiners leaves not in clusters 26
26\. Plants bulbous (inflorescence scapose) 27
26\. Plants non-bulbous, generally rhizomatous (inflorescence generally not scapose, rarely spicate) 28
27\. Inflorescence generally umbel-like . . . . **Alliaceae**
27\. Inflorescence racemose . . . . . **Hyacinthaceae**
28\. Chromosome complement strongly dimorphic ($x=30$; 5 large and 25 small) 29
28\. Chromosomes more uniform in size and not as above 30
29\. Scapose herbs; leaves strongly veined, pseudo-petiolate; flowers lilac to white, in a one-sided raceme . . . . **Funkiaceae**
29\. Generally large, with short or tall woody trunk; leaves linear, flowers white to yellowish, in panicles or racemes **Agavaceae** (subfam. **Yuccoideae**)
30\. Large rosette plants, often with a tall woody trunk, stomata paracytic, (flowers small, numerous, white, densely crowded in a spike; aril lacking) . . . . **Xanthorrhoeaceae**
30\. Habit different, if woody generally rosette plants, the flowers then not white; stomata generally anomocytic, sometimes tetracytic 31
31\. Plants generally producing anthraquinones instead of steroidal saponins; ovules generally hemianatropous or orthotropous; seeds generally arillate (microsporogenesis simultaneous) . . . . **Asphodelaceae**
31\. Plants producing steroidal saponins; ovules anatropous or (especially in Anthericaceae) campylotropous; seeds not arillate but sometimes with a caruncle (microsporogenesis generally successive, simultaneous in Hemerocallidaceae) 32
32\. Inflorescence a (scorpioid) cyme; perigone yellow to ferruginous, campanulate-infundibular, similar to that in *Lilium*; microsporogenesis simultaneous . . . . **Hemerocallidaceae**
32\. Inflorescence otherwise; flowers generally white, blue or violet; microsporogenesis successive 33
33\. Pollen grains spinulose . . . . **Asteliaceae**
33\. Pollen grains not spinulose . . . . **Anthericaceae**

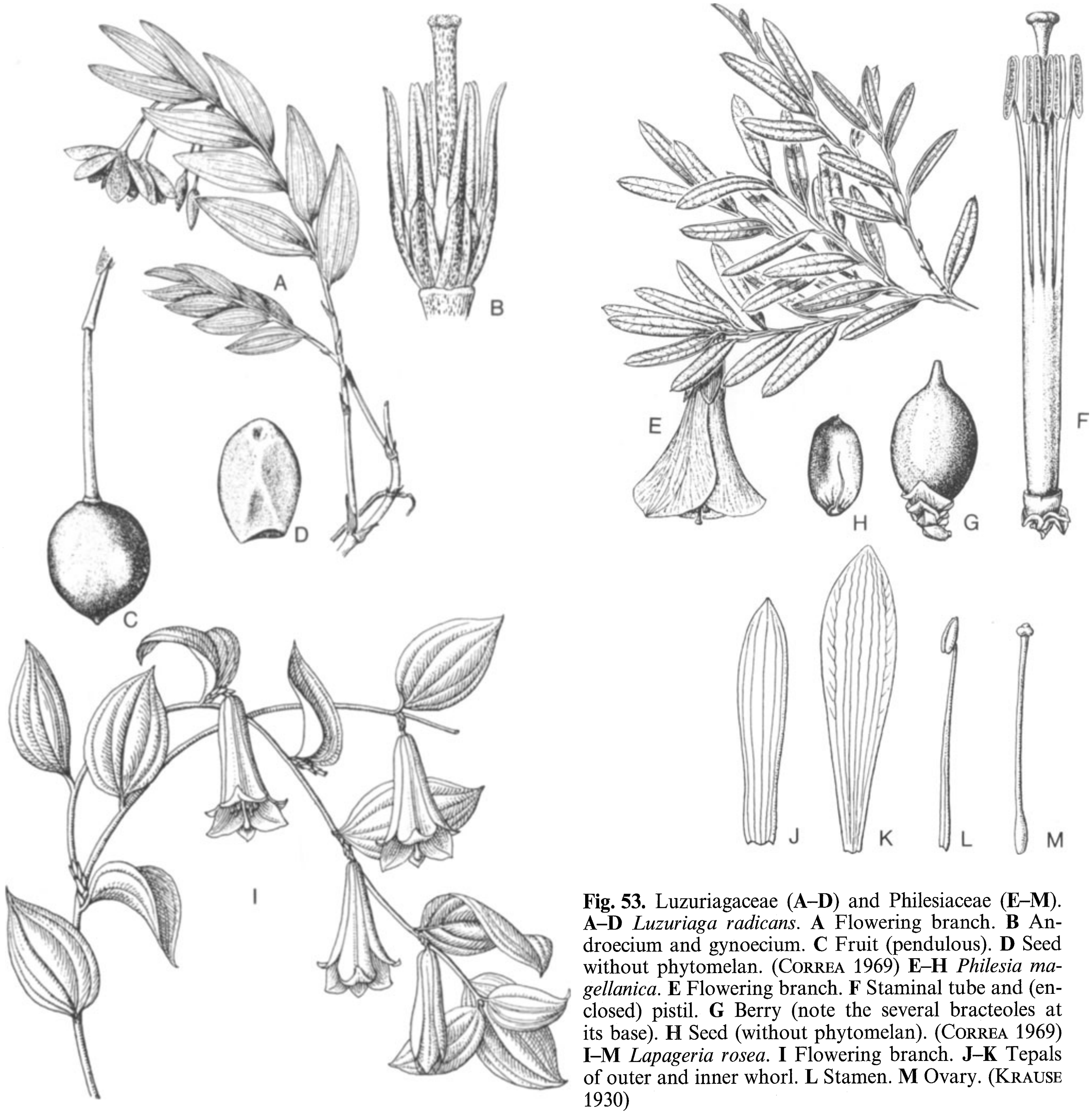


Fig. 53. Luzuriagaceae (**A–D**) and Philesiaceae (**E–M**). **A–D** *Luzuriaga radicans.* **A** Flowering branch. **B** Androecium and gynoecium. **C** Fruit (pendulous). **D** Seed without phytomelan. (CORREA 1969) **E–H** *Philesia magellanica.* **E** Flowering branch. **F** Staminal tube and (enclosed) pistil. **G** Berry (note the several bracteoles at its base). **H** Seed (without phytomelan). (CORREA 1969) **I–M** *Lapageria rosea.* **I** Flowering branch. **J–K** Tepals of outer and inner whorl. **L** Stamen. **M** Ovary. (KRAUSE 1930)

Philesiaceae Dumortier (1829) 2:2 (Fig. 53)

Erect undershrubs (*Philesia*) or vines (*Lapageria*) with woody branches, sometimes ascending from a branched rhizome. Spines are lacking, but crystals may be secreted on the stem surface. The leaves are alternate, sessile or petiolate, sometimes sheathing at the base, entire, ovate to lanceolate or broadly linear and twisted at the base, but the blade is not inverted. They have a few prominent parallel main veins, and between them a distinctly net-like or transverse venation. Vessels and vessel-tracheids occur in roots and stem, but not in the leaves. The stomata are anomocytic, and in *Lapageria* transversely oriented in relation to the leaf axis (CONOVER, 1983).

The flowers are solitary, situated in leaf axils or on the tips of short branchlets. Their pedicels characteristically bear a number of medial, dorsal and ventral scales (in a way superficially resembling that of some Epacridaceae and Ericaceae). The flowers are bisexual, actinomorphic and hypogynous. Their colour is variable, being at least partly rose or purple and more or less spotted on the inside. The two tepal whorls are very different in shape and size in *Philesia,* the outer short and nearly sepaloid. The tepals are free but form a funnel-shaped or campanulate structure. Nectary pouches occur on the base of the tepals.

The stamens are 3+3. Their filaments are free or fused half-way up. The anthers are subbasifixed, extrorse or introrse and dehisce longitudinally. Microsporogenesis is successive (CAVE 1966). The pollen grains are inaperturate and spinulose.

The style is erect and linear and the stigma is capitate or trilobate, and at least in *Lapageria* of the Wet Type (HESLOP-HARRISON and SHIVANNA 1977). The ovary is unilocular with intrusive parietal placentae. The ovules are anatropous and crassinucellate; a parietal cell is cut off before meiosis sets in; the embryo sac is formed according to the *Polygonum* Type; during meiosis the nucellar epidermis divides anti- and periclinally (CAVE 1966). The type of endosperm formation is unknown.

The fruit is a berry with few to numerous seeds, which are globose to ovoid. They sometimes shed the outer epidermis of the testa, which lacks phytomelan and collapses during its development (as with *Smilax*). The endosperm is massive and consists of cells with rather thin non-pitted walls. It contains aleurone and fatty oils. $n=15, 19$.

Chemistry. Steroidal saponins (diosgenin) occur in *Philesia.*

Distribution. The family consists of the genera *Philesia* (1) and *Lapageria* (1), both in South America (Chile).

Philesia magellanica is a sclerophyllous, pink-flowered shrub, with linear leaves. It grows up to one metre in *Nothofagus* forests. *Lapageria rosea* is a vine with elliptic leaves and large campanulate flowers having a drop-like pattern within. The two genera hybridize in cultivation (× *Philageria*).

Luzuriagaceae J. Dostal (1857) 4–5:6–8 (Figs. 53–54)

Slender shrublets or vines with thin, generally branched, woody aerial shoots. The roots in *Geitonoplesium* are fusiform and swollen. The leaves are alternate and distichously inserted, sessile or slightly petiolate, lanceolate to ovate or sometimes linear and nearly grass-like (the habit then approaching that of small bamboos), with the lamina inverted. Their parallel veins are closer and more numerous than in Philesiaceae and in contrast to this family they have only very slight reticulate or transverse venation between the parallel veins or none. Stipules and similar structures are lacking. Vessels are present in the roots and stems and also sometimes in the leaves; in *Geitonoplesium* the leaves may have vessel tracheids (WAGNER 1977). Oxalate raphides occur in most genera.

The flowers, (solitary or) few to several in axillary or terminal cymose inflorescences, are small and hypogynous. The tepals are white to pale violet, free almost to the base or, in *Behnia,* ± fused and campanulate. In *Eustrephus* the inner tepals are fimbriate. As in Philesiaceae the pedicel may bear a number of prophylls. Perigonal nectaries are present at least in *Luzuriaga.*

The stamens are 3+3 in number; their filaments are usually free, and the basifixed or dorsifixed, introrse or extrorse anthers are sometimes poricidal. The pollen grains are sulcate or trichotomosulcate (*Geitonoplesium*).

The style is erect, linear and sometimes short and the stigma is capitate to trilobate and, at least in *Geitonoplesium,* of the Dry Type. The ovary is trilocular with few anatropous or (in *Luzuriaga*) campylotropous, crassinucellate ovules. The fruit is a berry or, in *Eustrephus,* rather a fleshy capsule, as in that genus it opens and exposes the seeds. The seeds in *Geitonoplesium, Eustrephus* and, perhaps, *Behnia* have a testa encrusted with phytomelan, and otherwise agree in having a straight embryo and a massive endosperm, storing fat and aleurone. The seeds are arillate in *Eustrephus.* $x=10$ in *Luzuriaga* (CAVE 1966).

Chemistry. Saponins are lacking in *Luzuriaga,* at least.

Distribution. The family occurs in southern South America, South Africa, Australia and adjacent regions as far as Java, New Guinea, New Zealand and New Caledonia. *Luzuriaga* occurs in South America, New Zealand and the Falkland Islands, and *Behnia* in Southern Africa. *Eustrephus* and *Geitonoplesium* occur in Australasia (and *Drymophila,* which is a dubious member of the family, is Australian).

Luzuriaga (3) (Fig. 53 A–D) consists of shrublets, on which the leaves are horizontally directed. The flowers are rather small, with free white, entire tepals. *Behnia* (1) (Fig. 54) is characterized by having a campanulate syntepalous perianth, to which the filaments are attached. The berries are white

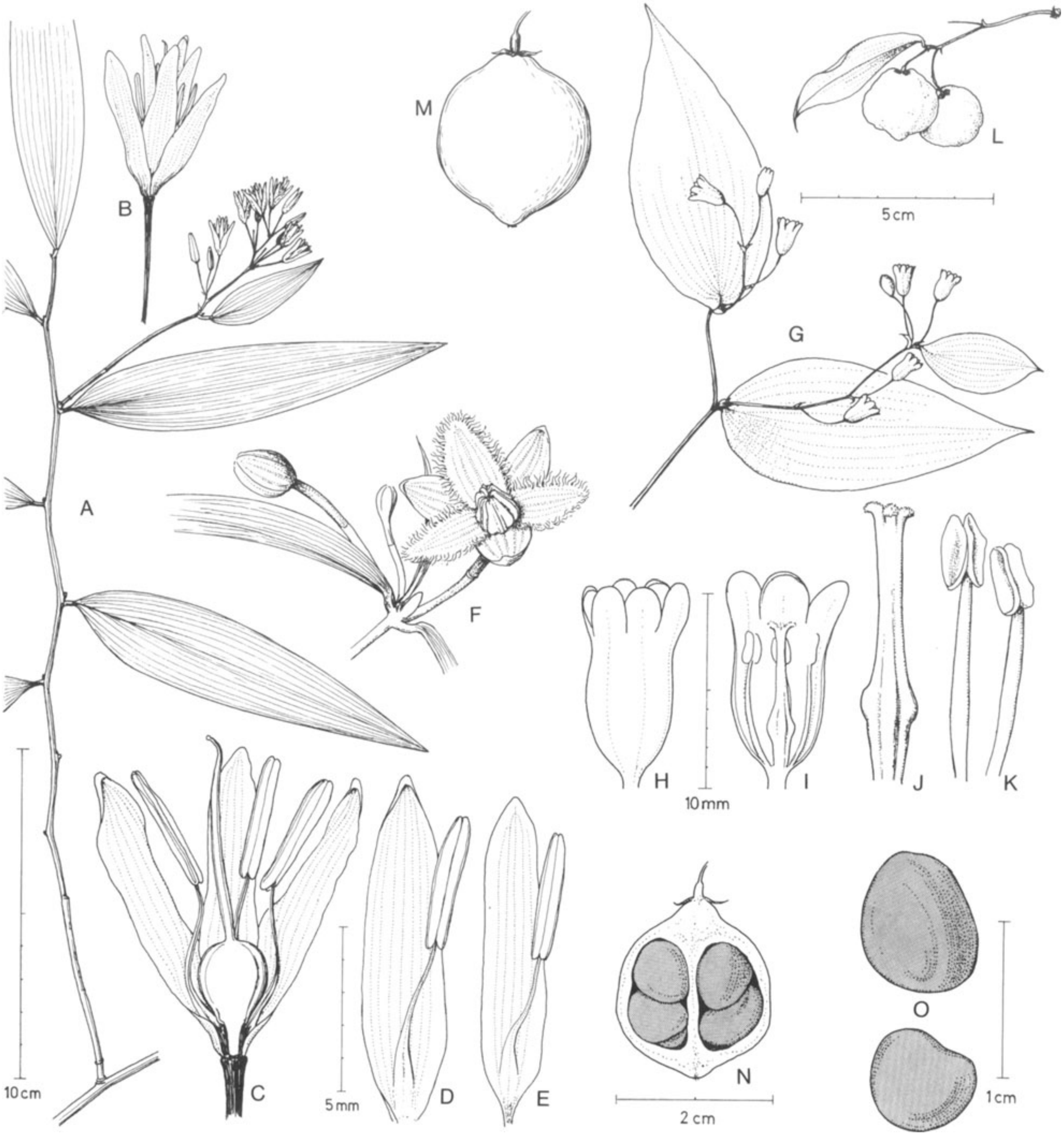


Fig. 54. Luzuriagaceae. **A–E** *Geitonoplesium cymosum*. **A** Flowering branch. **B** Flower. **C** Flower, late stage, with three tepals and three stamens removed. **D** A tepal and a stamen, each of the outer whorl. **E** A tepal and a stamen, each of the inner whorl. **F** *Eustrephus latifolus*. Inflorescence. **G–O** *Behnia reticulata*. **G** Flowering branchlet. **H** Flower. **I** Flower, half of perianth and stamens removed. **J** Pistil. **K** Stamens. **L** Fruiting branchlet. **M–N** Fruit, **N** in longitudinal section. **O** Seeds. The seeds of all these genera finally become dark, even where the fruit is a berry. (All orig. B. Johnsen)

and the large seeds remain almost white until the fruit is quite ripe, when they become dark.

Eustrephus (1) *latifolius* (Fig. 54), with fimbriate inner tepals and flowers basally prolonged into a "pericladium" and yellow fleshy capsules, occurs in Eastern Australia, Java, New Guinea and New Caledonia. *Geitonoplesium* (2; Fig. 54), with black berries, has a similar distribution and habit but extends to Fiji. These two genera have poricidal anthers and black, phytomelaniferous seeds.

Drymophila (2), in eastern Australia, with inverted leaf blades, is usually referred to Convallariaceae, but may be best placed in Luzuriagaceae or possibly in Uvulariaceae. This genus is at present being closely analyzed (Conran, personal communication). The genus *Elachanthera,* sometimes referred to this group of genera, is a synonym of *Myrsiphyllum asparagoides,* as shown by Burbidge (1963).

Convallariaceae P. Horaninow (1834) 19:110 (Figs. 55–56)

Perennial herbs with sympodially or monopodially branching rhizomes, which are often thick and nutrient-storing. A multilayered velamen occurs in the roots of several genera, including *Aspidistra, Tupistra, Ophiopogon* and *Polygonatum.*

The vegetative leaves may be restricted to the base of the aerial stem (as in *Convallaria*) or may be spirally distributed (distichous or non-distichous), opposite or verticillate on an aerial stem. They are sessile or sometimes (as in *Aspidistra* or *Maianthemum*) petiolate and are linear, lanceolate, ovate or cordate in shape. The venation is parallel; stipules and similar structures are lacking. The stomata are anomocytic. Crystal raphides are present and contained in cells or sacs filled with mucilage. Vessels with scalariform or simple perforation plates occur in the roots; very rarely vessels with scalariform perforations occur also in the stem.

The flowers are distributed in various kinds of inflorescences. They are bisexual, actinomorphic, generally hypogynous (hypogynous to epigynous in *Peliosanthes* and *Ophiopogon*), trimerous, except in *Maianthemum* and *Aspidistra,* and with the tepals of the two whorls more or less similar. The tepals are generally connate to form an urceolate or campanulate perigone and are only rarely almost free from each other. They are usually white or greenish, only rarely purplish or of other colour.

The stamens are usually 3+3 (rarely 2+2 or 4+4) in number and sometimes inserted high up in the perianth tube. In *Peliosanthes* the filaments are connate basally. The stamens are basifixed or rarely peltate (*Reineckea*). Anther dehiscence is longitudinal and introrse, and the connective is not protracted beyond the microsporangia, which are not confluent. Microsporogenesis is successive. The pollen grains are sulcate or inaperturate (at least in *Aspidistra*). They are dispersed in the two-celled or (at least in *Polygonatum multiflorum*) in the three-celled stage.

The pistil generally has an erect, simple style and a capitate or lobate stigma which generally or perhaps constantly has a Dry, papillate surface. The locules are separate and contain two or a few ovules each. Septal nectaries are present in most genera. The ovules are anatropous, campylotropous or nearly orthotropous and generally crassinucellate. A primary parietal cell is generally cut off from the archesporial cell. Embryo sac formation is unusually variable in Convallariaceae; generally it conforms to the *Allium* Type, but in certain genera to the *Scilla* (*Smilacina*) or *Drusa* Types (*Maianthemum, Smilacina*). Endosperm formation is of the Nuclear Type.

The fruits in Convallariaceae are normally berries, although those in *Liriope* and *Ophiopogon* are capsules and may rupture to expose the fleshy seeds. The berries vary from red to black or blue or may even be spotted (*Maianthemum*). Where the seeds are fleshy the testa is often bright blue, mimicking a fruit (*Ophiopogon*). In the seeds, the outer integument, which is several-layered, is almost completely obliterated during maturation, and a phytomelan crust is never formed. The inner integument, at least in the European genera, collapses during development (Huber 1969).

The endosperm cells are often thick-walled (with pitted walls) and store aleurone and lipids, but not starch. The embryo is usually more than half as long as the endosperm.

Chemistry. Like the related families, Convallariaceae is characterized by rich contents of steroidal saponins and sapogenins, such as diosgenin and gentrogenin. Poisonous cardenolide glucosides (used as heart poisons and medicines) occur in the berries of *Polygonatum* and *Convallaria,* being especially rich in the latter genus. Chelidonic acid is also found in the family, e.g. in *Convallaria.*

Distribution. Convallariaceae are found chiefly in the Northern Hemisphere. Many taxa occur in the Himalayas and eastern Asia, but also some in North America and Europe. All species are terrestrial, and many grow in montane forests.

The family is divisible into the following tribes:

Tribus Polygonateae

The rhizomes in this tribe are sympodial, the branch generations each ending in an erect stem with a variable number of cauline leaves. The inflorescences are terminal panicles or racemes; less commonly the flowers are solitary or few in the leaf axils. The basic chromosome number is $x=23$.

Fig. 55. Convallariaceae. **A–F** *Polygonatum odoratum*. **A** Flowering, aerial shoot. **B** Flower, half of perianth removed to show pistil. **C** Stamen, lateral view. **D** Style apex and stigma. **E** Berry. **F** Seed. **G–L** *Maianthemum bifolium*. **G** Plant. **H** Flower (note the dimerous condition). **I** Pistil, the wall opened to show placentation. **J** Infructescence. **K** Seed. **L** Berry, transverse section. (From Ross-Craig 1972) **M–Q** *Neolourya thailandica*. **M** Leaf. **O** Flower. **P** Same, longitudinal section. **Q** Fruit. (**M–Q** from Larsen 1966)

Smilacina (20) in Asia, particularly the Himalayas, and North and Central America, has terminal, often multiflorous paniculate inflorescences of flowers with almost free, spreading, white tepals. Some species are grown as ornamentals, e.g. *S. racemosa* with compound "racemes" and edible berries. *Polygonatum* (30) has erect leafy stems with solitary or few, axillary, pendulous, subcylindric flowers. The genus is subcosmopolitan, but chiefly developed in the Northern Hemisphere. The thick,

Fig. 56. Convallariaceae. **A–C** *Smilacina stellata.* **A** Aerial shoot with inflorescence. **B** Flower. **C** Berries. (Hitchcock et al. 1969) **D–G** *Peliosanthes cumberlegii.* **D** Leaf rosette. **E** Aerial shoot with inflorescence. **F** Flower. **G** Same, longitudinal section. (Larsen 1966) **H–K** *Streptopus streptopoides.* **H** Rhizome and fruiting aerial shoot. **I** Part of flowering aerial shoot. **J** Berry. **K** Flower. (Hitchcock et al. 1969). *Streptopus* is a dubious member of Convallariaceae

starch-rich, sympodial rhizomes of some species, mainly in Japan, are eaten as vegetables or preserved in syrup. *Maianthemum* (3) consists of small forest herbs with dimerous flowers.

Tribus Convallarieae

Tribus Convallarieae consists of rhizomatous geophytes. In this feature it agrees with Polygonateae, but while that tribe has a sympodial rhizome, the taxa of Convallarieae have monopodial, continuously growing rhizomes; the aerial stems are thus lateral. Generally there are only a few green assimilating leaves which are inserted at the base. However, in *Reineckea* the stem bears numerous leaves. The inflorescences in this tribe consist of axillary, scapose racemes or spikes with campanulate flowers. *Convallaria* (1) *majalis,* "Lily of the Valley", is a common Eurasian herb. It has usually two cauline leaves and white, campanulate, strongly scented flowers followed by red poisonous berries despite which it is often grown as an ornamental. *Reineckea* (1) *carnea,* in China and Japan, has pinkish, reflexed tepal lobes and large, one-seeded berries.

Tribus Aspidistreae

Tribus Aspidistreae agrees with the Convallarieae in having monopodial rhizomes and lateral aerial stems.

Aspidistra (3) and *Tupistra* (3) are centred in eastern Asia. The former has solitary, rather large, dingily coloured, fleshy flowers, which usually have eight perigone lobes and a large stylar head. It is often grown as an indoor ornamental, but the flowers are seldom observed as they are produced at soil level.

Tribus Ophiopogoneae

Tribus Ophiopogoneae is characterized by a short, thick rhizome, on which the fibrous roots are borne. These are sometimes developed as runners, sometimes thickened into storage organs. The leaves are narrow, lanceolate or linear, sometimes grass-like; the plants may be conspicuously tufted. The inflorescences are panicles, spikes or racemes with bracteate, often small flowers with white or violet tepals. *Liriope* has hypogynous and *Ophiopogon* and *Peliosanthes* hemi-epigynous flowers. In *Liriope* and *Ophiopogon* the tepals are free, in *Peliosanthes* fused into a campanulate perigone; in the last genus the filaments are also united into a ring. The fruit is a berry (*Peliosanthes*) or (the two other genera) a leathery irregularly rupturing capsule, and in these the seeds have a juicy, often bright blue sarcotesta.

This tribe consists of three genera, all Asiatic. The distribution ranges from the Himalayas to Japan and Malesia.

Liriope (5) occurs in China, Japan, and the Philippines. The roots of *L. spicata* are aromatic and have medical use. *L. platyphylla,* with pale violet pearl-like flowers, is grown as an ornamental. *Ophiopogon* (=*Mondo,* 3), from the Himalayas, eastwards, is also often grown as ornamentals ("Black Dragon"), forming tufts.

Peliosanthes (incl. *Lourya*; 10) is also distributed from the Himalayas to South-Eastern Asia.

There are strong indications that some genera normally placed in Convallariaceae, including at least the three southern Asiatic-North American genera *Disporum, Streptopus* and *Clintonia,* are misplaced in this family. As the bacciferous Asparagales generally lack phytomelan pigment in the epidermis of the seed coat, this criterion cannot be used to assign them definitely to the order. A secondarily bacciferous member of the Liliales, of the colchicaceous or uvulariaceous stock, might simulate the convallariaceous phenotype. The combination of attributes in *Disporum* and the other genera mentioned, namely absence of oxalate raphides, presence of perigonal rather than septal nectaries, lack of a parietal cell, and other embryological attributes (Björnstad 1970), suggests that they should be transferred to the Liliales (Uvulariaceae). Also the Australian genus *Drymophila* with coriaceous, inverted leaves may be better placed in Uvulariaceae or in Luzuriagaceae (Asparagales).

Asparagaceae A.L. Jussieu (1789)
3:305 (Fig. 57)

Shrubs, subshrubs or vines with woody or often partly herbaceous, persistent (evergreen) or annually withering branches growing from a short, sympodial rhizome. The roots are often swollen and fusiform, and sometimes provided with multiple velamen. Many species have green assimilating branchlets and a few have branchlets transformed into flat, leaf-like cladodes (phylloclades), as in *Myrsiphyllum* (sometimes included in *Asparagus*). The leaves on the long-shoots are normally reduced and more or less scale-like, as also are those of the short-shoots, if present. The fascicled, green, slender and needle-like to filiform assimilatory structures (as in *Asparagus officinalis*) were shown by Arber (1925) to be of axial (stem) nature. In some species, e.g. *Asparagus densiflorus,* they may bear minute, reduced scale leaves. The vascular tissue of the roots contains vessels with simple or scalariform perforations, and that of the stems usually has vessels with scalariform perforations. Raphide cells are widely distributed in the family. Hairs are mostly lacking.

The flowers are small and solitary or assembled in umbel-like or raceme-like inflorescences which are probably mainly determinate in nature. The flowers are inconspicuous, hypogynous, and either bisexual or unisexual. The 3+3 tepals are all similar in shape; they are free and spreading or fused basally to form a campanulate perigone. Their colour is usually white, yellow or green. In the male or bisexual flowers the stamens are 3+3 in number

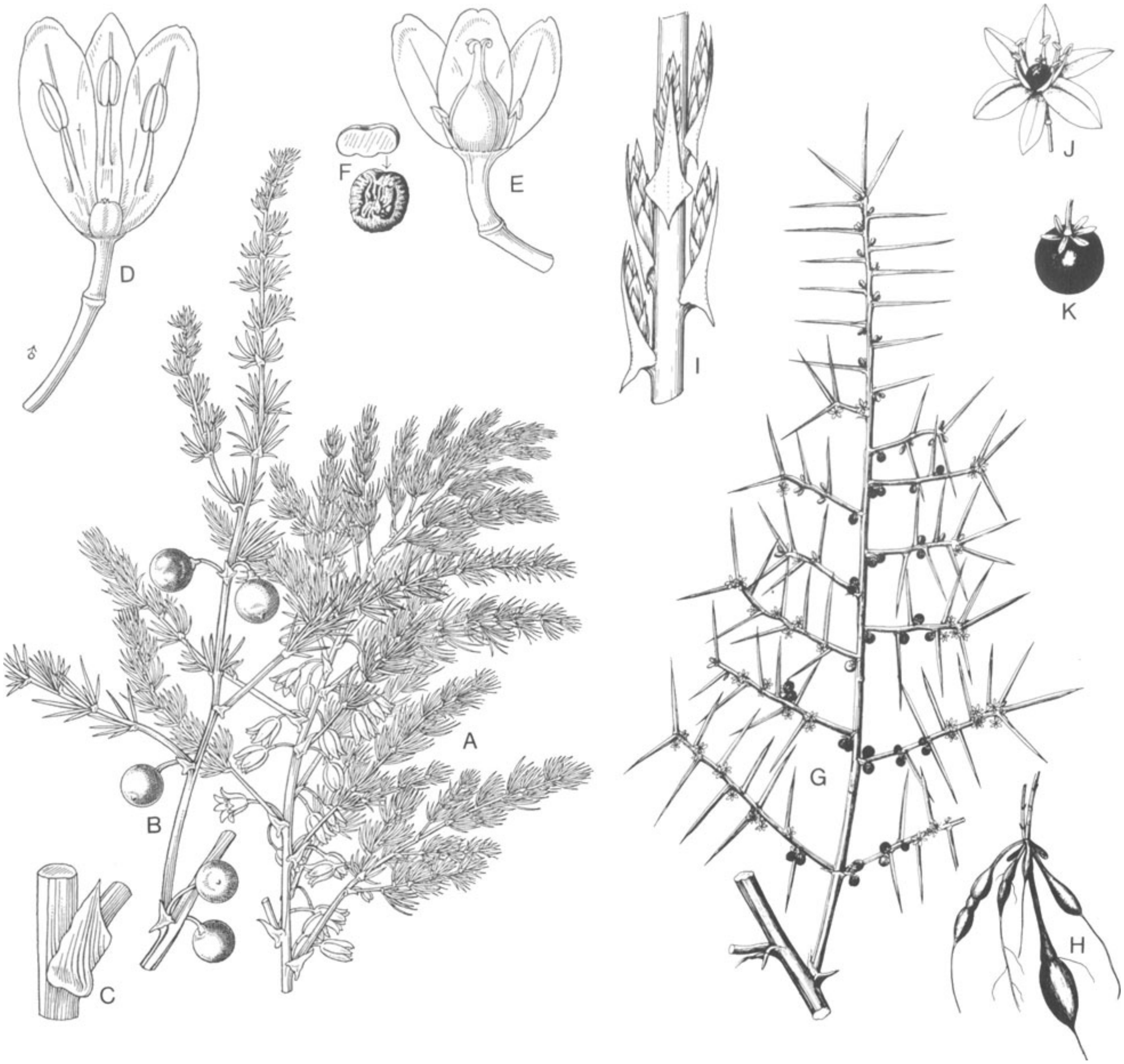


Fig. 57. Asparagaceae. **A–F** *Asparagus officinalis*. **A** Flowering branch. **B** Fruiting branch. **C** Scale leaf subtending lateral branch. **D** Male flower, longitudinal section. **E** Female flower, longitudinal section. **F** Seed. (Ross-Craig 1972) **G–K** *Asparagus stipularis*. **G** Flowering and fruiting branch. **H** Roots. **I** Scale leaves and axillary branchlets. **J** Flower. **K** Berry. (Jafri and El-Gadi 1978)

with the filaments free from each other, and their anthers are introrse-dorsifixed. Microsporogenesis is successive. The pollen grains are sulcate and dispersed in the two-cellular stage.

Where the flowers are unisexual stamens are always present but in the female flowers are nonfunctional (i.e. they do not produce pollen). The ovary is tricarpellary and trilocular and has a rather short style. The stigma is capitate or lobate and is either of the Dry or Wet Type. The placentation is axile and the ovules 2–12 per locule. The ovules are hemianatropous (or anatropous or almost orthotropous) and crassinucellate; a parietal cell is formed. Embryo sac formation is of the *Polygonum* Type and endosperm formation of the Nuclear Type.

The fruit is a globose, red, blue or otherwise coloured berry, the seeds of which have a deep black outer epidermis. The endosperm is starch-free and contains aleurone and lipids. The embryo in *Asparagus* may be slightly curved; it is from two thirds to almost as long as the endosperm.

Chemistry. Oxalate raphides are widespread in the family and chelidonic acid, acetidine carbonic acid and steroidal saponins are recorded in various species. Especially the rhizomes and swollen root tubers of *Asparagus* have been found to be rich in saponins, which can be obtained from, for example, rhizomes in *A. officinalis* and *A. acutifolius* or from roots of *A. thunbergianus*.

Distribution. Asparagaceae are widely distributed in the Old World; most species are found in regions with arid to Mediterranean climates, and extreme xeromorphic adaptations are common. Many species are practically leafless shrubs with thick underground stems or roots, which store water and nutrients. Assimilation is carried out by the green branch ends and branchlets.

Three genera may be distinguished: *Asparagus, Protasparagus* and *Myrsiphyllum,* the last two of which are perhaps best treated as subgenera of the first.

Asparagus and *Protasparagus* together comprise almost 300 species. *Asparagus* is widely distributed in the Old World, with many species in the Mediterranean Region and in Africa and part of Asia. It consists mainly of xeromorphic shrubs or shrublets but also of herbs. Common xerophytic species in the Mediterranean area are, for example, *A. stipularis, A. aphyllus* and *A. thunbergianus*. The young shoots of some species are used as vegetables, in particular those of *A. officinalis,* "Garden Asparagus", growing wild in temperate Eurasia. This species is widely cultivated and of great economic importance. Its seeds can be used as coffee substitute. Roots or tubers of some other species are edible, e.g. of *A. abyssinicus* in Northern Africa, of *A. lucidus* in China and Japan, and of *A. densiflorus* in Southern Africa. The more primitive genus, *Protasparagus,* with at least nearly 70 species, differs from *Asparagus* in several features. In *Protasparagus* the flowers are bisexual (whereas in *Asparagus* the flowers are unisexual and the plants dioecious), there are 4–12 ovules per locule (in *Asparagus* only 2), and the seeds are globose (in *Asparagus* they are dorsally convex and ventrally angular) (Obermeyer 1983). – Flat cladodes occur in the genus *Myrsiphyllum* (12) in Southern Africa.

Asparagaceae, when given family status, is often circumscribed so as to include also the Ruscaceae, but these two groups are widely different, as will be shown below, and we consider them distinct here. Both of these are probably most closely related to the Convallariaceae, Herreriaceae and Dracaenaceae.

Ruscaceae Hutchinson (1934) 3:8 (Fig. 58)

Subshrubs, often forming low thickets, or vines. The basal parts are woody and rather slender, and the branchlets are developed as flat assimilatory phylloclades which are ovate to lanceolate and pointed, (they are highly reminiscent of the leathery leaves in Luzuriagaceae). The phylloclades are alternate, opposite or even verticillate. The roots may have multiple velamen (known in *Semele*). The leaves are reduced and scale-like. The vascular tissues of the roots have vessels with scalariform and simple perforation plates, and vessels are either present or lacking in the stems, if present having scalariform perforation plates. Raphides occur throughout the plant. The stomata are anomocytic. Hairs are lacking.

The flowers are small and inconspicuous and occur in raceme-like clusters on the upper or the lower surface of the phylloclades (*Ruscus*), in umbel-like clusters on their margins (*Semele*), or in terminal racemes quite separately from the phylloclades (*Danaë*). In *Ruscus* and *Semele* the inflorescence is subtended by a single, scale-like or herbaceous leaf. The flowers are articulated with their pedicels. They are actinomorphic, hypogynous and bisexual or, in *Ruscus,* unisexual (bisexual and male occasionally in one species). The tepals are inconspicuous, greenish to pale yellowish-white, all more or less similar in size and shape; in *Danaë* they form an urceolate perigone. The stamens are fused by their filaments into a column and have extrorse, tetrasporangiate anthers. Microsporogenesis is successive and the tapetum glandular. The pollen grains are dissimilar to those in Asparagaceae in being inaperturate, at least in some taxa. They are dispersed in the two-celled stage.

The pistil is tricarpellary, and lacks or has only a very short style. The sessile or subsessile stigma has a Wet surface (at least in *Ruscus*). The ovary has one or three locules, each with (one or) two hemianatropous or orthotropous ovules. The embryo sac formation is reported to be of the *Allium* Type. The fruit is a red berry with one to four seeds. These are pale (not black as in Asparagaceae) and have a collapsed testa and a thick tegmen (unusual in Asparagales). The embryo is less than half as long as the endosperm. When germinated the seedling, except in some species of *Ruscus,* produces petiolate assimilating leaves with a flat lamina.

Chemistry. The chemistry of Ruscaceae is obviously similar to that in Asparagaceae, containing raphides, steroidal saponins, and chelidonic acid.

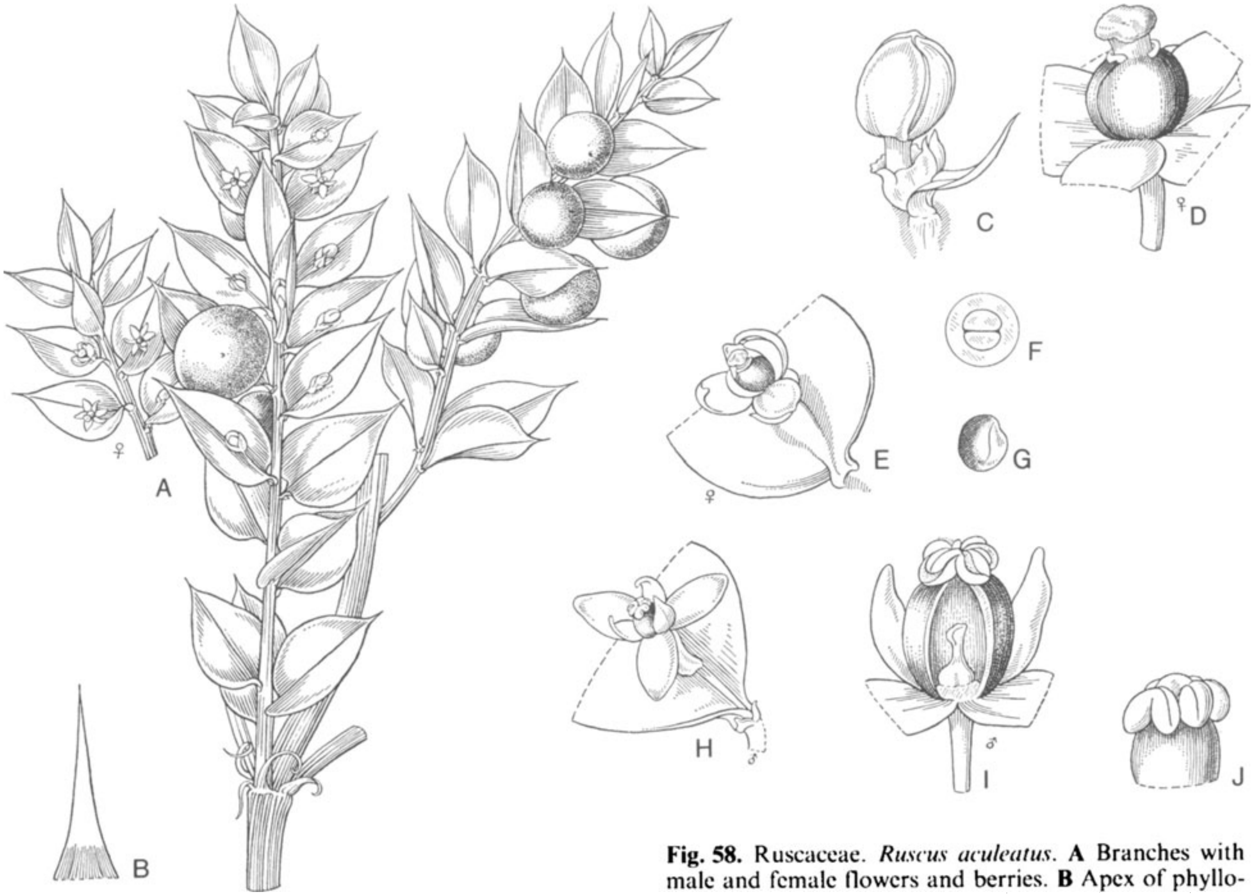


Fig. 58. Ruscaceae. *Ruscus aculeatus*. **A** Branches with male and female flowers and berries. **B** Apex of phylloclade. **C** Bract, bracteole and bud of female flower. **D** Pistil of female flower protruding from the staminal tube which has a rim formed by vestigial anthers. **E** Female flower in position on phylloclade. **F** Ovary, transverse section. **G** Seed. **H** Male flower in position on phylloclade. **I** Male flower, part of perianth cut away. **J** Staminal tube and anthers before dehiscence. (Ross-Craig 1972)

Rutin is found in the phylloclades of *Ruscus* and *Danaë*.

Distribution. Ruscaceae have a pronounced Mediterranean-Macaronesian distribution. The family consists of the following three genera.

Danaë (1), in forests from Syria to Iran, is a subshrub with terminal, raceme-like inflorescences with bisexual flowers free from the phylloclades, which are rather soft and mesomorphic. The flowers have six anthers. – *Semele* (1), a tall climber, in Macaronesia, has its inflorescences marginally on the phylloclades. The flowers, as in *Danaë*, are bisexual, and the anthers six in number.

Ruscus (6) (partly revised by Yeo 1968), which is mainly Mediterranean in distribution, has stems that are either unbranched or branched once (disregarding the cladodes). The inflorescences are generally situated centrally on the adaxial or abaxial side of the cladodes. The flowers are generally unisexual, their green tepals often minutely dotted with violet. The staminal tube is fleshy, papillate and violet. It is equally well developed in female and male flowers. There are three anthers, the 12 microsporangia of which are fused to the rim of the staminal tube. *R. aculeatus* is the commonest and most widely distributed species. It has stiff, ovate, pointed phylloclades. The young shoots, as in some *Asparagus* species, can be used as a vegetable.

Herreriaceae S.L. Endlicher (1836) 2:9 (Fig. 59)

Climbing or twining subshrubs with subterranean tuberous rhizomes and with stems sometimes armed with prickles (as in *Smilax*). Vessels with scalariform perforation plates are recorded in the stem of *Herreria*. The leaves are concentrated in lateral clusters. They are linear or linear-lanceolate, sessile and somewhat coriaceous (cladode-

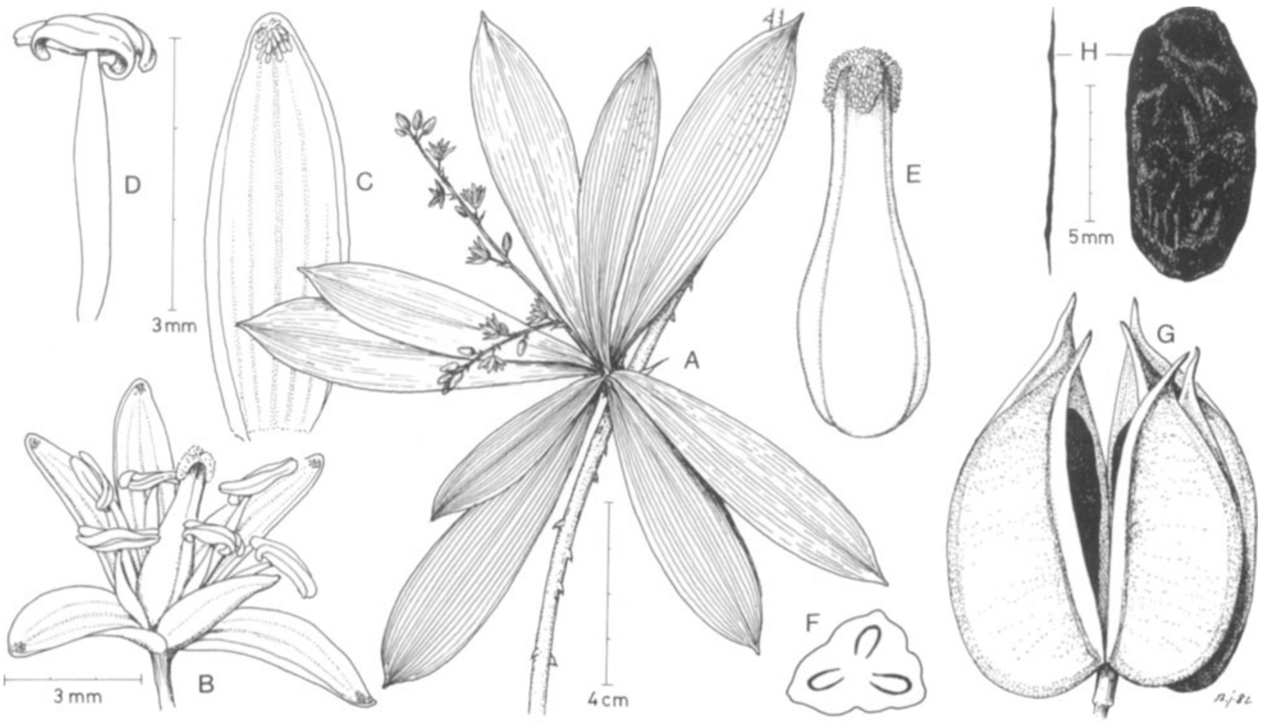


Fig. 59. Herreriaceae. *Herreria sarsaparilla.* **A** Part of branch with short shoot and inflorescence. **B** Flower. **C** Tepal. **D** Stamen. **E** Pistil. **F** Ovary, transverse section. **G** Capsule. **H** Seed in different views. (Orig. B. Johnsen)

like) with numerous parallel veins. Paniculate inflorescences, which are basally provided with several small, scale-like leaves, are situated in the leaf axils. The flowers have an articulate pedicel and are actinomorphic, hypogynous and bisexual. They have 3 + 3, spreading, free tepals, all of the same size and shape, 3 + 3 free stamens with basifixed, longitudinally dehiscent anthers, and a trilocular pistil with erect style and a small capitate stigma. The pollen grains are sulcate (Kuprianova 1948). Septal nectaries are present in the ovary. The ovules, one to many in each locule, develop into flattened, helically winged seeds, encrusted with phytomelan. Endosperm is copious and the embryo is small. The fruit is a trilobate, septicidal capsule.

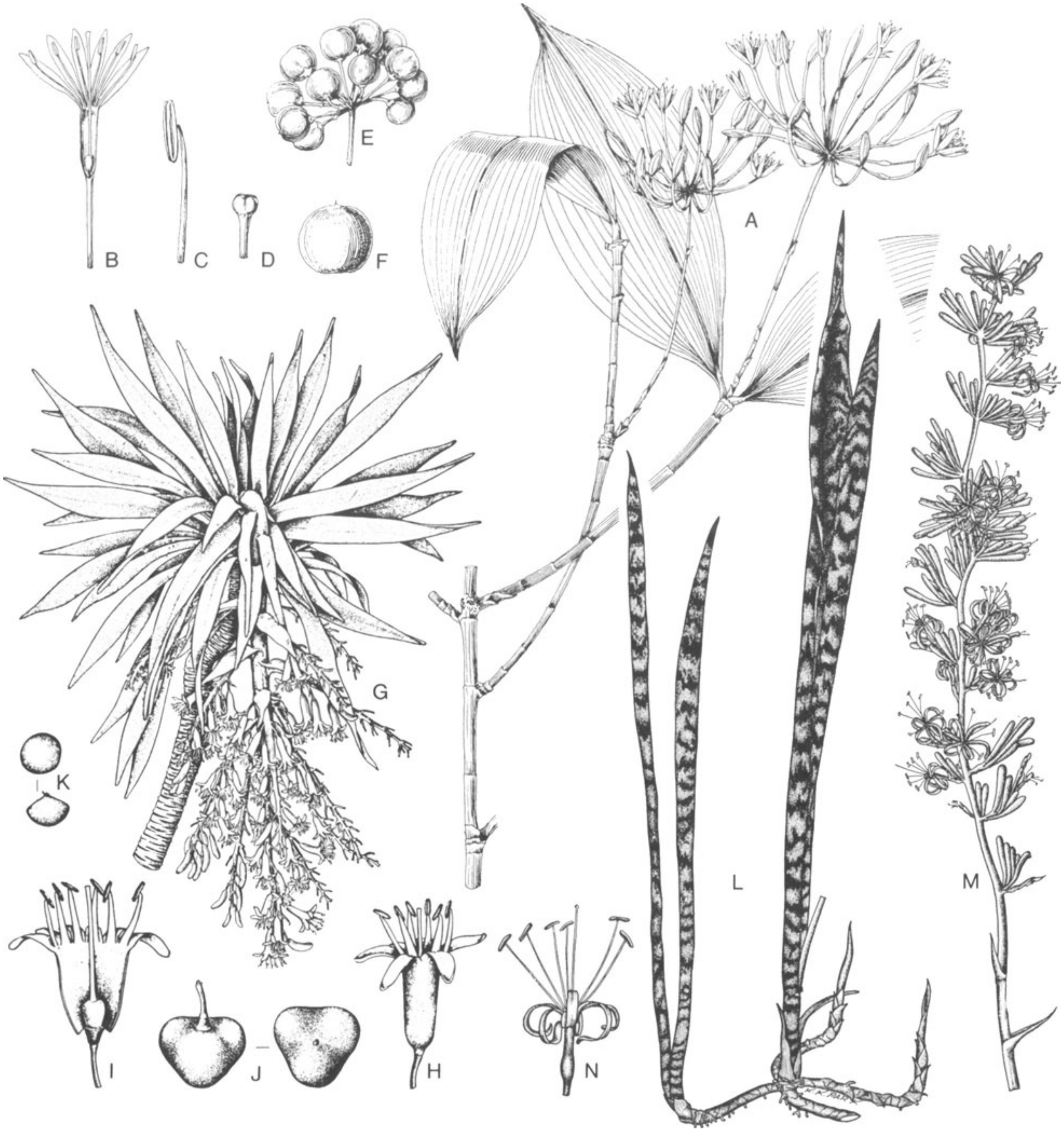
Herreria (7) occurs in temperate to subtropical South America and the other genus, *Herreriopsis* (2), occurs on Madagascar. *Herreria sarsaparilla* is common in moist forests in eastern Brazil.

The family, though having capsules, seems to approach the previous ones, but the exact affinities are not clear.

Dracaenaceae R.A. Salisbury (1866) 1–2:130 (Fig. 60)

Plants with a more or less woody trunk (*Dracaena*) or mostly without trunk (*Sansevieria*), the stem in the latter case short and partly subterranean. Trunk when present very variable in height and thickness, sometimes scandent, rarely considerable as with the trees of *Dracaena draco,* which may become many metres high and more than 2 m thick. In *Dracaena,* as well as *Sansevieria,* as in several genera of the Nolinaceae, there is extensive secondary thickening growth in the stem, caused by a meristematic zone continuously forming additional tissue in which new bundles are differentiated. The result is a great number of scattered vascular strands in which there are no real vessels, only tracheids. However, vessels are found in the roots and leaves, those in the roots mainly with simple and those in the leaves with scalariform perforation plates.

The leaves are narrowly linear to ovate and sessile, and have parallel venation. They may be of considerable size and in *Sansevieria* they are conspicuously succulent and sometimes terete or tubiform. They are frequently concentrated in rosettes either on the ends of aerial branches or (*Sansevieria*) from the apex of a mostly subterranean rhizome. The stomata are anomocytic; their guard



cells, unlike those in Nolinaceae, do not contain oil. Non-suberized, mucilage-filled cells with crystal raphides are present in the vegetative parts, whereas in Nolinaceae there are suberized cells with solitary, needle-like pseudo-raphides.

The inflorescences are axillary and pedunculate, emerging either from the leaf rosettes, i.e. from near the ground, in *Sansevieria,* or on the ends of the branches, in *Dracaena*. They consist of racemes or panicles, which may be elongate or may form pseudo-umbels. The flowers are articulated

Fig. 60. Dracaenaceae. **A–F** *Dracaena surculosa.* **A** Branches with inflorescences. **B** Flower, longitudinal section. **C** Stamen. **D** Style apex with stigma. **E** Infructescence. **F** Berry. (Hepper 1968) **G–K** *Dracaena fernaldii.* **G** Branch with inflorescence. **H** Flower. **I** Same opened to show pistil. **J** Berry. **K** Seeds. **L–N** *Sansevieria guineensis.* **L** Rhizome with leaves. **M** Inflorescence. **N** Flower. (**G–N** from Degener and Greenwell 1956)

on the pedicel, and are bisexual and hypogynous, with the elongate perianth members all of the same shape and size and connate at the base. The 3+3 stamens are inserted at the base of the lobes, and have dorsifixed, epipeltate, introrse anthers which dehisce longitudinally. Microsporogenesis is successive. The pollen grains are sulcate and two-celled.

The pistil is trilocular with an erect, simple, rather slender style and a trilobate or capitate stigma, which has been reported to be of the Wet Type in *Dracaena.* The ovary has septal nectaries. There is only one anatropous ovule in each locule (two in the Nolinaceae). No parietal cell is cut off from the archesporial cell but periclinal divisions occur in the nucellar epidermis, giving rise to a nucellar cap over the embryo sac (STENAR 1942). Embryo sac formation is of the *Polygonum* Type and endosperm formation is probably nuclear.

The fruit is generally a red or orange-coloured berry with up to three globose or elongate seeds, but sometimes it is hard and woody. The seed coat has a three to four-layered outer integument, the outer epidermis of which is thick-walled and lacks phytomelan, while the cells of the inner integument have collapsed and form a reddish brown membrane. The endosperm consists of cells with pitted walls and it stores aleurone and lipids but no starch.

Chemistry. Steroidal saponins occur in both genera; chelidonic acid is known at least in *Dracaena.* Resins are often secreted in the bark of species of *Dracaena;* by oxidation with nitric acid they yield the polycarbonic dracaenic and draco acids.

Distribution. The Dracaenaceae occur in subtropical-tropical regions of the Old World, both in rain forests and savannah.

Although the two genera are fairly different in appearance, they are very closely related and even dubiously distinct from each other.

Dracaena, with perhaps 80 species, but sometimes considered to contain up to 150 species, ranges from Macaronesia and subtropical Africa through Asia to northern Australia. It has a slender or occasionally very thick stem which may be of considerable height and the leaves vary from linear (almost grass-like) to broadly lanceolate. – *D. draco,* the "Dragon Blood Tree", on the Canary Islands may reach a height of 15 m or more and finally develops a thick trunk. Resins extracted from the stems can be used for varnishes, paper pigment and medicines. Other tree-like species are *D. reflexa* and *D. arborea* on Mauritius. Many species are slender subshrubs or shrubs. Other resin-producing species are *D. cinnabari* on Socotra and *D. schizantha* in Arabia and tropical East Africa. The shoots of *D. mannii* in eastern Africa can be used as a vegetable. *D. draco* is often grown as an ornamental tree and *D. fragrans, D. marginata* and other species are ornamental foliage plants.

Sansevieria (50), ranging from Africa through Asia to Burma, consists of acaulescent rosette plants with more or less stiff, often variegated, leaves which contain tough fibres. The panicles are scapose and have pale yellow or cream-white flowers. Several species (*S. trifasciata, S. zeylanica, S. senegambica,* etc.) yield hemp, and various forms of *S. trifasciata* are common and tolerant foliar ornamentals.

Nolinaceae T. Nakai (1943) 3–4:50 (Fig. 61)

Woody, generally large, arborescent plants with a stout, simple or sparingly branched trunk up to a few metres tall, with terminal leaf rosettes. Stem with secondary thickening growth of the kind described for Dracaenaceae. Vessels have not been recorded in the stems, but may occur in the leaves, where they have scalariform perforation plates (*Nolina*). The leaves are generally linear, sessile, parallel-veined, and have sunken stomata with oily contents. Suberized cells with pseudo-raphides (but not bundles of true raphides) occur in the family.

The inflorescences are panicles, often considerable in size and profusely flowered. The flowers are articulated on their pedicels, actinomorphic, hypogynous and polygamodioecious or dioecious. Their tepals are all equal, and are free from each other. There are 3+3 stamens, which have epipeltate anthers. The pollen grains are sulcate.

The pistil is generally trilocular, as in Dracaenaceae, rarely unilocular (*Dasylirion*). The ovary has septal nectaries. The style is relatively short. Each locule has two axially inserted ovules; in the unilocular ovary of *Dasylirion* there are three to six basally situated ovules. The ovules are anatropous; no parietal cell is cut off from the archesporial cell, nor are there any periclinal divisions in the nucellar epidermis; the embryo sac therefore becomes situated immediately below the epidermis. Nuclear endosperm formation has been recorded in *Nolina.* The fruit, unlike that in Dracaenaceae, is more or less dry and indehiscent, functioning rather as a nutlet than a berry (to

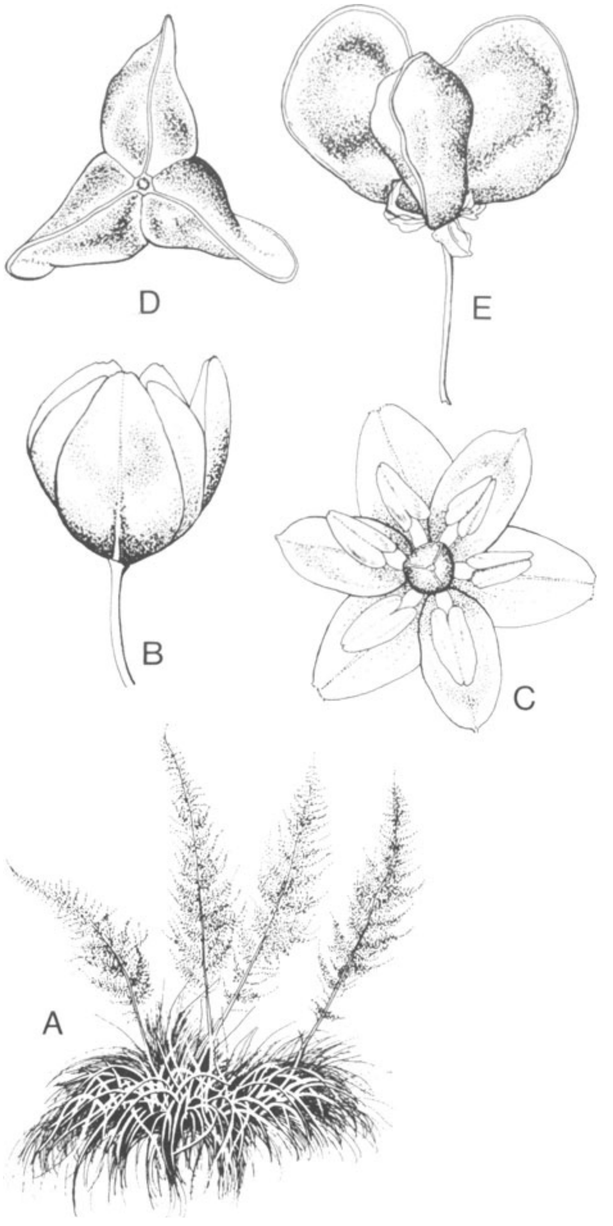


Fig. 61. Nolinaceae. *Nolina microcarpa*. **A** Habit, the inflorescences are to 2 m or more. **B–C** Flower in side and front view. **D–E** Fruit, top and side views. (Cronquist et al. 1977)

which, however, it closely corresponds). The seeds lack phytomelan and are similar to those in Dracaenaceae (Huber 1969).

Chemistry. At least *Nolina* contains rich amounts of diosgenin, a steroidal saponin.

Distribution. Nolinaceae comprise three (to four) genera in the warm parts of America.

Nolina (25) in Texas, California and Central America has linear, tough leaves. Its flowers have trilocular ovaries which develop into triangular or three-winged fruits. The leaves are used for thatching, mats, baskets, hats, etc. – *Dasylirion* (20–25), in the same regions, has inflorescences which are often of considerable size. The pulp from the shoot apex of *D. texanum* contains sugar and was used by the Indians as food or for preparing a beverage ("sotol"). The leaves of *Dasylirion* may also be used for basket work.

Asteliaceae Dumortier (1829) 4:50 (Fig. 62)

Dwarf to quite large herbs or woody rosette trees or shrubs, some species of *Cordyline* (e.g. *C. australis*) forming veritable trees up to 10 m high. Secondary thickening growth occurs at least in *Cordyline*. The herbs have a thick, tuberous underground rhizome. The leaves are spirally set or sometimes (in *Cordyline*) distichous. They are dorsiventral, mesomorphic to leathery and stiff, parallel-veined, linear to broadly lanceolate or elliptic, and occasionally constricted between sheath and lamina, or even pseudo-petiolate, e.g. in *Cordyline fruticosa*. The leaves at least in *Astelia* have paracytic stomata. Raphides are present in most taxa, e.g. *Cordyline* (they are absent, however, in *Astelia banksii*). In *Cordyline* the axis of the shoot may contain suberized cells with pseudo-raphides, but raphide cells may be present as well (Huber 1969). Vessels seem to be lacking both in the stems and leaves.

The inflorescence consists of a system of bracteate racemes (or spikes), situated on the ends of leafy or leafless shoots. The flowers are hypogynous, trimerous and actinomorphic and have 3 + 3 tepals which are free or basally connate, and all of the same size and shape. They may be brownish or greenish (*Astelia*) or violet or white (e.g. *Cordyline*). The stamens are 3 + 3 in number and have basifixed or nearly basifixed, introrse anthers, which dehisce by longitudinal slits. The tapetum is secretory, and microsporogenesis, as far as known, is successive. The pollen grains are sulcate, spinulose in at least *Astelia* and *Milligania*, but non-spinulose in *Cordyline*.

The pistil is usually tricarpellary, either trilocular with axile placentation or, rarely, in some species of *Astelia* (where there may be four carpels), unilocular with parietal placentation. The style, although relatively long and simple in *Cordyline* and in some species of *Milligania*, is generally short or is lacking altogether in the other taxa, so that the stigma is subsessile or sessile. The stigma is

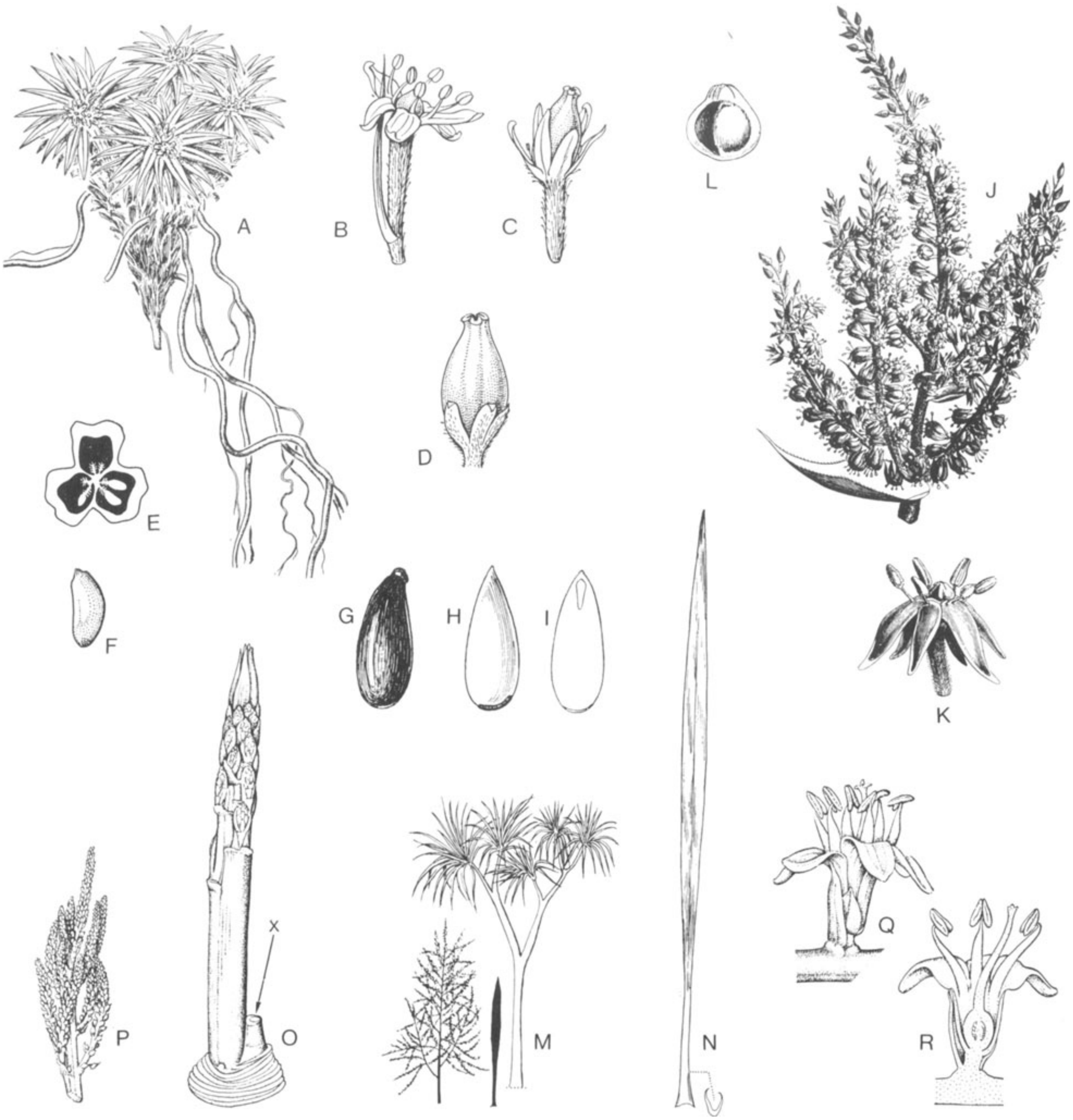


Fig. 62. Asteliaceae. **A–I** *Astelia pumila.* **A** Habit. **B** Flower. **C** Flower in late stage. **D** Fruit. **E** Ovary, transverse section. **F** and **G** Seeds. **H** Same, testa removed. **I** Seed, longitudinal section. (**A** from CORREA 1969; **B–D** and **F** from TAKHTAJAN 1982; **E** and **G–I** from CABRERA 1968) **J–L** *Astelia cunninghamii.* **J** Part of inflorescence. **K** Flower. **L** Fruit. (KRAUSE 1930) **M–N** and **Q–R** *Cordyline banksii.* **M** Tree, inflorescence and leaf, schematic. **N** Leaf. **Q** flower. **R** Same, longitudinal section. **O–P** *Cordyline australis.* **O** Young inflorescence (*x* lateral renewal shoot). **P** Inflorescence in early bud stage. (**M–R** from TOMLINSON and FISHER 1971)

Dry (at least in *Astelia* and *Cordyline*). Each locule contains 4 to ca. 15, anatropous or (in *Cordyline*) campylotropous ovules. The embryological information is incomplete.

The fruit is mostly more or less baccate, varying from fleshy to fairly dry (species of *Cordyline*), but in *Milligania* it is a globose capsule splitting from the apex. The seeds are ovate and often angular. Their testa is encrusted with phytomelan (even in the baccate forms). The embryo is straight and only a third to half the length of the endosperm.

Chemistry. Steroidal saponins occur in *Cordyline* and saponins have also been recorded in *Astelia*.

Distribution. Asteliaceae are distributed mainly in the Southern Hemisphere, but are absent from South Africa. *Astelia* itself has a highly disjunct distribution including Chile, Hawaii, the Marquesas, Tahiti, Samoa, Fiji, New Zealand, New Guinea, Australia and Reunion. *Cordyline* is even more widely distributed, occurring in Africa and South America as well as around the Pacific.

Astelia (25) consists of large to diminutive rhizomatous herbs with somewhat grass-like leaves. The stomata in the genus are reported to be paracytic, which is of particular interest. The colour of the tepals is green, dull red or fawn. All species are normally dioecious. Some species are large-growing herbs with leaves up to more than 2 m long, while others, like *A. pumila* (Fig. 62A–J) in Chile, are small and cushion-like with leaves only about 2–5 cm long. *A. grandis* in New Zealand is used for its tough fibres; another species, *A. nervosa,* in the same country, has edible berries, once used as food by the Maoris. *A. cunninghamii* is sometimes cultivated as an ornamental. *Milligania* (4), in Tasmania, differs from *Astelia* in having bisexual flowers and capsular fruits.

Cordyline (20) is distributed over Indomalaysia, New Zealand, Polynesia, Hawaii, Australia and even Africa, with one species, *C. dracaenoides,* in Brazil. The genus consists of shrubs and arborescent forms with leathery or stiff leaves, concentrated towards the ends of the branches. The flowers are yellow, greenish, blue or lilac. Their tepals are basally fused, with the lobes often recurved. Unlike *Astelia* the style is rather long and the ovules are campylotropous, but the genera agree (convergence?) in having baccate fruits with black seeds. *C. roxburghiana* and *C. australis* (Fig. 62O–P) are used for their fibres, and the underground parts of *C. terminalis* are fermented and used for a beverage, and the leaves to wrap fish, etc. The last two species among others are commonly grown as ornamentals.

It may seem that the Asteliaceae form a somewhat heterogeneous assemblage, but a small genus, *Cohnia* (2), in the Mascarenes and New Caledonia, may connect *Cordyline* with *Astelia* and *Milligania*. The basic chromosome numbers, $x=8$ in *Astelia* and $x=19$ in *Cordyline,* do not indicate a close connection. The former and the latter pairs of genera doubtless form two easily defined tribes within the family.

The family Asteliaceae shows some connection with the Asphodelaceae, and in the baccate fruit with black seeds it also resembles the Phormiaceae, although the similarity is most probably due to convergence. The two families differ markedly in pollen morphology.

Hanguanaceae Airy Shaw (1965) 1: >2 (Fig. 63)

Somewhat grass-like perennial herbs with thick creeping rhizomes, having a distinct endodermis and a loose central tissue with scattered, closed fibrovascular bundles. Aerial stems erect, with the linear or lanceolate leaves mostly concentrated towards the base. The leaf base is sheathing and pseudopetiolate and the lamina has supervolute ptyxis and pinnate-parallel venation with the distinct main veins diverging at intervals, and at a narrow angle, from the midvein (Cronquist 1981). Vessels are lacking in stems and leaves, but present in the roots, where they have scalariform perforation plates (Tomlinson 1969). The aerial parts have short, uniseriate but branching hairs. Tanniniferous cells are common. The stomata are tetracytic (Tomlinson 1969). Scattered cells with granular silica bodies occur in the endodermal cells around the vascular bundles, and larger silica bodies in hypodermal and mesophyll cells on the abaxial side of the leaf.

The inflorescence is a much-branched, bracteate panicle with small, unisexual flowers terminating the branchlets. The plants are dioecious, and the flowers actinomorphic. There are 3+3 tepals, which are small, rounded and pale, the outer being somewhat smaller than the inner. The male flowers have 3+3 stamens with long slender filaments (wind pollination) and basifixed, tetrasporangiate anthers which dehisce longitudinally. The axis in male flowers has conspicuous fleshy bodies. The pollen grains are inaperturate and spinulose. The female flowers have 3+3 staminodes, and a tricarpellary ovoid to globose pistil with a sessile, broad, triangular stigma (similar to that in *Astelia*). The ovary is trilocular and has one axile, nearly orthotropous ovule in each locule. The ovule has a funicular obturator and develops into a bowl-shaped seed with extensive endosperm and a small embryo.

The genus *Hanguana* (syn. *Susum*) (>2), occurs in Ceylon and Eastern Asia (Thailand to Australia). Its position is not yet settled. The presence of silica bodies, the tetracytic stomata, and the

Fig. 63. Hanguanaceae. *Hanguana malayana.* **A** Erect shoot and part of rhizome, the latter in longitudinal section. **B** Part of male inflorescence. **C** Male flower, note the basal callosities. **D** Part of female inflorescence. **E–F** Buds of male flowers. **G** Fruit. **H** Fruit, longitudinal section showing the seed. **I** Seed. **J** Seed, longitudinal section. (Orig. B. JOHNSEN)

seed shape do not support a position in Asparagales, but lack of vessels in the stem, lack of starch in the endosperm and other features indicate that *Hanguana* is after all closest to Asteliaceae (or Dasypogonaceae).

On Ceylon the species grows on the borders of pools and in swamps, where the rhizomes may form a veritable mat. Flowering of this form is rare. The forest floor *Hanguana* found in South-Eastern Asia is rather different and often flowers. These are probably not conspecific.

Dasypogonaceae Dumortier (1829) 7:53
(Figs. 64–65 and 68)

Mainly xeromorphic, rhizomatous perennial herbs or, more often, woody plants, which rarely may have a trunk up to 5 (−9!) m (the rosette tree *Kingia*) or which may form copiously branched shrublets, the branches of which are covered with short, stiff leaves or with leaf scars (see Staff and Waterhouse, 1981). Stout, generally unbranched trunks with a terminal leaf rosette occur in *Kingia* and *Dasypogon* (*D. hookeri*), in at least the former of which there is a mantle of concealed aerial roots ramifying amongst the persistent leaf bases (reminiscent of the condition in Velloziaceae). Secondary thickening growth in the stem has been reported in *Lomandra,* where the stem is short.

The leaves are tough and xeromorphic, resembling those in some Cyperaceae. They are linear, dorsiventral, sheathing at the base, parallel-veined, and vary from one or a few centimetres (in *Acanthocarpus*) to more than 1 m long (*Kingia, Dasypogon*). They are generally tapering, but in *Chamaexeros* rounded-obtuse at the apex. The stomata are anomocytic. Raphides are reported in the *Lomandra* group (see below), but seem to be absent in the other genera. Vessels are always absent in the stem, but occur in the roots, where their perforation plates are usually simple (scalariform in *Kingia* and *Baxteria*). In *Acanthocarpus* vessels, with scalariform perforations, occur in the leaves (Fahn 1954).

The inflorescences are generally borne on separate branches with sparsely or often very densely set (imbricate) bracteal leaves. They may be elongate and loosely branched or consist of globose partial inflorescences (*Lomandra*) or they may constitute dense, multiflorous, often globose heads, which are obviously of paniculate or thyrsoid character, the flowering starting from the equator and proceeding towards both the base and apex (as often seen in *Dasypogon bromeliifolius*).

The flowers are generally small and inconspicuous (but ca. 6 cm long in *Baxteria*), hypogynous, actinomorphic, and either bisexual or unisexual; if they are unisexual the plants are dioecious. The flowers are not articulate on the pedicel. They have 3+3 free or basally connate tepals, which are white, cream or yellowish, and sometimes dry and scarious, but more often hyaline or petaloid to fleshy (as in several species of *Lomandra*). The two whorls of tepals may, as in *Dasypogon,* be conspicuously different in appearance, the inner much narrower and different in shape. A constriction may be present between a distal and a basal portion. The large flowers of *Baxteria* are tubular. Hairs or bristles may be present on the outer surface of the tepals. Flowers with fleshy tepals are beetle-pollinated. Septal nectaries are present (*Dasypogon*) or absent (*Lomandra*).

The stamens are 3+3 in number, the 3 inner sometimes fused basally to the inner tepals. The filaments are generally rather long and filiform, and the anthers ovate to elongate, basifixed or slightly dorsifixed, introrse, and longitudinally dehiscent. Microsporogenesis seems to be unknown.

Pollen morphology (Chanda and Ghosh 1976) is extraordinarily variable, varying from sulcate (*Kingia, Dasypogon*) to bisulculate (-circumsulculate) (*Acanthocarpus, Chamaexeros*) or circumsulculate to more or less spiraperturate, multiaperturate or irregular, spinulose (*Lomandra*).

The pistil is tricarpellary and trilocular (unilocular in *Dasypogon*), containing one ovule per carpel. The style is simple or apically tribrachiate, and in *Lomandra* very short. The stigma (in *Lomandra*) is of the Wet Type. Placentation is axile (in *Dasypogon* basal) and the ovules anatropous or half-campylotropous and crassinucellate. A parietal cell is formed at least in *Lomandra* and in this genus embryo sac formation is of the *Polygonum* Type (Schnarf and Wunderlich 1939). Endosperm formation does not seem to have been investigated.

The fruits are capsules or nutlets: in *Acanthocarpus* and *Lomandra,* for example, there are loculicidal one- to three-seeded capsules, in *Baxteria* there are explosively opening capsules, while *Dasypogon* and *Kingia* have nutlets. The seeds, unlike those in *Xanthorrhoea,* lack phytomelan on the testal epidermis and are pale in colour. They are also smaller than in *Xanthorrhoea,* only 2–4.5 mm, elliptic to bean-shaped and circular in transverse section. Their outer epidermis consists of thick-walled, pitted cells, storing hemicellulose, aleurone and fat. The embryo is often relatively small (Huber 1969). The basic chromosome number is $x=7$, 8, 9.

Chemistry. Chemical data seem to be lacking.

Distribution. The Dasypogonaceae are almost restricted to Australia, where they are richly differentiated and adapted to arid habitats, mainly in a Mediterranean type of climate. *Lomandra* extends to New Guinea and New Caledonia.

The heterogeneity within Dasypogonaceae has long been recognized and several of the genera or groups of genera have been considered for family status (note that *Calectasia* often referred here is treated by us under Calectasiaceae). A tentative classification follows below.

Fig. 64. Dasypogonaceae. *Dasypogon bromeliifolius*. **A–B** Plant. **C** Inflorescence. **D** One of the longer bracts from the inflorescence. **E** A short bract (subtending a flower). **F** Flower. **G** Stamen with dorsifixed hypopeltate anther. **H** Pistil, longitudinal section. **I** Ovary, transverse section (more compressed than in the natural state). (Orig. B. Johnsen)

Kingia (1) and *Dasypogon* (3), both in the south of Western Australia have tough, long leaves, and both genera include veritable trees (*K. australis, D. hookeri*) with a single (rarely branched) trunk. Both genera have thick branches densely covered with imbricate bract-like leaves, and globose heads with small flowers. The tepals of both genera are hairy on the outer surface, the fruit is indehiscent, and the pollen grains are sulcate. – *Kingia* (1) *australis* (Fig. 68) has linear, glossy, arching leaves, and is similar in habit to arborescent species of

Xanthorrhoea. – *Dasypogon* (2) includes one species without an aerial trunk, *D. bromeliifolius* (Fig. 64), and one of trees, *D. hookeri*.

Baxteria (1), in the south of Western Australia, is a rosette plant, with a woody rhizome and linear leaves. The large, tubular flowers are situated at ground level in the rosette. The fruit is a capsule that opens explosively.

The remaining genera, *Lomandra, Romnalda, Acanthocarpus* and *Chamaexeros* form another possibly natural complex. They are shrublets or

Fig. 65. Dasypogonaceae. **A–E** *Chamaexeros serra*. **A** Plant. **B** Leaf margin; note the hyaline, dentate appendage. **C** Leaf, transverse section. **D** Flower. **E** Same, in detail, two tepals and stamens bent to show pistil; note the thick torus of the flower. **F–L** *Acanthocarpus preissii*. **F** Part of branch with fruits. **G** Fruit, seen from the base, with the six persistent tepals. **H** Same, lateral view. **I** Same, longitudinal section. **J** Seed (not with a black phytomelan layer). **K** Branchlet. **L** Flower. (Orig. B. Johnsen)

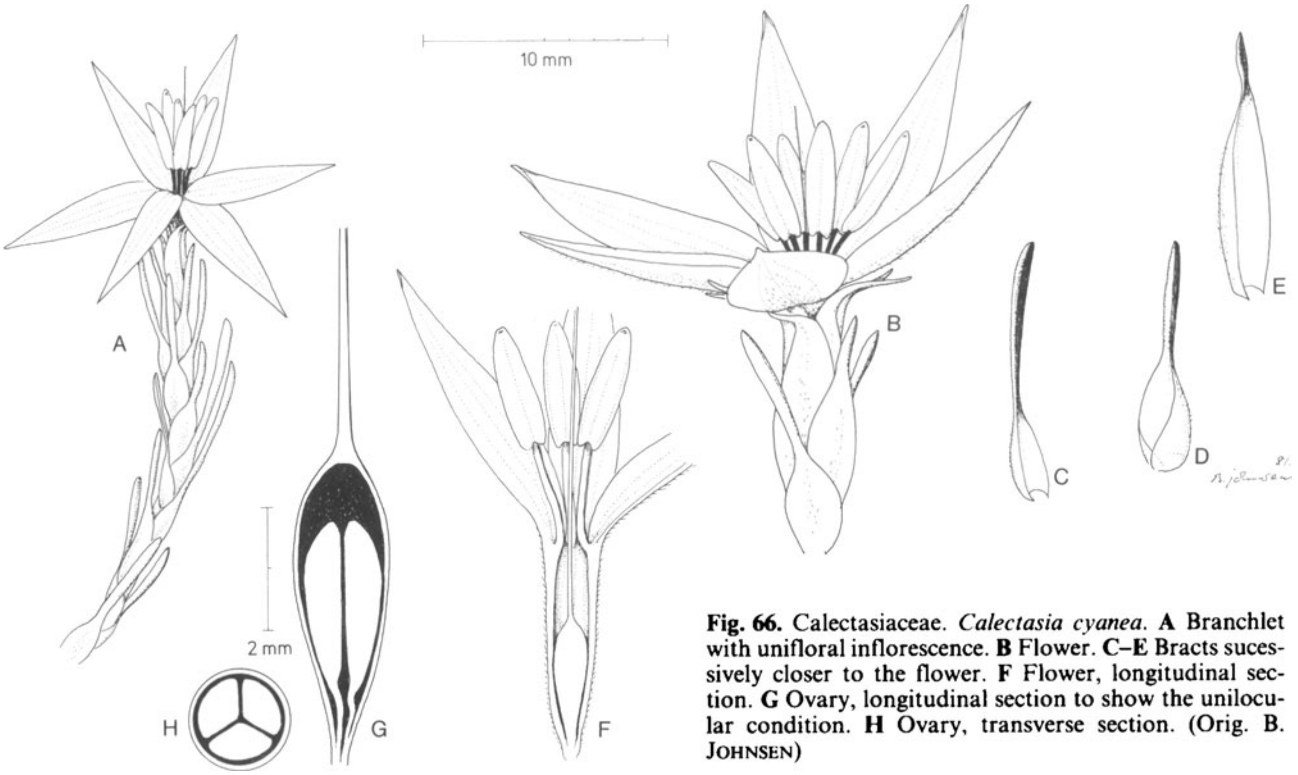


Fig. 66. Calectasiaceae. *Calectasia cyanea.* **A** Branchlet with unifloral inflorescence. **B** Flower. **C–E** Bracts sucessively closer to the flower. **F** Flower, longitudinal section. **G** Ovary, longitudinal section to show the unilocular condition. **H** Ovary, transverse section. (Orig. B. Johnsen)

herbs with a woody rhizome, and are all of moderate size, with a graminoid habit and the leaves concentrated basally or dispersed along the woody branches (*Acanthocarpus*). The inflorescences are generally dense, simple or complex heads or spikes but are sometimes looser, paniculate assemblages of flowers, which have generally yellow, brownish, or purple, hyaline or fleshy tepals. Raphides occur in the genera of this group. The pollen grains in this group are bisulculate, zonisulculate, spiraperturate or irregular. The fruits are capsular.

Lomandra (42) has the widest distribution in the family (see above) and is very variable in the appearance of the leaves as well as the inflorescences. The plants are dioecious and often have fleshy tepals eaten by beetles. Wind pollination may also occur. The anthers are dorsifixed and the pollen grains zonisulculate or spiraperturate.

Acanthocarpus (3) (Fig. 65) in the south of Western Australia is a shrublet with rather short, stiff, prickly leaves and a relatively large globose capsule covered with a scaly surface. *Chamaexeros* (3), (Fig. 65) in the same region, has a basal rosette of linear leaves with rounded apex and a cluster of small flowers.

The great variation in Dasypogonaceae may possibly justify a division into three families sketched above, although subfamilial status seems more appropriate. Family names such as Lomandraceae Lotsy and Kingiaceae Endl. are thus regarded as synonymous with Dasypogonaceae Dum.

Calectasiaceae S.L. Endlicher (1836) 1:1 (Fig. 66)

Xeromorphic, rhizomatous, branched shrublets up to ca. 50 cm high, with slender, stiff branches covered by old leaf sheaths or leaves. Branchlets pubescent, with small, stiff, flat or concave, lanceolate, parallel-veined leaves with pointed apices and laminae disarticulating from the open sheaths. The stomata are anomocytic and raphides are lacking. Vessels are lacking in the stem but present in the roots and have simple perforation plates.

The flowers are solitary on the ends of short branchlets. They are subtended by a great number of small, imbricate leaves. The flowers are bisexual, hypogynous, actinomorphic and trimerous. They have 3 + 3 lanceolate, lilac-blue to purple tepals which are fused basally into a short tube but are otherwise more or less spreading to form a funnel-shaped or nearly open, stellate perigone, which has a glossy metallic sheen. The stamens, 3 + 3 in number, are inserted in the perigone tube

and have rather short, flat filaments. The anthers are erect, basifixed, tetrasporangiate, introrse and stand close together to form a tube around the style. They each dehisce by two apical pores. The pollen grains are sulcate.
The pistil is tricarpellary. It has an erect filiform style and a unilocular ovary with three basal, erect, anatropous ovules. The embryology is incompletely known.
The fruit is dry, indehiscent and one-seeded (a nutlet), and the seed is elongate with a thin membranous testa lacking phytomelan. Unlike the Dasypogonaceae it has a basic chromosome number of $x=9$.

The chemistry is unknown.

Calectasiaceae consists of the monotypic genus *Calectasia* only. *Calectasia cyanea* is restricted to Australia, where it grows in heath vegetation in the states of Western and South Australia and Victoria.

Calectasiaceae is evidently most closely allied to the Dasypogonaceae, in which its habit is matched by the genus *Acanthocarpus*. *Calectasia* deviates in several conspicuous floral characters and in the chromosome number. It is treated here as separate from Dasypogonaceae with some reservations.

Blandfordiaceae Dahlgren & Clifford, fam. nov. 1:4 (Fig. 67)

Herbae perennes, rhizomatosae, erectae, ad 1.5 m altae. Folia in parte basali caulis aggregata, disticha, tenacia, linearia, dorsiventralia, ad 1 m longa et 8 mm lata, nervo centrali prominenti marginibusque asperis. Stomata anomocytica. Caulis rigidus foliis caulinis bracteatis instructus. Flores 1–20 ampliores, pendentes, campanulati, bracteati, pedicellati in racemo terminali dispositi. Pedicelli bibracteolati. Perianthium peristens. Tepala 6 in tubo aurantiaco, ca. 4/5 longitudinis coalita, partes libera lutea saltem ad margines. Stamina 6, filamentis in tubo inclusis, antheris dorsifixis, latrorsis, longitudinaliter dehiscentibus. Grana pollinis subglobosa, sulcata, bicellularia. Pistillum triloculare, breviter stipitatum; loculi ovula 40–50, anatropa, crassinucellata continentes. Saccus embryonis typi Polygoni formans; endospermium helobiale. Capsulae erectae, elongatae, septicidales. Semina 5–6 mm longa, fusco-pubescentia, sine phytomelano. Embryo linearis, longitudine seminis dimidius; endospermium inamyloideum. Plantulae Allii similes.

Fig. 67. Blandfordiaceae. *Blandfordia grandiflora.* **A** Leaf. **B** Inflorescence. **C** Winged capsule. **D** Seed, note the indumentum. (TAKHTAJAN 1982)

Genus typicus *Blandfordia* Sm.

Erect, herbaceous perennials to about 1.5 m tall, shortly rhizomatous with thick fibrous roots. The leaves are distichous and usually crowded at the base of the stem. They are linear, dorsiventral, glabrous, 30–100 cm long and 4–8 mm wide and have a prominent midrib and rough edges. The stomata are anomocytic.
The stem is rigid and its cauline leaves are bracteal and generally anthocyanic in colour. It ends in a raceme with 1–20 large, pendulous and more or less campanulate flowers, which are each subtended by a bract and (generally) two smaller bracteoles on their pedicels. Rarely, the flowers occur singly in the leaf axils. The perianth is persistent with the 3 + 3 tepals fused into a tube for about four-fifths of their length. The perianth tube is usually orange-red and the lobes yellow, at least on the margins.
There are 3 + 3 stamens, the filaments of which are inserted in the perianth tube about one third of the distance from the base. The anthers are dorsifixed and open latrorsely by longitudinal slits. The pollen grains are subsphaeroidal, sulcate and dispersed in the two-celled stage.
The pistil is tricarpellary and shortly stipitate, the stipe lengthening in fruit. The ovary is trilocular and surmounted by a short style that terminates in a small three-grooved stigma. Septal nectaries are lacking.
The ovules are 40–50 in each locule, inserted in two rows on axile placentas. They are anatropous

and crassinucellate. The embryo sac is of the *Polygonum* Type and endosperm formation helobial (Di Fulvio and Cave 1964).

The fruit is an erect, elongate, septicidal capsule 4–10 cm long (including the stipe). The seeds are 5–6 mm long with a soft felted surface of short brown hairs. Phytomelan is lacking. The embryo is about half the length of the seed and is embedded in a starchless endosperm. The seedlings are like those of *Allium*.

The single genus *Blandfordia* (4) is restricted to Eastern Australia and Tasmania, and generally grows in sandy, damp places or acidic moorland.

We consider this genus so distinct that familial recognition is justified. The habit is somewhat reminiscent of that of some Haemodoraceae, e.g. *Conostylis* (incl. *Blancoa*), but several details, such as the anomocytic stomata and starchless seeds, of *Blandfordia* argue against a position in Haemodoraceae. Possibly it is most closely allied to the Dasypogonaceae.

Xanthorrhoeaceae Dumortier (1829) 1:15 (Fig. 68)

Xeromorphic plants, either rhizomatous with a woody trunk or nearly acaulescent, with a woody rhizome, the former comprising "Rosette Trees" with a trunk up to ca. 2 m tall. Where a trunk is developed this has secondary thickening growth of the kind described under Dracaenaceae. The trunk is covered with old leaf scars and leaf bases, and carries green leaves on the apical parts. The stems secrete large quantities of yellow, red and brown acaroid resins, which contain small amounts of essential oils. The leaves are spirally inserted on the stem, linear, dorsiventral, parallel-veined and tough, and may be up to more than 1 m long, but are sometimes only 3–5 cm, as in *Xanthorrhoea pumilio*. The stomata are paracytic. Vessels are present in roots and leaves and sometimes also in the stems; perforation plates are simple in the roots and scalariform in the leaves and stems. Crystal raphide cells are abundant.

The inflorescence is complex, dense, spike-like and multiflorous, with infinitely short secondary branches, and is situated on the end of a long, leafless peduncle. The flowers are small, actinomorphic, hypogynous and bisexual and are supplied with a relatively large bract and bracteole. The 3+3 perianth members are free from each other, and are more or less bract-like and partly hyaline, the outer somewhat stiffer and shorter than the inner and generally hairy. There are 3+3 stamens with narrow filaments, which are free from each other and longer than the tepals. They bear peltate, elongate and introrse anthers dehiscing longitudinally. Microsporogenesis and tapetum do not seem to have been described. The pollen grains are sulcate.

Copious nectar exudes from septal nectaries, attracting trigonid bees (reported from Queensland).

The ovary is trilocular and has a long, erect, simple style and a trilobate or capitate to punctiform stigma. Each locule contains a few anatropous ovules, the embryological features of which have not yet been fully investigated. The fruit is an ovate, woody or cartilaginous capsule. Each capsule contains one or two ovoid-elongate seeds, rounded at one end, pointed at the other, and slightly compressed and trigonous in transection. The outer integument consists of several cell layers and its epidermis has a thick crust of phytomelan. The endosperm consists of rather thin-walled, isodiametric cells containing aleurone and fatty oils but no starch. The embryo is transversely situated in the centre of the endosperm; it is fusiform, straight or curved and about as long as the breadth of the seed (Huber 1969). $x = 22$.

Chemistry. The family is well known for its contents of acaroid resins, which may contain p-cumaric acid, p-oxybenzoic aldehyde and essential oils like citronellol, paeonol, etc.

Distribution. The genus is restricted to Australia, where it is widely distributed.

Xanthorrhoea (15) shows a considerable variation in size and habit. Some species form veritable trees, which are characteristic components in the Australian chaparral. *X. preissii*, "Black Boy" (Fig. 68A–H) has a stem up to more than 2 m high, leaves more than 1 m, and an inflorescence of 3–3.5 m. The wood of this species can be used for bowls and other wooden vessels. *X. australis* and *X. hastilis* yield a gum, "Grass Tree Gum" or "Red Acaroid Gum", which is used for varnishes. In *X. minus* the short trunk is mainly subterranean; *X. pumilio* has leaves only about 3 cm long and a scape of only ca. 30 cm.

The Xanthorrhoeaceae in terms of seed shape recall *Agapanthus* or *Phormium*, but are probably not most closely related to either of these, nor, perhaps, to the Dasypogonaceae, among which they resemble *Kingia* in habit and flower characters. The phylogenetic connections are still unsettled.

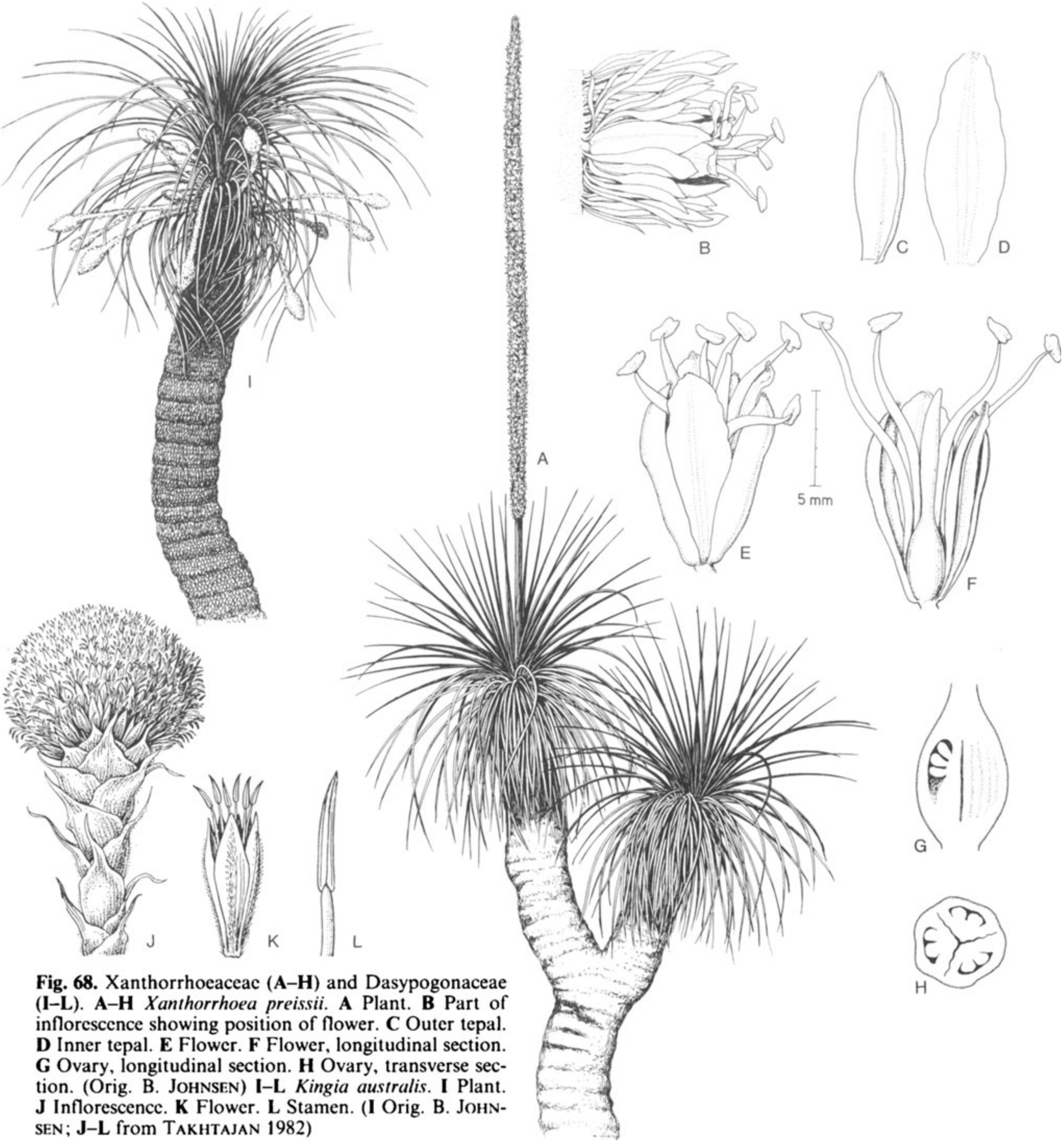


Fig. 68. Xanthorrhoeaceae (**A–H**) and Dasypogonaceae (**I–L**). **A–H** *Xanthorrhoea preissii.* **A** Plant. **B** Part of inflorescence showing position of flower. **C** Outer tepal. **D** Inner tepal. **E** Flower. **F** Flower, longitudinal section. **G** Ovary, longitudinal section. **H** Ovary, transverse section. (Orig. B. JOHNSEN) **I–L** *Kingia australis.* **I** Plant. **J** Inflorescence. **K** Flower. **L** Stamen. (**I** Orig. B. JOHNSEN; **J–L** from TAKHTAJAN 1982)

Agavaceae S.L. Endlicher (1841) 8:300
(Figs. 69–70)

Predominantly large rosette herbs to giant rosette trees, which may have a stout trunk with secondary thickening growth. The underground parts consist of rhizomes or bundles of roots. The leaves are spirally set, dorsiventral, thick and succulent or tough and fibrous. They are lanceolate, linear or subulate, often broadest near the base and gradually tapered to a sharp point; their margins often bear lateral spines or teeth. In *Agave* and related genera, the leaves are fleshy and thick, with stomata more frequent on the upper than on the lower surface (otherwise stomata are mostly confined to the lower surface). The stomata are ano-

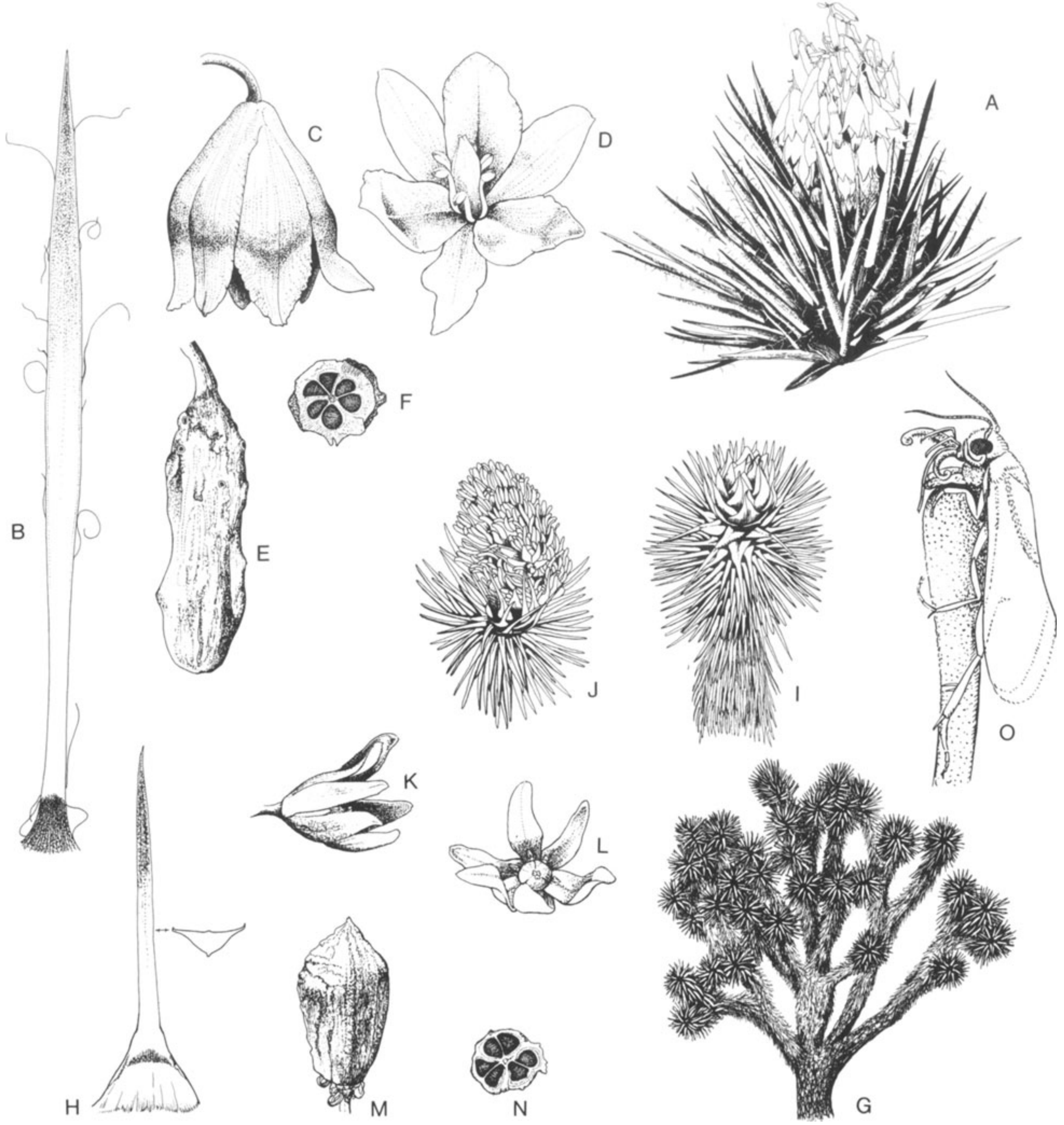


Fig. 69. Agavaceae. **A–F** *Yucca baccata*. **A** Branch with inflorescence. **B** Leaf. **C** Flower, lateral view. **D** Same, front view, to show hypogynous condition. **E** Fruit (baccate). **F** Fruit, transverse section. **G–N** *Yucca brevifolia*. **G** Whole tree. **H** Leaf with transverse section. **I** Branch before flowering stage. **J** Branch with inflorescence. **K** Flower, lateral view. **L** Flower, front view. **M** Fruit. **N** Same, transverse section. (**A–N** CRONQUIST et al. 1977) **O** The pollinator, a female of *Pronuba yuccasella*, collecting pollen on a *Yucca* stamen. (LOTSY 1911)

mocytic and generally deeply sunk. While crystal raphides are lacking, so-called pseudo-raphides contained in suberized cells and solitary crystals in small cells are typical of the family. The vascular bundles of the leaves are accompanied by thick and tough fibres, hence the use of several species as textile plants. The spines of the leaves in some species are filled with sclerenchymatous tissue.

The inflorescence-bearing stem is large and terminal, in some species 2 to several metres high and covered with few or numerous bracteal leaves. In

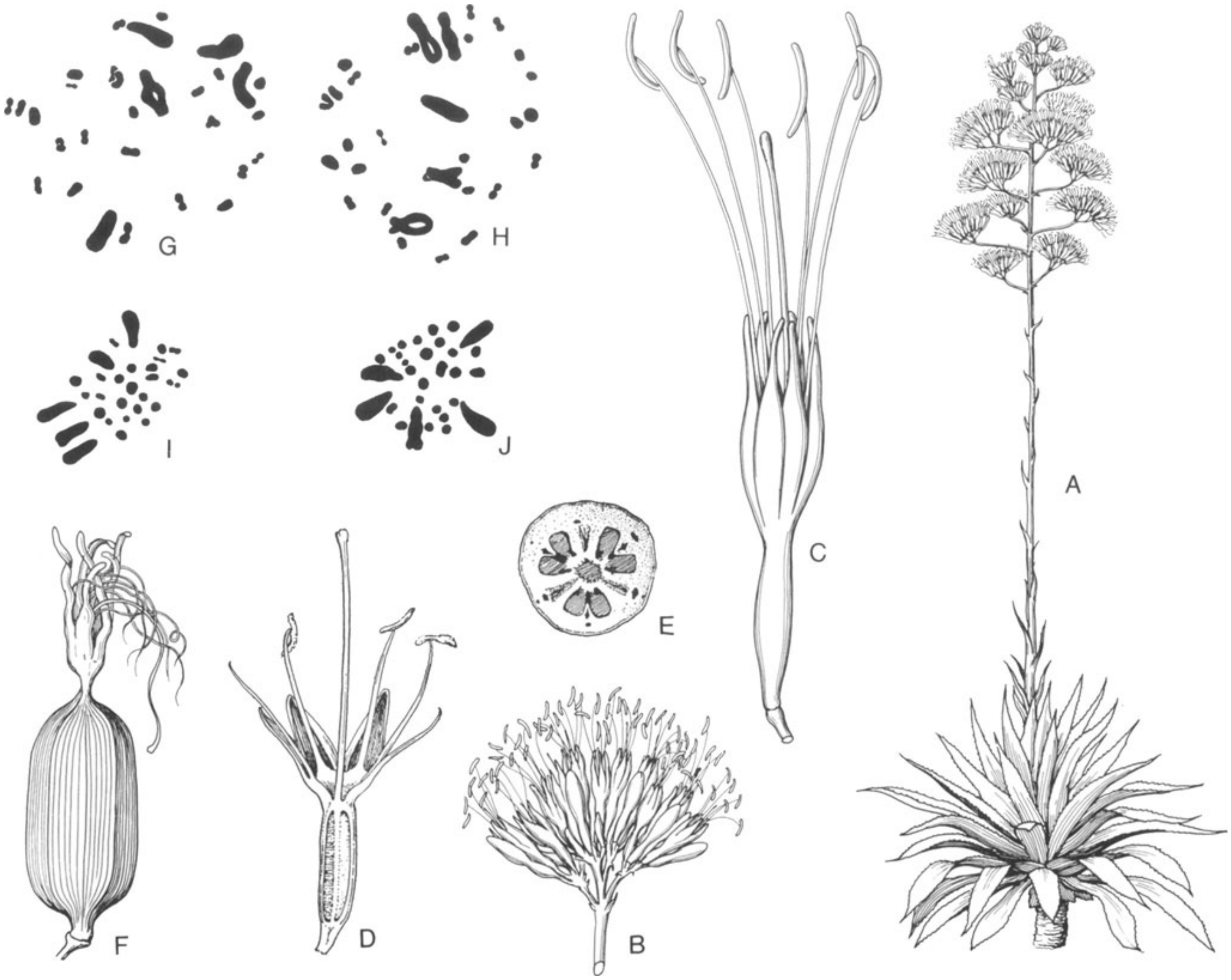


Fig. 70. Agavaceae. **A–C** and **F** *Agave* sp. **A** Plant. **B** Branch of inflorescence. **C** Flower. **F** Fruit. (LARSEN 1973a) **D–E** *Agave* sp. **D** Flower, longitudinal section. **E** Ovary, transverse section. (A.M. JOHNSON 1931) **G–J** Chromosome configurations of *Yucca flaccida* (**G** diakinesis), *Agave virginica* (**H** diakinesis), *Yucca filamentosa* (**I** metaphase), and *Agave virginica* (**J** metaphase). (MCKELVEY and SAX 1933)

most genera the inflorescence is a complex, much-branched panicle, the lateral components of which are cymose, consisting of monochasial units. In the hapaxanthic genera, after several years the plants produce a giant inflorescence and then die.

The flowers are mostly bisexual, trimerous, hypogynous or epigynous, actinomorphic or slighty zygomorphic and generally situated in the axils of well-developed bracts. The tepals, which are generally white or yellow, are free or more or less fused into a tubular or campanulate perigone; sometimes this is abruptly widened and urceolate in the outer part.

The stamens are 3 + 3 in number and are inserted at the base of the tepals or on the inner side of the perigone tube. The filaments are sometimes basally widened; in *Yucca* they are relatively stout and short-hairy; in *Agave* they are filiform and often extend far beyond the perigone. The anthers are long or short, introrse, peltate ("epipeltate") or in *Yucca* nearly impeltate, and dehisce longitudinally. The tapetum is glandular (secretory) and microsporogenesis is successive. The pollen grains have a reticulate exine and a sulcate or (in *Polianthes* and *Prochnyanthes*) bisulculate aperture (ERDTMAN 1952). They are dispersed singly or rarely in tetrads (*Furcraea*; species of *Agave* and *Beschorneria*).

The ovary is trilocular, each locule having several to many anatropous ovules. The style is short (subfam. Yuccoideae) or rather long and simple (subfam. Agavoideae), with a punctiform or small and capitate to trilobate stigma with Dry or Wet stigma surface. A parietal cell is cut off from the archesporial cell. Embryo sac formation conforms to the *Polygonum* Type, and endosperm formation is helobial (rarely, as in *Furcraea,* nuclear). Haustoria in connection with the embryo sac and endosperm are lacking. In *Yucca* part of the nucellus divides actively before and after fertilization and forms a considerable perisperm tissue.

The fruit is a capsule or, in some *Yucca* species, rather a berry. It contains several or many seeds. These are sometimes flat and plate-like, crescent-shaped or semi-circular, but sometimes less compressed (as in *Yucca*), and then with a furrowed endosperm. The outer integument of the testa consists of several to many (up to 20) cell layers; its epidermis has a thin crust of phytomelan. The endosperm contains aleurone and fatty oils.

The karyotype in all Agavaceae is uniform: $x=30$, with 5 large and 25 small chromosomes (McKelvey and Sax 1933).

Chemistry. The family is rich in steroidal saponins, the sapogenins of which have 27 C-atoms. Of the simple sapogenins may be mentioned smilagenin, sarsasapogenin, tigogenin, neotigogenin, diosgenin and yamogenin. The saponins produced especially from species of *Agave* and *Yucca* are of great importance as hormonal substances (and form the active principle of contraceptive pills). Chelidonic acid is also widely distributed in the family, and the leaves may contain a certain amount of ascorbic acid. Essential oils can be obtained from the scented flowers of some taxa.

Distribution. The Agavaceae form an embryologically and cytologically homogeneous, but morphologically somewhat heterogeneous family. Both subfamilies, Yuccoideae and Agavoideae, are entirely American in origin, but *Agave* especially is now widely distributed in warm, arid areas all over the world. The members are prevailingly large prairie and steppe plants. The centre of distribution is in Mexico and adjacent warm and arid parts.

Subfamily Yuccoideae

This consists of two genera with short to considerable trunks, sometimes several metres high, with secondary thickening growth. The leaves are not as succulent as in many Agavoideae, but are stiff or tough and fibrous, and are sometimes supplied with marginal fibres (Fig. 68B). In the flowers, which are hypogynous, the tepals are free or more or less connate basally and the anthers only weakly epipeltate.

Subfamily Yuccoideae is wholly American and consists of *Yucca* (incl. *Hesperoyucca, Clistoyucca* and *Samulea*) and *Hesperaloë* (2), which are both concentrated to the warmer parts of America.

Yucca (40) occurs in the plains and arid mountains of western North America. It consists of large or medium-sized plants which often have a woody stem: *Y. ("Clistoyucca") brevifolia,* "Joshua Tree" (Fig. 69G–N) is a veritable tree with relatively short leaves covering considerable parts of the branches. In other species the stem is shorter and bears terminal leaf rosettes. The large flowers have almost free tepals. The stamens have rather stout, shortly hairy, filaments and small, arrow-like anthers. Some species have berry-like fruits; in others the fruits are dry or spongy. – The leaves of several species, especially *Y. australis,* yield fibres used locally for twine, cloth and baskets. The seeds or fruits of some species are eaten locally, and the young stems and leaves of *Y. australis* are fermented to an alcoholic beverage. – Several species are grown as ornamentals, in particular *Y. aloifolia, Y. brevifolia, Y. filamentosa, Y. glauca, Y. gloriosa* and *Y. smalliana.*

Yucca provides a classic case of interdependence between a plant and its pollinator, which in this case is the genus of small moths, *Tegeticula* (*Pronuba*). One species of *Tegeticula* is specific to each of the two monotypic subgenera *Hesperoyucca* and *Clistoyucca* in the southwestern U.S.A., while a third pollinates the several *Yucca* species occurring here and further east. The moths, exhibiting a specific behaviour pattern, gather pollen into a ball, which is held under the head by the proboscis. They then fly to another flower and carry out alternate ovipositions (one egg at a time) and acts of pollination, in which they press pollen into the canal of the tubular style. Usually one egg is laid in each loculus of the ovary. Ovules in the neighbourhood of a moth's egg form gall tissue which nourishes the larva, while causing irregularities on the capsule (Fig. 69E).

Subfamily Agavoideae

Subfamily Agavoideae represents the epigynous genera of the family. Many taxa are giant herbs with secondary thickening growth and some, like *Furcraea longaeva,* have a considerable trunk. The leaves are often strongly succulent and contain tough fibres that are economically exploited. The plants, though often reaching considerable age, flower only once and then die, and so are hapaxanthic. They are generally propagated vegetatively. Their inflorescences are mostly profusely flowered and complex and may appear on tall axes with sparsely or closely set scale-like leaves. Some such species (in *Agave*) are adapted for bat pollination, while the syndrome of bird pollination is prominent in *Beschorneria*. The flowers are syntepalous with a very short to quite long perianth tube, and they mostly have long, slender, exserted filaments with epipeltate, versatile anthers. In some genera the pollen grains cohere in tetrads, and bisulculate pollen grains occur in other genera. The fruits are always capsular and the seeds mostly flattened.

Here belong *Agave, Furcraea, Beschorneria, Manfreda, Polianthes* and *Prochnyanthes*. Among other genera referred here at least *Littaea* is probably best treated as a subgenus of *Agave*.

Agave (300) in the southern U.S.A., central America and part of tropical South America consists of plants with a short, often woody stem, which at least in several species has secondary thickening growth. The fleshy leaves end in a spine and frequently (as in species of *Aloë,* Asphodelaceae) have lateral spines. The inflorescence in some species, like *A. americana,* is gigantic and reaches a height of 3 m or more. The flowers generally have yellow and greenish tepals, exceeded much in length by the stamens.

The leaves are covered with wax. The young inflorescence can be tapped for sugar-rich sap, which in large specimens may amount to hundreds of litres. When brewed this yields the alcohol-rich "Pulque", from which "Mescal" and "Tequil" are distilled. Many species are useful for their fibres.

A. americana, "Century Plant", from Mexico, is one of the commonest and largest species, cultivated in warm parts of the world as an ornamental or border plant and now widely naturalized. *A. sisalana* ("Sisal Agave") and *A. fourcroydes,* indigenous in the same region, are widely cultivated in the world for the sisal hemp fibres retted from the leaves and used for cordage and strings. Used in the same way are *A. funkiana, A. gracilispina,* and especially *A. cantala,* from Mexico, and *A. letonae* from Central America. Species used for "Pulque" are, for example, *A. complicata, A. atrovirens, A. mapisaga,* etc. The leaves of several species yield saponins.

Besides *A. americana,* many other species are grown as ornamentals, some being rather small in size.

Furcraea (20) and *Beschorneria* (7) from tropical America have flowers with tepals fused higher up than in *Agave*. The pollen in these genera is generally dispersed in tetrads. *Furcraea* includes some almost trunkless species, while others have a considerable trunk. The inflorescence of some species forms an enormous panicle. *Furcraea* yields fibres, which are of better quality than those from *Agave; F. gigantea,* "Piteira", cultivated mainly on Mauritius, *F. hexapetala* and *F. humboldtiana* are fibre plants. *Beschorneria* species are rosette plants without an aerial trunk. Their inflorescence is an erect panicle or raceme with pendent flowers.

Hypoxidaceae R. Brown (1814) 10:150 (Figs. 71–72)

Herbs with a tuberous rhizome or a corm covered with a membranous coat of fibres. The leaves are radical and sometimes longer than the inflorescence. They are mostly tristichous and are dorsiventral, linear to lanceolate, sessile or, for example in some *Curculigo* species, constricted above the leaf base into a pseudopetiole. The lamina is prominently parallel-veined, and the ptyxis may be plicate. They are often clothed with fairly long, uniseriate hairs, but branched, multicellular hairs are also present in the family. Stomata, at least in most cases, are paracytic, rarely tetracytic. Raphide cells occur at least in *Curculigo,* and are probably widespread in the family. The inflorescence-bearing stem has only one circle of vascular bundles. Vessels are lacking in the stems and leaves, but are present in the roots where they have scalariform perforation plates.

The flowers are borne on a leafless, usually hairy scape arising from the rhizome or corm. The inflorescence consists of spikes, racemes or umbel-like clusters, or it may be reduced to a single flower.

The flowers are sometimes situated in the axils of fairly large bracts. They are actinomorphic, bisexual, trimerous and epigynous, with 3+3 tepals free or fused into a sometimes long and narrow tube above the ovary. The tepals of the two whorls are more or less equal and generally yellow or white, rarely red (in *Rhodohypoxis*); in most taxa they have attenuate apices and are hairy on the outside. Nectaries (of any kind) seem to be lacking.

There are 3+3 or rarely (*Pauridia*) 3 stamens inserted at the base of the perianth lobes; they have narrow filaments and basifixed or epipeltate, introrse anthers dehiscing longitudinally. The tapetum becomes periplasmodial at an early stage, and may be classified as amoeboid, which is exceptional in Asparagales. Microsporogenesis is successive.

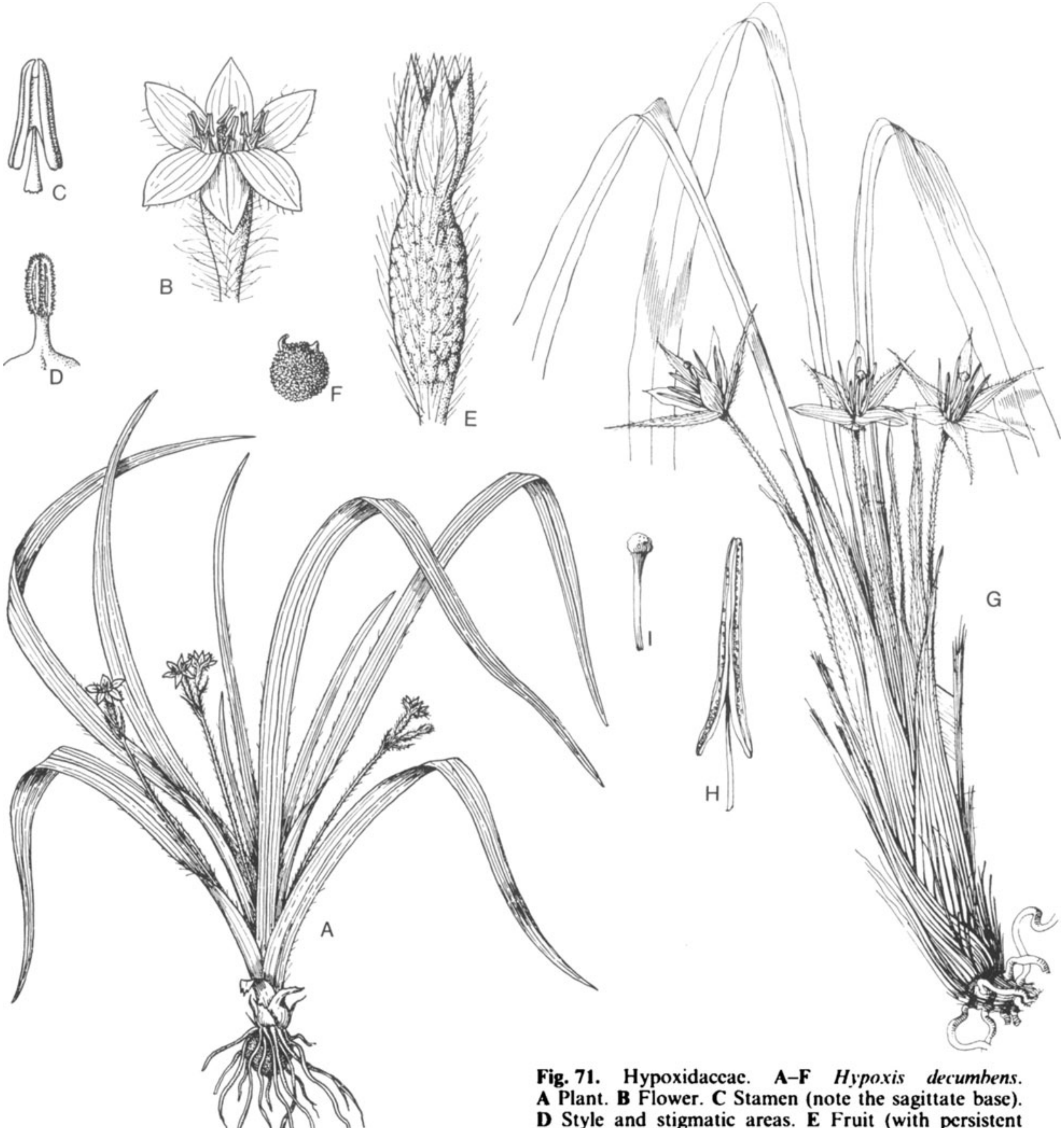


Fig. 71. Hypoxidaceae. **A–F** *Hypoxis decumbens*. **A** Plant. **B** Flower. **C** Stamen (note the sagittate base). **D** Style and stigmatic areas. **E** Fruit (with persistent tepals). **F** Seed. (CABRERA 1968) **G–I** *Curculigo pilosa*. **G** Plant (some leaves omitted). **H** Stamen. **I** Style apex and stigma. (HEPPER 1968)

The pollen grains are sulcate, with a finely reticulate exine, and are dispersed in the two-celled state.

The ovary is trilocular (unilocular in *Empodium*) and bears a short style which is apically divided into three branches. The stylodial branch tips are covered with a Dry stigmatic surface. The locules have several centrally (in *Empodium* parietally) inserted, anatropous or hemianatropous ovules. The archesporial cell functions directly as the megaspore mother cell and parietal tissue thus is lacking, but the epidermis often divides periclinally to form a nucellar cap. Embryo sac formation follows the *Polygonum* Type, more rarely the *Allium* Type. Endosperm formation is generally helobial but nuclear in *Pauridia,* where the chalazal part is somewhat haustorial.

The fruit is generally a capsule, which is mostly crowned by the remaining parts of the perianth,

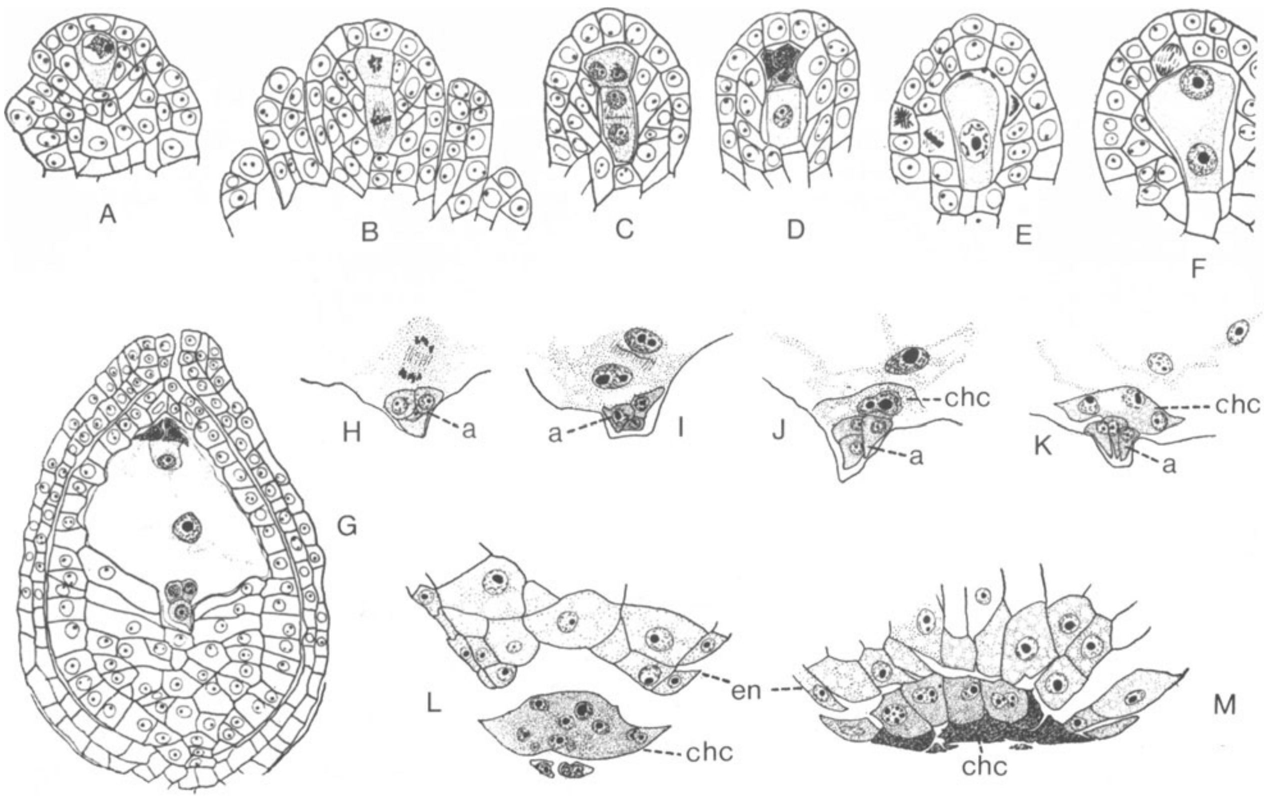


Fig. 72. Hypoxidaceae, embryology. **A–G** *Spiloxene aquatica,* embryo sac formation. A parietal cell is not formed here. **A–D** show the meiosis resulting in four megaspores, out of which the chalazal one continues to form an 8-nucleate embryo sac (**E–G**) according to the *Polygonum* Type. **H–M** *Spiloxene schlechteri,* helobial endosperm formation; **H–J** showing division of the primary endosperm nucleus with the formation of a wall between the micropylar and chalazal chambers; **K–M** showing the subsequent ab initio nuclear divisions in each chamber, with walls formed subsequently in the micropylar chamber (*en*) but not in the chalazal chamber (*chc*) (**L**), and then the degeneration of the chalazal chamber (**M**). (All after DE Vos 1948)

and opens by short vertical slits near the top; it may also be fleshy and indehiscent (*Curculigo* s. lat.). In all taxa the seeds are small and globose, with a prominent raphe. An elaiosome occurs at least in *Curculigo*. The seed coat consists of a few cell layers, the epidermis of which is palisade-like and has a thick, black phytomelan crust. The endosperm is composed of thin-walled, isodiametric cells storing aleurone and fatty oils, but no starch.

Chemistry. Alkaloids and steroidal saponins seem to be lacking, at least in *Hypoxis,* while chelidonic acid occurs in the family.

Distribution. The family is found mainly in the Southern Hemisphere, with centres in Southern (to Central) Africa, South America, Australia and the coastal regions of Asia. About 90 species in at least five genera occur in Southern Africa. The plants mostly grow in meadows, grassland or low macchia vegetation.

Hypoxis (90) is distributed in Africa, America, southern Asia and Australia. It has a vertical tuberous rhizome, and an often rather short inflorescence-bearing scape, the flowers of which have a yellow, stellate perianth and exserted stamens. Some species, e.g. the American *H. hirsuta* and the South African *H. stellata,* are occasionally cultivated as ornamentals. *Rhodohypoxis* (4) with red or white flowers and stamens hidden in the basal perianth tube occurs in the Drakensberg Mountains of Southern Africa. The South African genus *Spiloxene* (30) should probably also be distinguished from *Hypoxis,* differing in having a more bulb-like corm and in lacking pubescence on most parts. Besides, it generally has one or a few rather large flower(s) with spreading, orange, yellow or white (rarely partly green and black) tepals. – The small-sized species of *Pauridia* (2) in the same region have only three stamens and are doubtfully included in the family.

Curculigo (10) has about the same distribution as *Hypoxis.* The inflorescences are mostly more or less concealed by the far longer and larger leaves, and the indehiscent fleshy fruits are prolonged into a rostrum formed by the perianth tube. *Empodium* (10) in South Africa has a unilocular ovary with parietal placentae.

Further investigations are required to determine whether *Pauridia,* with nuclear endosperm formation and only three stamens, properly belongs in Hypoxidaceae.

The combination of attributes: paracytic stomata, lack of nectaries and tapetum which soon becomes periplasmodial is a peculiar one, the constancy of which needs further investigation. The closest affinities of the family are somewhat uncertain and also need further study. Sometimes Hypoxidaceae have been associated with orchids, an affinity that does not seem at all convincing to us.

The paracytic stomata, the fibrous leaf bases and the epigynous flowers may be taken to suggest an affinity with the Velloziaceae, but the phytomelan-coated, starchless seeds of the Hypoxidaceae show little similarity to the seeds of Velloziaceae, and the lack of vessels in stem and leaves indicates that Hypoxidaceae are best placed in the Asparagales, and the similarities with Velloziaceae are obviously due to convergent evolution.

Tecophilaeaceae Leybold (1862) 5–7:15–20 (Figs. 73–74)

Moderate-sized or fairly small, generally glabrous herbs with thick, often tunicated rhizomatous corms. The stem is erect and partly leafy, although the leaves may be concentrated at the base. The leaves are dorsiventral, linear to lanceolate, entire, parallel-veined and sheathing at the base. Vessels are lacking in the stems and leaves, but present in the roots; they have scalariform perforation plates (CHEADLE 1969). The stomata are anomocytic.

The inflorescences are simple or compound racemes or thyrses in which the flowers are subtended by bracts of variable size. The flowers are bisexual, trimerous, generally partly epigynous, and actinomorphic or, in particular with regard to the androecium, zygomorphic. The 3 + 3 tepals are free from each other or shortly connate at the base, generally lanceolate and in most taxa blue, violet, white or pale yellow. They are frequently somewhat reflexed. There are 3 + 3 stamens or stamen homologues, some stamens (often the upper) being often transformed into linear staminodes or being dwarfed and sterile (see the genera, below). The filaments are short and glabrous and the anthers, which are mostly basifixed (peltate in *Tecophilaea*), are sometimes connivent, with the connective sometimes produced at both ends. Anther dehiscence is by means of apical pores or by apical longitudinal slits. Microsporogenesis is simultaneous (at least in *Cyanella* and *Odontostomum*). The pollen grains are sulcate (with operculate sulcus) and two-celled when shed.

The ovary is generally half-inferior and the style erect and subulate to filiform, straight or slightly curved, ending in a small capitate stigma. There are three locules in the ovary, each with several to many ovules in two rows. The ovules are anatropous and crassinucellate, and a primary parietal cell is cut off from the archesporial cell. Embryo sac formation is of the *Polygonum* Type. In *Cyanella,* at least, the mature embryo sac forms a tubular chalazal haustorium. Endosperm formation is nuclear (recorded in *Cyanella*). Adventive embryony leading to polyembryony has been observed in *Cyanella.*

The fruit is an apically loculicidal capsule with rather numerous and small seeds. The outer integument of the testa consists of four or more cell layers, the outermost of which collapses and becomes encrusted with a thin layer of phytomelan. The endosperm cells contain lipids and aleurone.

Chemistry. The chemistry of Tecophilaeaceae seems to be practically unknown.

Distribution. As circumscribed here, Tecophilaeaceae are a mainly Southern Hemisphere group with centres in Chile, South America, (*Conanthera, Tecophilaea, Zephyra*) and in South Africa (*Cyanella* and perhaps *Lanaria,* see below). *Odontospermum* occurs in California.

Conanthera (5) (Fig. 73), in Chile, has flowers with six equal, functional stamens. The anthers are connate into a cone-like structure with projecting connectives. *Tecophilaea* (2), found in the same region, has blue flowers with three functional stamens and three linear staminodes. In contrast to the other genera, the stem is leafless in this genus. *Cyanella* (7) (Fig. 73) in South Africa are leafy plants with iridaceous habit and light blue or light yellow flowers in sparse racemes. The number of functional stamens is variable. Six similar functional stamens occur in *C. alba;* three are more common, as in *C. orchiformis,* and in *C. lutea* there is only one functional stamen, five being non-functional and reduced in size.

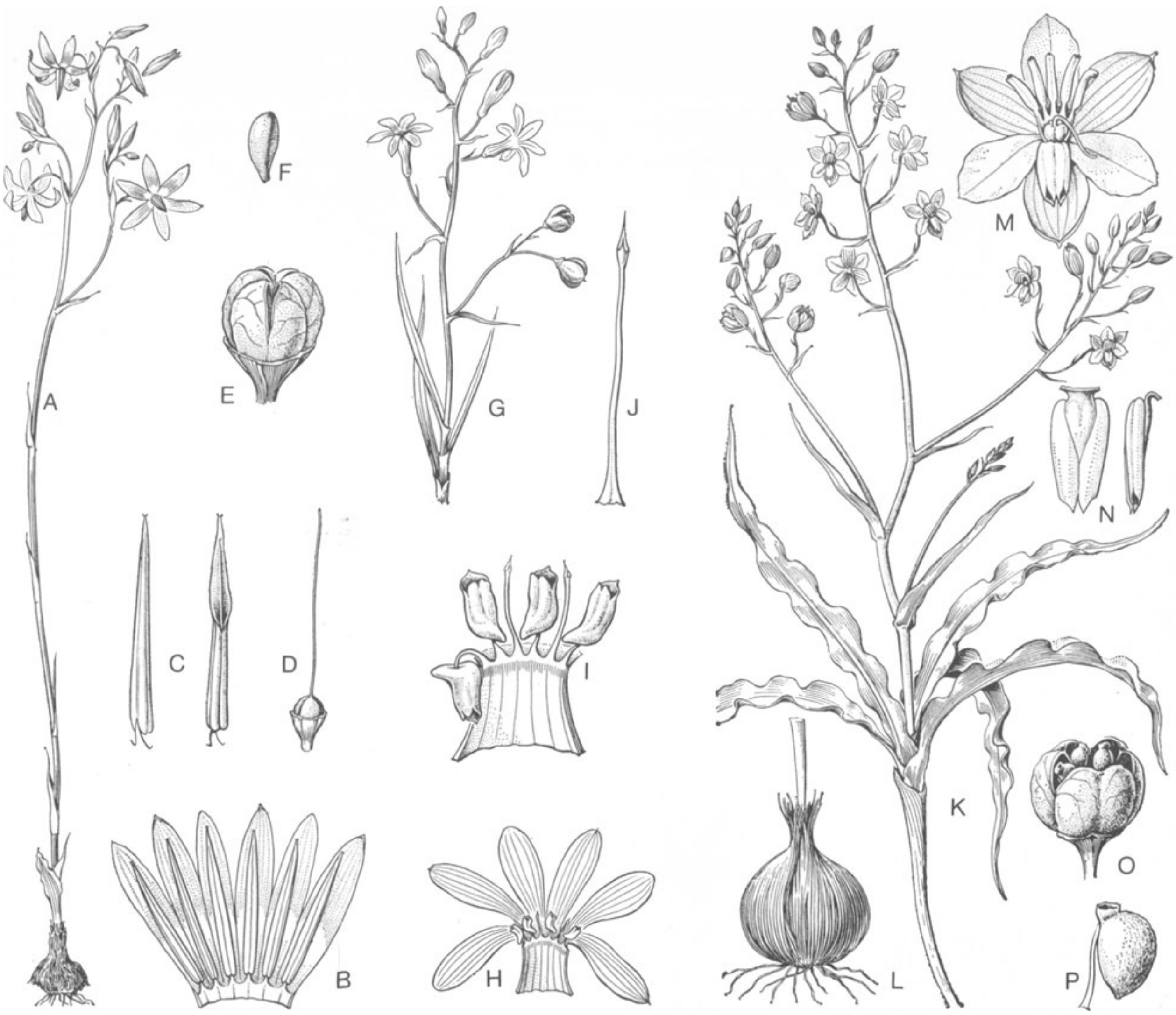


Fig. 73. Tecophilaeaceae. **A–F** *Conanthera bifolia.* **A** Plant with corm. **B** Perianth and stamens, spread open. **C** Stamen in different views; note the poricidal dehiscence. **D** Pistil (semiepigyny). **E** Capsule. **F** Seed. **G–J** *Zephyra amoena.* **G** Plant. **H** Perianth tube with attached stamens, spread open. **I** Androecium. **J** Staminode. **K–P** *Cyanella capensis.* **K** Plant. **L** Corm. **M** Flower; note that the upper five stamens are small and functionally sterile. **N** Functional stamen in different views. **O** Capsule. **P** Seed. (All from TAKHTAJAN 1982)

The South African genus *Lanaria* (1) has, according to DE VOS (1963), an embryology which coincides best with the Tecophilaeaceae, although it does not have poricidal anthers. *Lanaria plumosa* (Fig. 74) is a herb with distichous leaves with fairly small semi-epigynous flowers in a dense corymb-like panicle with monochasial components. The tepals are densely woolly. Of the six stamens, the three inner somewhat shorter than the outer and the anthers are peltate as in other Tecophilaeaceae, but open by longitudinal slits. The ovary is subinferior and trilocular, with biovulate locules, but develops into a one-loculed and mostly one-seeded capsule. Its seeds are similar to those of Hypoxidaceae and the stomata are also of the same type (paracytic). However, microsporogenesis is simultaneous and the tapetum secretory. The position of *Lanaria* may best be left open, although a position in Tecophilaeaceae may be considered. – *Lophiola* (1) *aurea,* occurring from New Jersey to Florida, with three stamens, may also belong to Tecophilaeaceae (see ZAVADA et al. 1983).

Walleria (1–5), in Southern Africa and Madagascar, is here included in Tecophilaeaceae with great reservations. It is a herb with a corm and with leafy stem and *Solanum*-like, hypogynous

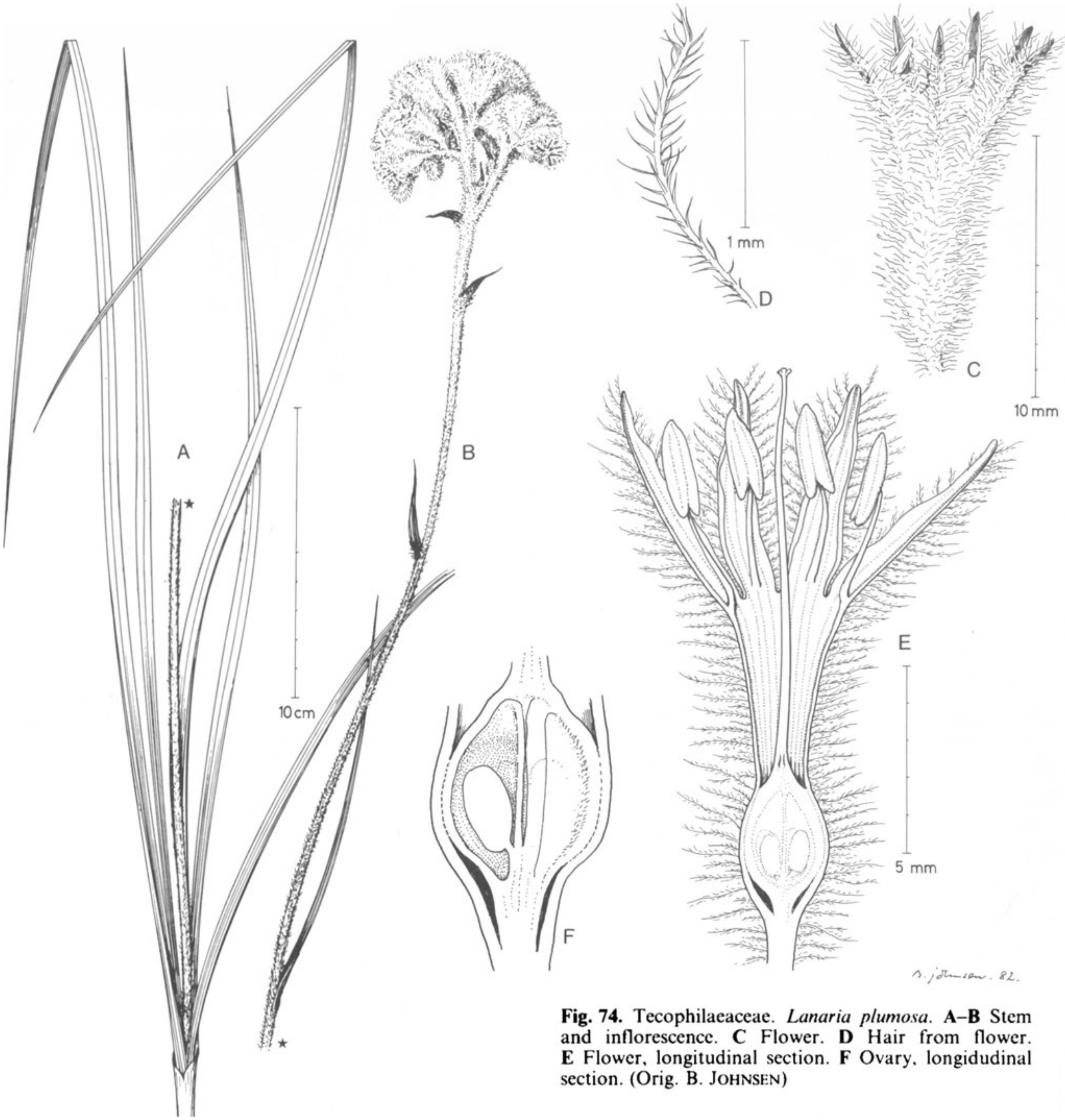


Fig. 74. Tecophilaeaceae. *Lanaria plumosa*. **A–B** Stem and inflorescence. **C** Flower. **D** Hair from flower. **E** Flower, longitudinal section. **F** Ovary, longidudinal section. (Orig. B. Johnsen)

flowers with somewhat recurved, violet tepals and large, coherent and apically poricidal anthers. The somewhat bean-like seeds are unique in being warty and lacking a phytomelan crust. The outer integument (testa) of the seed coat is multi-layered, and its warts are multicellular, hemispheric (although much longer at the chalazal end). The cell layers of the inner integument have collapsed completely in the seed into a thin membrane (Huber 1969). A group of apical cells on each wart continue each into a thin hair, which might suggest affinity to *Eriospermum,* although this is highly uncertain.

Cyanastrum, here treated in a separate family, could also with some justification be included in Tecophilaeaceae (see further under Cyanastraceae).

The Tecophilaeaceae are probably most closely related to Cyanastraceae, Ixioliriaceae, Phormiaceae, Hemerocallidaceae and Asphodelaceae.

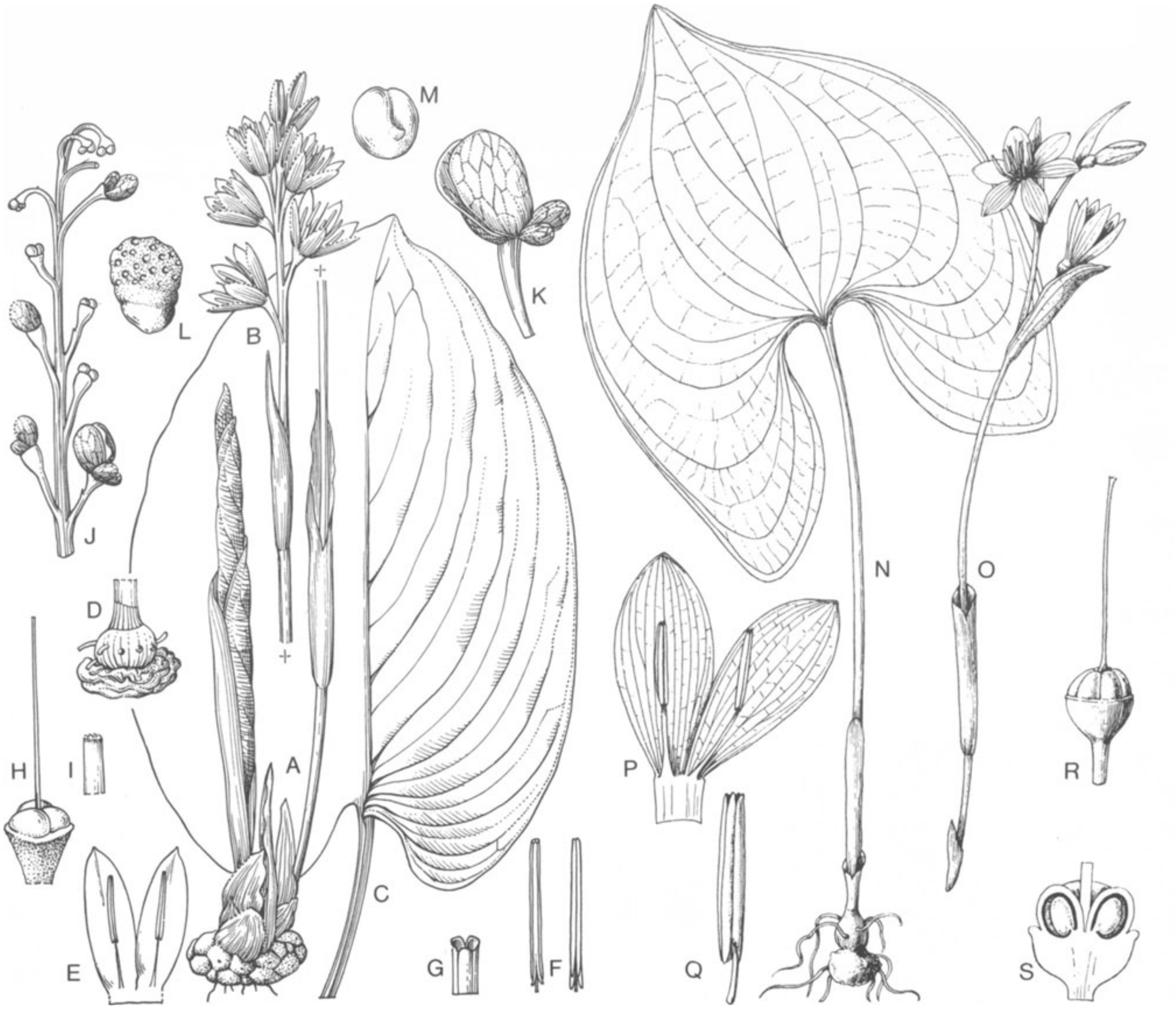


Fig. 75. Cyanastraceae. **A–M** *Cyanastrum johnstonii.* **A** Tuber, erect stem and leaf bud. **B** Inflorescence. **C** Leaf. **D** Tuber. **E** Two tepals and opposite stamens. **F** Anther in different view, note the poricidal dehiscence. **G** Apex of poricidal anthers. **H** Pistil. **I** Style apex with stigma. **J** Infructescence. **K** Fruit, this is a schizocarp where two mericarps have not come to development. (Carter 1969) **N–S** *Cyanastrum cordifolium.* **N** Tuber and foliage leaf. **O** Inflorescence. **P** Two tepals and the opposite stamens. **Q** Stamen. **R** Pistil. **S** Young fruit, longitudinal section. (Hepper 1968)

Cyanastraceae Engler (1900) 1:6 (Fig. 75)

Herbs with a thick corm constricted at intervals. The leaves are few and concentrated basally, the lowest being usually bract-like, one or more being large, green and dorsiventral, sheathing the base and in some species with the base of the lamina constricted into a pseudopetiole. The lamina is lanceolate or ovate-cordate and in some species distinctly parallel-veined with fine transverse veinlets. Vessels are confined to the roots and have scalariform perforation plates. Raphides are lacking. The stomata are paracytic. The inflorescence is situated on an erect leafless scape which is basally subtended by a bract-like or spathe-like cataphyll. It represents a panicle, a raceme or a thyrse.

The flowers are bisexual, actinomorphic, trimerous and half-epigynous. The 3 + 3 tepals are similar in size and shape, generally blue, and often spreading but basally fused into a short tube, at the mouth of which the 3 + 3 stamens are inserted. These have short, often S-curved filaments and basifixed, elongate anthers which dehisce by an apical pore or a short slit. The tapetum is secretory and microsporogenesis is simultaneous. The pollen grains are finely reticulate and sulcate or sometimes trichotomosulcate (Erdtman 1952).

The pistil, which is only half-superior, is tricarpellary and trilocular, with a central simple, almost gynobasic style bearing a terminal punctiform stigma. The locules are separated from each other and from the style in a way reminiscent of the boraginaceous or ochnaceous pistil. Septal nectaries are present. Each of the locules contains two anatropous, basally inserted ovules with a funicular obturator. A primary parietal cell is cut off from the archesporial cell. Embryo sac formation is probably of the *Polygonum* Type. Endosperm formation is probably nuclear (helobial according to some reports). An extraordinary condition is that the tissue in the chalazal part of the ovule, opposite the micropyle, enlarges by cellular division to form a chalazosperm (Fries 1919), in which the cells are swollen and filled with compound starch grains. The chalazosperm functionally but not histologically corresponds to a perisperm, which it resembles in being diploid.

In the three-lobed ovary only one seed normally ripens, the two remaining ones degenerating. The pericarp is membranous, and the fruit may be classified as a mericarp of a schizocarp. The testa consists of several layers of isodiammetric cells and completely lacks phytomelan. The embryo is depressedly globose and fills up about half of the seed. The chalazosperm is well-developed and starchy, whereas the endosperm is almost completely used up during seed development. The embryo has a large, terminal cotyledon and a sunken, lateral plumule. $x = 11, 12$.

Chemistry. The family seems to lack accumulation of calcium oxalate and tannins, but schizogenous spaces with an oil-like excretion are present in the leaves. They probably represent so-called cyanocysts (tissue masses enclosing anthocyanic contents).

Distribution, Taxonomy. The family consists of the genus *Cyanastrum* (6), in tropical Africa, which grows in shady forests. The species are quite variable in the shape of the leaves and the size, shape and number of flowers of the inflorescence.

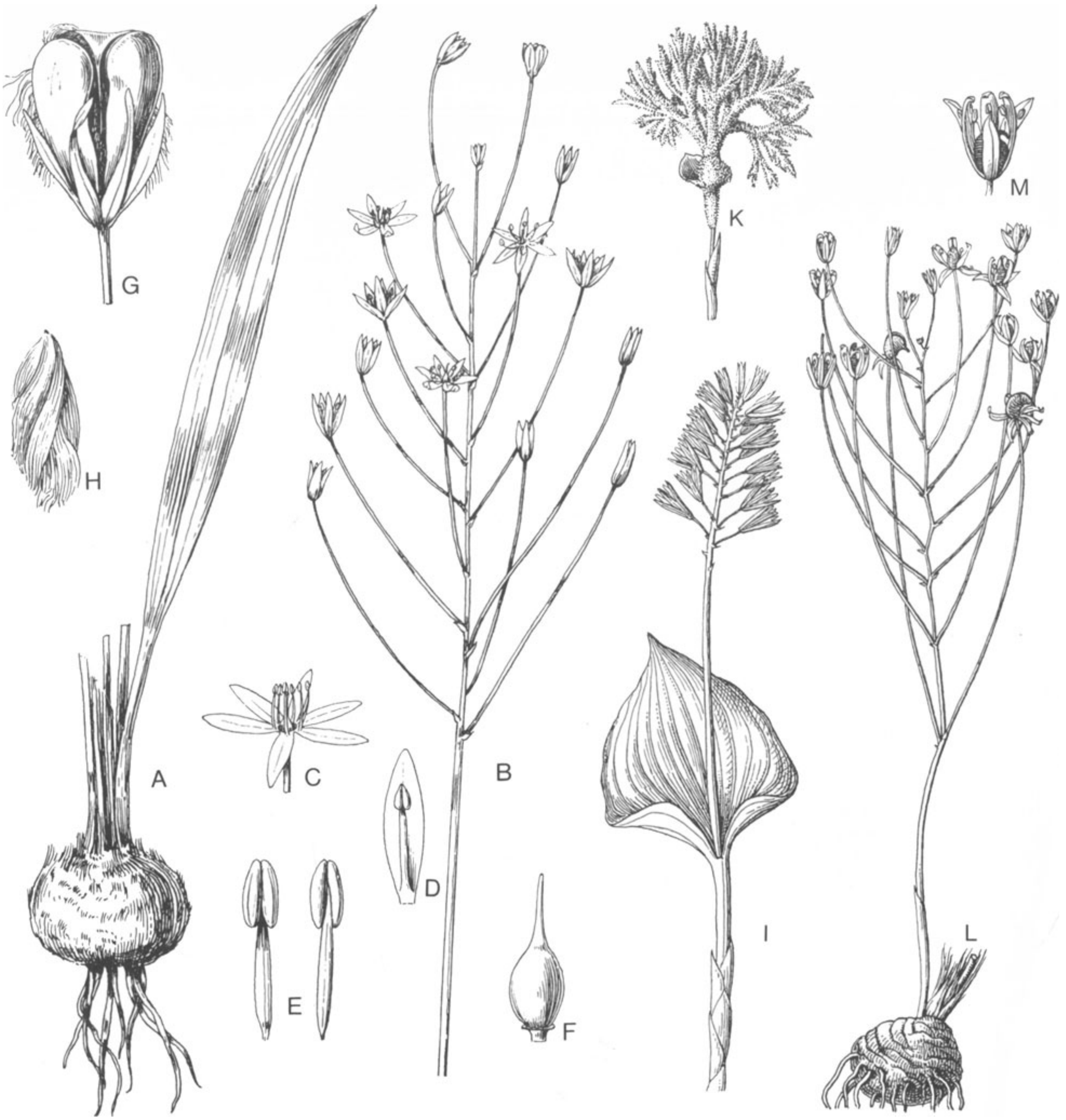
The relationships of the family are somewhat uncertain. Some features, such as the corms, the petiolate leaves with distinct main veins and fine transverse veinlets discernible in between, and the simultaneous microsporogenesis, suggest an affinity with various Dioscoreales. The closest affinity is, however, no doubt with Tecophilaeaceae, with which *Cyanastrum* shares the corm, the general floral construction, the blue tepal colour, the basifixed poricidal anthers, the glandular tapetum, the simple style, and the simultaneous microsporogenesis. There is also some similarity to Eriospermaceae and Phormiaceae.

It is interesting to note that in *Walleria*, which is considered by Huber (1969) to be related to *Cyanastrum* and the Tecophilaeaceae, the tissue of the raphe is rich in starch grains. In the Eriospermaceae, where chalazosperm is poorly developed, the endosperm, as in Cyanastraceae, is used up during the ripening of the seed, and the embryo is large and well developed. *Eriospermum* also shows some vegetative similarities to *Cyanastrum*, such as the corm or tuber and the solitary or few broad leaves.

Eriospermaceae S.L. Endlicher (1836) 1:80 (Fig. 76)

Perennial herbs with a single, globose or sausage-like tuber or with a complex of tubers and stolons. The cut surface of the tubers is opaquely white, yellow, pink or red. In addition to some scale-like, reduced basal leaves there is a single leaf or there are up to three, rarely more, basally concentrated dorsiventral leaves each with a well-developed lamina. The leaf lamina varies from linear to ovate or cordate and sometimes lies flat on the ground; it is parallel-veined and either glabrous or clothed with simple or compound hairs. Of particular interest is the frequent presence of complex enations or a pubescent deeply dissected appendage at the base of the leaf blade. This appendage may have the shape of a "bottle brush", it may consist of a few filiform threads, or may resemble a bunch of feathers, the leaf itself being in these cases very small (Marloth 1915). In *Eriospermum dregei* and *E. paradoxum* the appendage is almost dichotomously branched, with linear, thick and fleshy segments (Fig. 76K).

The inflorescence-bearing stem is an erect scape, leafless or with bracteal leaves, ending in an often sparse raceme with bracteate and sometimes long-pedicelled flowers. It develops in the summer after the green, assimilating (leaf or) leaves have withered. Fasciculate hairs, matched only in Haemodorales, are found on the inflorescence in some species (Huber 1969). The flowers are hypogynous, actinomorphic, trimerous and bisexual, those uppermost in the raceme being sometimes minute and sterile. Their 3 + 3 tepals are free from each other, white, pink or yellow, and persistent, the outer being upright or spreading. The 3 + 3 stamens are adnate at the base to the tepals and have narrow or flat filaments and peltate, introrse, lon-



gitudinally dehiscent anthers. Tapetum is glandular and microsporogenesis is successive. The pollen grains likewise are poorly known but probably sulcate.

The tricarpellary, trilocular pistil has an erect simple style and a punctiform stigma. Each locule contains a few axile ovules, which are anatropous, bitegmic and weakly crassinucellate. A parietal cell is cut off from the archesporial cell. Embryo sac formation is of the *Polygonum* Type. Endosperm formation is nuclear(?), but the endosperm is used

Fig. 76. Eriospermaceae. **A–I** *Eriospermum abyssinicum.* **A** Corm with one leaf. **B** Inflorescence. **C** Flower. **D** Tepal and stamen attached to its base. **E** Stamens. **F** Pistil. **G** Capsule in state of dehiscence. **H** Seed with pubescence. (HEPPER 1968) **I** *E. majanthemifolium,* shoot. **H** *E. paradoxum,* young plant with one foliage leaf and, opposite this, an appendage of the unique kind found in part of this genus. **L–M** *E. abyssinicum.* **L** Plant, in flowering and fruiting stage. **M** Flower, in late stage. (**L–M** from KRAUSE 1930)

up in the course of seed ripening. The embryo becomes large and conical-cylindrical. Embryo formation follows the Solanad Type. Nucellar tissue envelops the chalazal parts of the embryo (Lu, unpublished). The embryology is thus very unusual.

The fruit is a loculicidal, subglobose or often three- or six-lobed capsule with a few seeds. These are unique in the monocotyledons in being clothed with long, unicellular hairs consisting of epidermal cells which have grown up to a length of 8 mm, and form processes filled with air. The hairs are white or reddish brown. The seeds are pear-shaped to narrowly ovate and their testa lacks phytomelan. In addition to the hirsute epidermis the outer integument of the testa consists of two cell layers, which may be compressed and colourless or pigmented with phlobaphene (Huber 1969). The endosperm of the ripe seed has thus been used up in connection with the extensive embryo, and nucellar tissue forms a cap around part of the embryo. This tissue accumulates fatty oils and aleurone, but no starch.

The chemical contents are otherwise not known.

Eriospermum (80) is confined to Africa with about 50 of its species concentrated in Southern Africa. Because the leaves and inflorescence are developed at different times, the taxonomy is somewhat difficult. The tubers of *Eriospermum* are edible. They contain mucilage but no starch or solid protein.

The genus is extraordinary in many respects, such as the occurrence of the peculiar leaf appendages, the epidermal hairs of the seed and the embryological attributes. Huber (1969) associates *Eriospermum* with *Walleria* and *Cyanastrum* on the basis of seed characters, but the successive microsporogenesis and thin testa argue against this. The relations are still uncertain and *Eriospermum* is probably best treated as a separate family.

Ixioliriaceae T. Nakai (1943) 1:1–4 (Fig. 77)

A perennial, erect herb up to ca. 60 cm tall. The underground stem is developed as a bulb-shaped, tunicated corm, which seems to range over more than one internode (lateral corms being developed at some distance from its base; Fig. 77F). The aerial stem is erect and leafy with the dispersed leaves flat and linear, sheathing at the base and supplied with a cylindrical-subulate apex. The tissues are rich in raphides (Oganezova 1981; Arroyo 1982). The stomata are anomocytic.

The inflorescence is a panicle varying much in degree of branching and number of flowers; it is often few-flowered and quite frequently umbel-like. The flowers are bisexual, actinomorphic, trimerous and epigynous, superficially similar to those in Amaryllidaceae, in which *Ixiolirion* is often placed. The linear-oblanceolate tepals of the two whorls are similar in size and shape, the outer somewhat narrower than the inner, and with a more prominent point emerging slightly below and outside the apex. The tepals are blue, bluish violet, pale-blue or nearly white, and are free from each other. There are 3+3 stamens, with their narrow filaments attached basally to the tepals opposite which they are inserted. Their anthers are basifixed, tetrasporangiate, introrse-latrorse and longitudinally dehiscent. Microsporogenesis is simultaneous, and the pollen grains are sulcate.

The style is erect, slender and apically tribrachiate, with Dry stigmatic surfaces. The ovary is inferior and trilocular, with rather numerous axially inserted, anatropous, crassinucellate ovules. A parietal cell is cut off from the archesporial cell. Endosperm formation is helobial. The fruit is a capsule with numerous seeds. These are ovate to pear-shaped, reticulate and have a testal epidermis with phytomelan, making them black. Apart from the elongate, hexagonal epidermal cells, the testa consists of several cell layers with thin reddish brown walls; the tegmen is thin and membranous and the endosperm cells thin-walled and starch-free. The embryo is straight and fusiform and nearly as long as the endosperm (Huber 1969). $x=12$ (Fedorov 1969).

Chemistry. Unlike the Amaryllidaceae, *Ixiolirion* lacks alkaloids. Chelidonic acid is present, but there seems to be no information on steroidal saponins.

The Ixioliriaceae consist of the single genus *Ixiolirion* (1–4) which is distributed in South-West Asia (Wendelbo 1970). Some taxonomists claim that the genus contains only one species.

Ixioliriaceae is to be separated from Amaryllidaceae on the basis of its corm, inflorescence structure and lack of alkaloids. Rather it could be most closely related to some Alliaceae (e.g. Brodiaeeae), to Tecophilaeaceae or Phormiaceae. The combination of simultaneous microsporogenesis and corms is important for drawing this conclusion. A close link with Liliaceae or Alstroemeriaceae is excluded because of the seeds which are coated with a phytomelan layer.

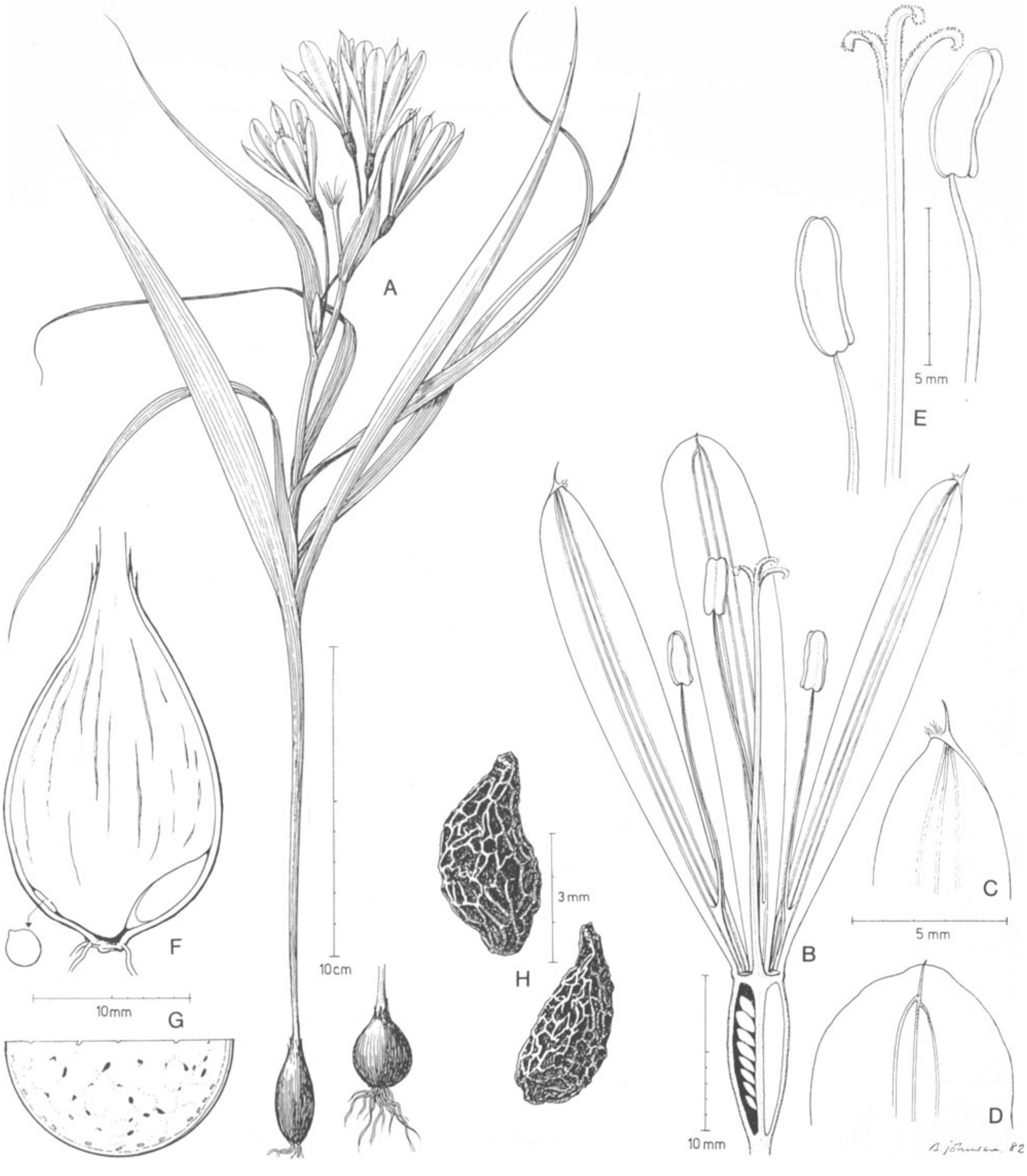


Fig. 77. Ixioliriaceae. *Ixiolirion montanum* s. lat. **A** Plant. **B** Flower, longitudinal section. **C** Apex of outer tepal. **D** Apex of inner tepal. **E** Style and two stamens, one of each whorl in the relative positions they have in the flower. **F** Corm; note the lateral new corms formed on both sides in the lower part. **G** Corm, transverse section. **H** Seeds, black from the phytomelan layer. (All orig. B. Johnsen)

Phormiaceae J.G. Agardh (1858) 7:32 (Figs. 78, 79)

Medium-sized to tall, rhizomatous herbs or subshrubs without secondary thickening growth. Rhizome often thick, with fascicled, fibrous roots. The leaves are distichously inserted and concentrated on the base and lower part of the stem. They are linear, often rigid and tough, and the lowest are developed as scale-like cataphylls. The foliar leaves are long, linear, parallel-veined, basally strongly compressed and nearly unifacial, otherwise dorsiventral and V-shaped or flat. Short antrorse teeth may be present on the leaf margins and midribs, making them rough or serrulate. Raphides are often present except in *Phormium,* where suberized cells with pseudo-raphides are present, a similarity to Nolinaceae. Stomata are of the anomocytic type and more or less sunken. The fibres of the leaves are sometimes conspicuous but not very strong (they are exploited in *Phormium,* as "New Zealand Flax"). Vessels seem to be lacking in the stem and leaves, but are present in the roots, and have simple and scalariform perforation plates.

The inflorescence, which is terminal on the stem, is a sparingly to densely branched panicle, which varies from rather few-flowered to very many-flowered. The pedicel is sharply demarcated from the perigone (Fig. 79G). The flowers are bisexual, actinomorphic or slightly zygomorphic, hypogynous or nearly so (*Phormium*). There are $3+3$ tepals, which are free or nearly free from the base, the outer often slightly smaller than, and sometimes different in texture and colour from the inner, which are more petaloid and often have rounded and/or recurved tips. The tepal colour varies from (greenish) yellow to red (*Phormium*), but is more often blue, violet or white.

The $3+3$ stamens have narrow, basally somewhat thickened filaments. Rarely, they are fused at the base into a ring (*Excremis*). Sometimes they are of unequal length (*Phormium*). They may also have papillate or villous hairs (*Stypandra*). In *Dianella* and some other genera they are thickened apically near the attachment point of the anther to form a globose or ovoid structure covered with nectar-secreting papillae. The anthers are elongate, basifixed or dorsifixed-epipeltate, and dehisce with apical pores (as in *Dianella* and *Stypandra*) or longitudinal slits. The tapetum is glandular and microsporogenesis simultaneous. All the genera seem to have trichotomosulcate pollen grains.

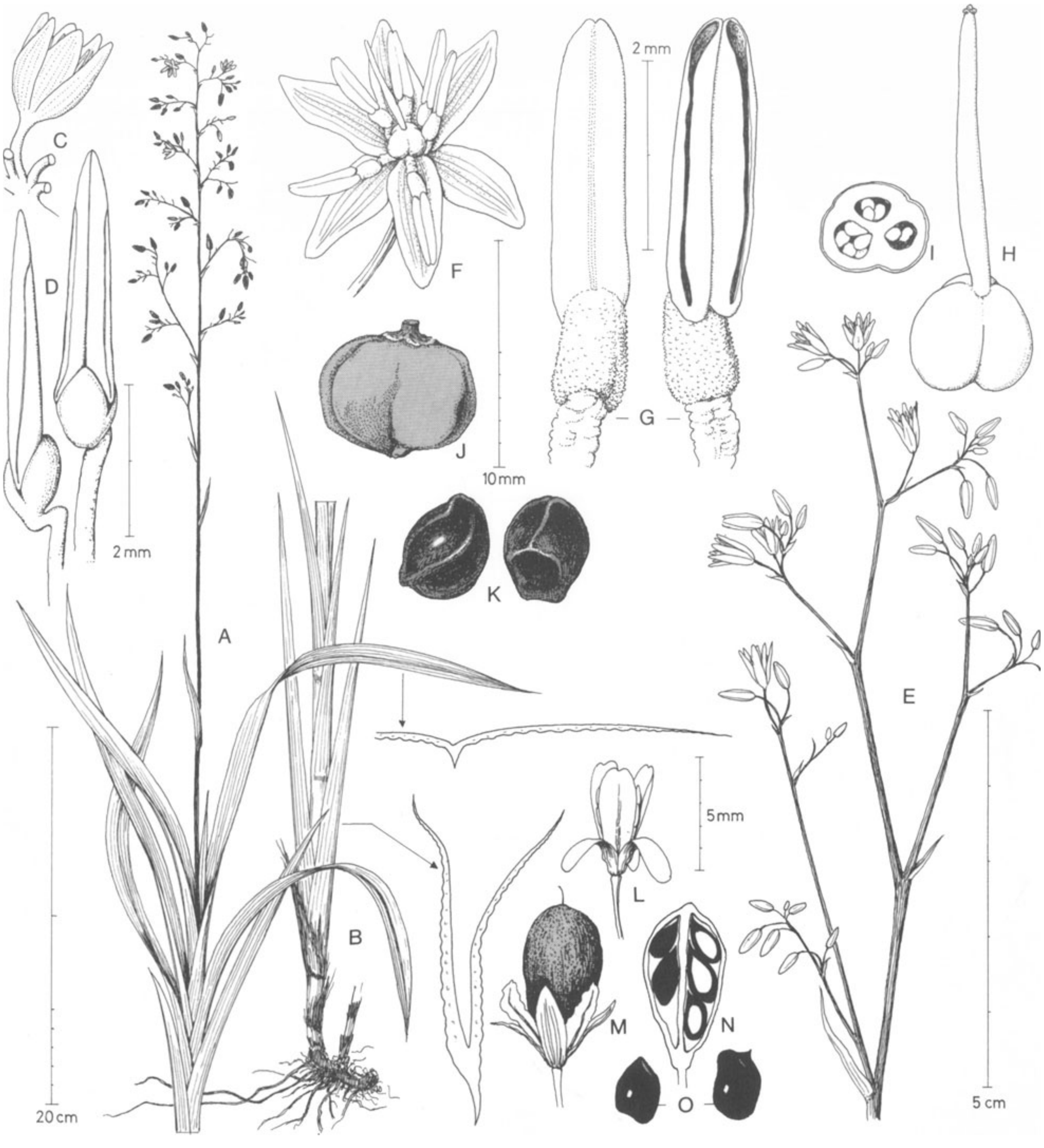
The pistil is tricarpellary and trilocular and has an erect, narrow style, which may be slightly upcurved in lateral flowers of *Phormium.* The stigma is punctiform and has a Dry surface. The locules each contain from four to rather numerous anatropous (epitropous) ovules which are weakly crassinucellate. No parietal cell is formed as the archesporial cell functions directly as the megaspore mother cell; periclinal divisions of the nucellar epidermis may (*Stypandra, Phormium*) or may not (*Dianella*) occur, in the former case forming a nucellar cap three to four cells in thickness. Embryo sac formation follows the *Polygonum* Type, and endosperm formation is helobial (CAVE 1955, 1975).

The fruits are either capsules or berries, the capsules in *Phormium* being elongate and often curved, those in other genera shorter. The berries in *Dianella* are often blue. The seeds are ovoid in most genera but elongate, elliptic-oblong and surrounded by a wing in *Phormium.* They are always provided with a black layer of phytomelan (even where the fruit is baccate). The seed coat has a multilayered outer integument with compressed but not collapsed cells, and a tegmen which has collapsed to form a thin membrane. The endosperm cells are relatively thin-walled and contain aleurone and lipids. The embryo varies from only about a third of the length of the endosperm to almost the same length. The basic chromosome number is $x=8$.

Chemistry. The chemical content seems to be little known. Steroidal saponins seem to be lacking in *Phormium;* the rhizome in this genus contains wax (ca. 1%) and its leaves contain "rubber", a hemicellulose-like polysaccharide.

Distribution. Phormiaceae occur mainly in South-East Asia and Australia and on the Pacific Islands, including New Zealand, *Dianella* extending, however, westwards to Africa, Madagascar and the Mascarene Islands. *Excremis* occurs in tropical South America.

Dianella (25) is widely distributed in the Old World tropics. It is a remarkable genus in its blue (to white) flowers and its often blue berries. Its branches are herbaceous or somewhat woody and the panicles are slender and often much branched. *D. ensifolia* (Fig. 78A–D) reaches a height of up to 2 m. Another species with wide distribution is *D. nemorosa,* ranging from Indomalesia to Madagascar and East Africa. *Stypandra* (3) in Australia has woolly filaments and capsular fruits. Some species are toxic if grazed. – *Agrostocrinum* (1), in South-Western Australia, has a capsular fruit



enclosed by the persistent base of the perianth. – *Excremis* (1) is a plant of the paramos from Peru to Colombia growing up to 1.5 m tall. – *Phormium* (2), occurs primarily in New Zealand but the best-known species, *P. tenax,* is also found on Norfolk Island. It is a large herb with leaves up to 2.5 m long and an inflorescence axis 2–4.5 m long; it grows mainly in lowland swamp habitats.

Fig. 78. Phormiaceae. **A–D** *Dianella ensifolia* (specimen from Kew). **A–B** Plant, transection of leaves shown to the *right.* **C** Flower. **D** Stamen in different views. **E–K** *Dianella* sp. **E** Inflorescence. **F** Flower. **G** Anther, different views. **H** Pistil. **I** Ovary, transverse section. **J** Berry. **K** Seeds, note the black colour caused by the phytomelan layer. **L–O** *Dianella nigra.* **L** Flower. **M** Berry. **N** Same in longitudinal section. **O** Seeds. (Orig. B. JOHNSEN)

Fig. 79. Phormiaceae. **A–B** *Phormium cookianum*. **A** Inflorescence and leaf. **B** Flower. (Redrawn from EVERARD and MORLEY 1970) **C–E** *Phormium tenax*. **C** Flower bud. **D** Stamen from flower bud. **E** Pistil, in same bud. (Orig. from Kew Gardens) **F–I** *Phormium cookianum*. **F** Capsule, transverse section. **G** Lateral branch of infructescence; note the sharp delimitation ("joint") between pedicel and flower. **H** Seeds. **I** Same, transverse section. (Orig. from Kew Gardens; B. JOHNSEN)

The species is known as "New Zealand Flax" and was used by the Maoris as a source of fibre for making cloth and cord. At present it is grown commercially on a moderate scale in New Zealand, the U.S.A., Central Africa, Mauritius, etc., and is used mostly for cordage and sacking material. A smaller species, *P. cookianum* (Fig. 79A–B), with which it hybridizes, grows in open heath and montane scrub.

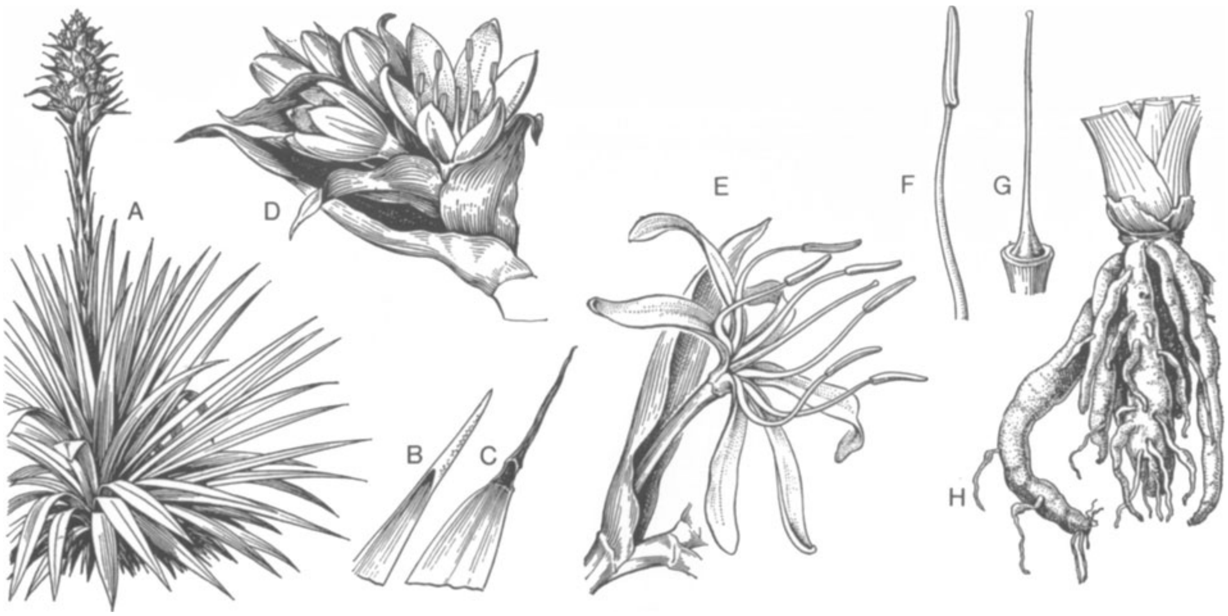


Fig. 80. Doryanthaceae. **A–D** *Doryanthes palmeri.* **A** Plant. **B–C** Apex of young and old leaf. **D** Branch of the thyrsoid inflorescence. **E–H** *Doryanthes excelsa.* **E** Flower. **F** Stamen. **G** Pistil. **H** Root system. (All from TAKHTAJAN 1982)

It is possible that the genus *Xeronema* (2) (EVERARD and MORLEY 1970), on New Zealand and New Caledonia, consisting of large herbs with one-sided panicles of reddish flowers, is closely related to *Phormium* and also belongs to Phormiaceae, although further studies on its embryology and pollen morphology are needed. Alternatively, a position in or near Asteliaceae or Doryanthaceae is to be considered.

Phormiaceae, which is here circumscribed as by TAKHTAJAN (1980), is probably rather closely related to Doryanthaceae in which, however, the leaves are spirally set and not basally compressed, and the pollen grains are not trichotomosulcate. Both families have developed large flowers with the bird-pollination syndrome and have the simultaneous microsporogenesis and nucellar cap in common. Although these details do not convincingly prove a close relationship the shared geographical distribution may be regarded as a support.

Doryanthaceae Dahlgren & Clifford, fam. nov. 1:3 (Fig. 80)

Plantae giganteae foliis in rosula maxima spiraliter aggregatis. Folia linearia, crassa, carnosa, dorsiventralia, ad 1.5 m longa vel longiora, apice tereti infuscato vel ferrugineo quasisuberoso munita. Contextus partium vegetativarum sine rhaphidibus pseudorhaphidibusque. Stomata paracytica. Caules floriferi usque ad 5 m alta, recti, rigidi, foliis reductis instructi et inflorescentiis thyrsoideis elongatis vel subcapitatis terminati. Flores diametro 10–15 cm, laete rubri, raro candidi, epigynici, actinomorphi vel parum zygomorphi, bisexuales. Tepala patentia, interiores ad basin leviter dilatati. Stamina 3+3, antheris elongatis pseudobasifixis, longitudinaliter dehiscentibus. Microsporogenesis simultanea. Grana pollinis sulcata. Ovarium triloculare; stylus simplex trisulcatus, in stigma triangulare terminans. Nectaria septalia praesentia. Ovuli quoqueloculo plures vel multi, anatropa, crassinucellata. Saccus embryonis typi Polygoni formans; endospermium helobiale. Fructus capsula loculicidalis. Semina aliquot compressa et alata vel conica, sectione transversali saepe triangularia, sine phytomelano. Endospermium olea pinguia et aleuronem continens; embryo obconicus.

Genus typicus: *Doryanthes* Corréa.

Giant rosette plants with a short basal stem. The leaves are spirally set, linear, thick, dorsiventral, up to more than 1.5 m long, with a terete, brownish tip, 1–2 cm long. The leaves lack raphides as well as pseudoraphides, but cells with twin crystals are common (raphides, however, are found in the tepals). The stomata are of the paracytic type (BLUNDEN and JEWERS 1973).

The inflorescence is borne on straight, stiff aerial branches up to 5 m long, with numerous short leaves; it is a thyrse, elongate or sometimes globose, with numerous, large flowers, which may be substituted by bulbils. The flowers are 10–15 cm long, with tepals varying in colour from nearly white to bright maroon-red. The flowers are epigynous, actinomorphic or slightly zygomorphic and bisexual. The six tepals are spreading, the inner being slightly dilated at the base.

The 3+3 stamens have linear-subulate filaments, broadening towards the base, and elongate anthers which are "pseudobasifixed", i.e. in reality peltate but with the apex of the filament enclosed in a tube formed by the connective (as in *Tulipa,* for example). Anther dehiscence is longitudinal. The tapetum is of the Secretory Type. Microsporogenesis is simultaneous (as in Phormiaceae; CAVE 1955). The pollen grains are sulcate.

The inferior ovary is trilocular and the style is simple, with three furrows, and bears a triangular stigma. Septal nectaries are present. There are several to many, anatropous, crassinucellate ovules in each locule. A primary parietal cell is cut off from the archesporial cell and, additionally, the nucellar epidermis divides periclinally to a nucellar cap (CAVE 1955). The embryo sac formation follows the *Polygonum* Type, and the endosperm formation is helobial (NEWMAN 1928–29).

The fruit is a loculicidal capsule with several seeds per locule. The seeds vary from somewhat compressed and winged (*D. palmeri*) to conical; they are often triangular in transection and elongated transversely. They lack phytomelan entirely. The testal layer of the seed coat consists of seven to many cell layers; its epidermis consists of isodiametric cells, reddish brown (with phlobaphene). The inner integument is thicker than in Agavaceae and has a distinct cuticle. The endosperm consists mainly of isodiametric cells storing aleurone and fatty oils, but not starch. The embryo varies in size and has a broadened obtriangular cotyledon (HUBER 1969). Saponins are now known to occur in the family.

Doryanthaceae consists of the single genus *Doryanthes* (3) in Queensland and New South Wales, Australia, impressive rosette plants with large, brightly coloured flowers. They are known as "Spear Lilies", and are sometimes grown as ornamentals.

The affinity of Doryanthaceae is somewhat uncertain. Possibly it comes closest to Phormiaceae. Doryanthaceae was first suggested as a family by HUBER (1969) and was also acknowledged by TAKHTAJAN (1980), but has not formally been published.

Hemerocallidaceae R. Brown (1810) 1:16 (Fig. 81)

"Lily-like", glabrous herbs to ca. 1 m tall with short rhizomes and fleshy, swollen, sometimes nearly fusiform roots. The larger leaves are concentrated at the base, and are dorsiventral, linear, mesomorphic, sheathing at the base and parallel-veined. The stomata are anomocytic. Crystal raphides are present. Vessels are lacking in stem and leaves; those of the roots have scalariform perforation plates (CHEADLE and KOSAKAI 1971).

The inflorescence is borne on a bracteate, but otherwise largely leafless scape, and is considered to represent one (or two) double helicoid cymes (KRAUSE 1930). The flowers are fairly large and few (mostly 5–12) and are not delimited from the pedicel by a joint. They are hypogynous, trimerous and funnel-shaped (*Lilium*-like) in outline, having 3+3 petaloid, yellow to orange or brick-red tepals, which are basally connate into a tube. They may be striped (but not variegated with a drop-like pattern) and may be recurved apically.

The stamens, which are inserted in the tubular part of the perigone, are all slightly upcurved, making the flowers zygomorphic. Their filaments are long, glabrous and free from each other; the anthers are epipeltate-versatile, often twisted, and dehisce longitudinally. The tapetum is secretory. Microsporogenesis is simultaneous (CAVE 1955). The pollen grains are sulcate, two-celled and rather similar to those in Funkiaceae.

The pistil is trilocular and has a long, slender, slightly upcurved style and a punctiform-capitate stigma with a Wet surface. Septal nectaries are present in the rather triangular ovary. Each of the locules contains numerous anatropous ovules, in which the archesporial cell functions directly as the megaspore mother cell. There are no periclinal divisions in the nucellar epidermis. The embryo sac formation follows the *Polygonum* Type, and the endosperm formation is nuclear.

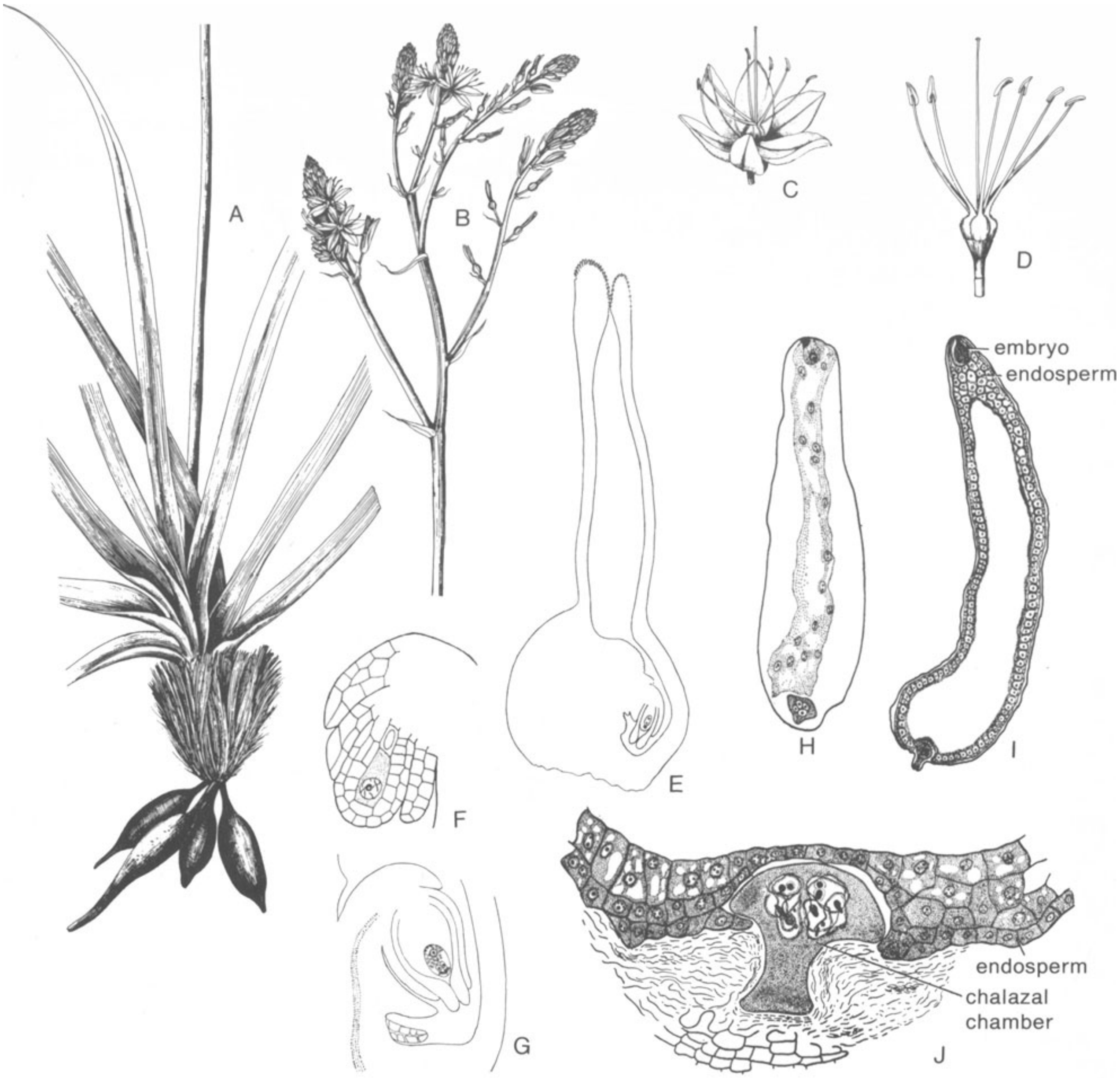
The fruit is a loculicidal capsule opening from the apex. The seeds are subglobose to prismatic or slightly elongate (not flat) and have a smooth, shiny black epidermal layer encrusted with phytomelan; the inner layers of the outer integument are compressed and rust-coloured, while the inner integument is collapsed. The endosperm contains aleurone and fat, but not starch, and the embryo is of about the same length as the endosperm.

The chemistry seems to be unknown.

It is interesting to note that the chromosomes ($x=11$) are not dimorphic, as they are in *Hosta,* with which *Hemerocallis* is sometimes associated.

The family Hemorocallidaceae ("Day Lilies") consists of the single genus *Hemerocallis* (16), distributed mainly in temperate regions of Asia but extending into southern Europe. *H. fulva* and several garden hybrids with different perigone colours are grown as ornamentals and are reminiscent of

Fig. 81. Hemerocallidaceae. **A–E** *Hemerocallis fulva.* **A** Roots and young shoot. **B** Inflorescence. **C** Flower bud, longitudinal section. **D** Anther in different views. **E** Ovary, transverse section, note the septal nectary cavities. **F–H** *H. middendorfii.* **F** Infructescence. **G** Opening capsule, one valve removed. **H** Seeds. (Orig. B. Johnsen)



certain lilies (*Lilium*), from which they are easily distinguished by their rhizome and the black, prismatic to rounded (not pale brown and flat) seeds.

The closest affinities of *Hemerocallis* are uncertain. Although in seed coat structure the genus agrees with the Alliaceae (HUBER 1969) its simultaneous microsporogenesis, the lack of parietal tissue, and its inflorescence type exclude it from that family. Comparisons with the Asphodelaceae, Anthericaceae and Funkiaceae suggest no valid reasons for including *Hemerocallis* in any of these families, most features being perhaps concordant with Asphodelaceae subfam. Asphodeloideae.

Fig. 82. Asphodelaceae. **A–D** *Asphodelus aestivus*. **A** Lower part of plant. **B** Inflorescence. **C** Flower. **D** Androecium and gynoecium, the filament bases widened to conceal ovary. (JAFRI and EL-GADI, 1978). **E** *Asphodelus fistulosus,* carpel in early stage, showing ovule with beginning of aril formation. (STENAR 1928a). **F** *Echeandia ternifolia.* Ovule. (SCHNARF and WUNDERLICH 1939). **G** *Bulbine annua,* anatropous ovule with aril. (STENAR 1928a). **H–J** *Asphodelus tenuifolius,* endosperm formation. **H** Helobial endosperm, the lower dark portion being the chalazal chamber. **I** Later stage; wall formation has taken place in the micropylar chamber. **J** Details of same section, showing the chalazal chamber. (EUNUS 1952)

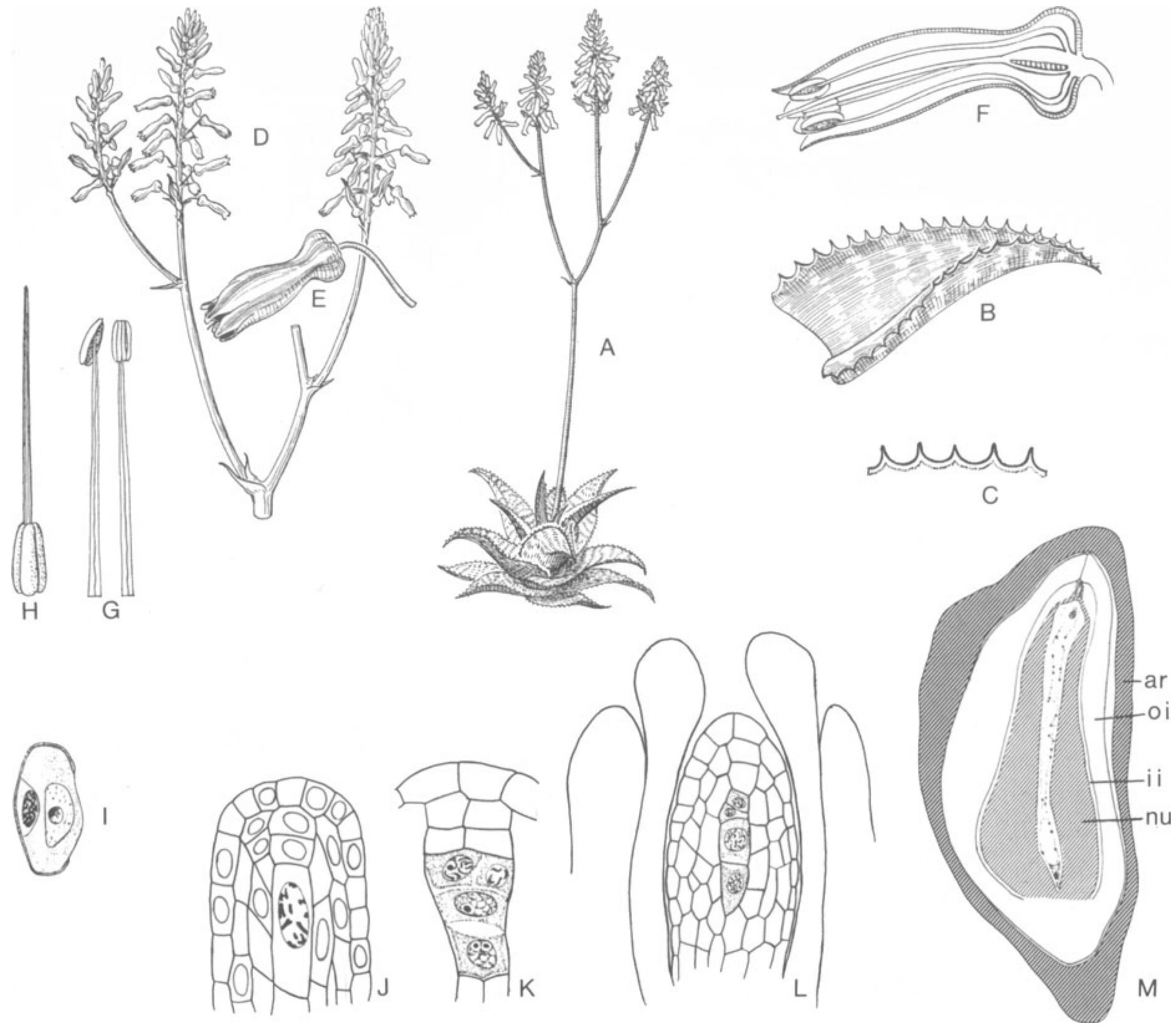


Fig. 83. Asphodelaceae. **A–H** *Aloë macrocarpa*. **A** Plant. **B** Apical part of leaf. **C** Leaf margin. **D** Part of inflorescence. **E** Flower. **F** Same, longitudinal section. **G** Stamens. **H** Pistil. (Hepper 1968). **I** *Aloë humilis*, pollen grain (sulcate, two-celled). **J** *A. ciliaris*, nucellus with parietal cells. **K** *A. variegata*, T-shaped megaspore tetrad. **L** *A. brownii*, linear megaspore tetrad. **M** *Kniphofia praecox*, ripe seed (*ar* aril; *oi* outer integument; *ii* inner integument; *nu* nucellus; the endosperm, with a small basal chamber, is seen in the *centre*). (**I–M** from Schnarf and Wunderlich 1939)

Asphodelaceae A.L. Jussieu (1789) 18:750–800 (Figs. 5, 82, 83, 84G–L, 89Q–T)

Mostly herbs, but also woody forms provided with a trunk up to several metres high. The latter forms bear rosettes of succulent leaves at the ends of the branches, whereas the leaves are otherwise normally radical. Secondary thickening growth occurs in species of *Aloë* and *Kniphofia*. The roots sometimes (e.g. in *Asphodelus*) are inflated and fusiform; multi-layered velamen is known in some genera. The leaves are generally dorsiventral and often thick and succulent; they may be terete but are never ensiform. They are usually spirally set (occasionally distichous, as in several species of subfam. Alooideae), from linear or subulate to thickly conical or even elliptic, sheathing at the base and, in the succulent genera, often serrate-dentate and apically spiny. The veins are longitudinal but are indistinct or invisible when the leaves are succulent. The stomata are generally anomocytic or tetracytic, rarely paracytic. Vessels, with scalariform perforation plates, are only occasionally present in the stem (species of *Asphodelus*). Raphide cells are abundant. So-called aloine cells, which are parenchymatous cells arranged as a cap at the phloem pole of most vascular bundles of the leaf, occur in many taxa, and are characteristic of subfam. Alooideae. These cells secrete a range of anthraquinones and other substances. In subfamily Alooideae the aloine cells generally contain coloured secretions. The parenchyma cap may be replaced by sclerenchyma. In other genera of the family (i.e. taxa of subfam. Asphodeloideae) typical caps of aloine cells are lacking, but there may be a large parenchymatous region at the xylem pole of the vascular strands (e.g. in *Kniphofia*). Tannin cells then replace cells with anthraquinones (CUTLER, personal communication).

The inflorescences are simple or compound racemes or spikes. They are situated on the ends of terminal peduncles, which are sharply demarcated from the vegetative part of the shoot and are either nearly leafless or beset with bracteal leaves (densely so in *Jodriella,* for example). The growth of the shoot is often sympodial, so that the inflorescence-bearing axes, which are terminal, are pushed aside and appear lateral. As in the Anthericaceae, the flowers may have a basal "pericladium".

The flowers are hypogynous, trimerous and normally bisexual. In certain genera (e.g. *Asphodelus*) the tepals are free or nearly free from each other, while in subfam. Alooideae they are often more or less fused with each other into a tube. The perigone may then be conspicuously zygomorphic, with the apical parts (together with the filaments) somewhat curved (*Gasteria*) or slightly two-lipped (*Haworthia*). The tepals vary much in colour, from white or rose-coloured to bright red and/or yellow or pale purple and greenish (but not blue or blue-violet); in large-flowered, ornithogamous forms they may be rather stiff. The inner tepals may be more or less different from the outer.

The stamens are 3+3 in number and generally inserted at the base of the ovary. The filaments are linear and free from each other, and rarely (*Bulbine, Jodriella, Simethis*) provided with hairs. The anthers are dorsifixed-epipeltate and introrse and dehisce longitudinally. Microsporogenesis is simultaneous (a noteworthy difference from Anthericaceae, where it is successive). The pollen grains are sulcate and two-celled when dispersed.

The pistil is syncarpous, tricarpellary and trilocular and has a simple, long style with a small stigma of the Dry or, more rarely, of the Wet Type. Septal nectaries are present in the ovary walls. Placentation is axile. The ovules (Fig. 5) are two to rather numerous per locule, anatropous, hemianatropous or (as in species of *Aloë* and *Asphodelus*) nearly orthotropous, and crassinucellate, with a parietal cell usually cut off from the archesporial cell. Embryo sac formation conforms to the *Polygonum* Type, and endosperm formation is of the Helobial Type (Fig. 89Q–T). An aril frequently develops as an annular invagination at the distal part of the funicle and envelops the seed to a variable extent during its growth, as if it were a "third integument" (SCHNARF and WUNDERLICH 1939). The aril is two or more cells thick; it is well developed in *Bulbine, Kniphofia* and the genera of subfam. Alooideae; in *Kniphofia* it is supplied with purple pigment; an aril, although thinner, is also present in *Asphodelus, Verine, Bulbine* and *Bulbinopsis.*

The fruit is a loculicidal capsule, which is carnose in *Lomatophyllum*. The generally arillate seeds (see above) are elongate and ovoid, winged in some species of *Eremurus*. The outer epidermis of the outer integument develops a black phytomelan crust while the layers of the inner integument become more or less collapsed. The endosperm cells store lipids and aleurone, and the embryo is straight, linear and generally at least three-quarters the length of the endosperm. $x=7$ (in *Kniphofia* 6).

Chemistry. Chemically the Asphodelaceae differ from the Anthericaceae in lacking steroidal saponins and in synthesizing, quite frequently, anthraquinones, which are accumulated in the aloine cells mentioned above. Chelidonic acid is often present. The underground organs accumulate fructans and other carbohydrates but not starch.

Distribution. The family consists of ca. 17 genera and has a wide Old World distribution with a clear centre in Southern Africa, in particular subfamily Alooideae.

Subfamily Asphodeloideae

This consists of a number of herbaceous genera with mesomorphic to succulent or otherwise xeromorphic, rarely subterete, leaves and a central, branched or unbranched, pedunculate inflorescence. The plants are rhizomatous and may have thickened storage roots (as in species of *Asphodelus,* Fig. 82A). Typical caps of aloine cells are obviously not formed at the phloem poles of the vascular strands of the leaves, not even in *Kniphofia,* which has previously been referred to the *Aloë* group of genera (see below). The stomata are generally anomocytic. The flowers are usually white or pink, but are yellow in, for example *Bulbine,* and yellow and red in most species of *Kniphofia.*

The locules of the ovary have two or, in *Kniphofia, Eremurus* and *Trachyandra,* more ovules. An aril is present in some genera, but it is often thin and devoid of lipids. Although the information is incomplete, anthraquinones seem to be present in some taxa of the subfamily, e.g. in *Simethis* (HEGNAUER 1963; GIBBS 1974); aloine reactions are also reported in *Bulbine* (HEGNAUER 1963). Tannin contents rather than anthraquinones are, however, found in the mesenchymatous cells at the vein endings of the leaves in *Kniphofia* (CUTLER, personal communication).

The Asphodeloideae form a varied group of genera, often with a less African concentration than in the Alooideae. *Eremurus* is Asiatic with most species in the U.S.S.R. and Afghanistan and *Asphodelus* is Mediterranean and West Asiatic; *Trachyandra, Bulbine* and *Kniphofia* are, however, centred in Southern Africa.

Asphodelus (12) (Fig. 82) is chiefly Mediterranean-West Asiatic and includes small to fairly tall herbs with white or pink flowers. The roots are swollen and fusiform; those of *A. albus* are used for fermenting alcohol, those of *A. ramosus* for gum. *A. aestivus* is a common plant on disturbed ground in the Mediterranean Region; it can be used for dyeing carpets. – Related is *Asphodeline* (20) in the same region. – *Eremurus* (35) is concentrated in the steppes of the high plateaus in central Asia, up to 6,000 m in the Himalayas. It consists of herbs with scapose racemes up to 3 or more metres high with white, pinkish or yellow flowers on rather slender pedicels. The seeds in some species have broad wings. – *Trachyandra* (50), mainly in South Africa, has scabrid filaments but otherwise superficially resembles *Anthericum,* in which it was long included.

Simethis (1) (Fig. 84G–L), in western Europe and the western Mediterranean, has often been placed in the *Anthericum* group of genera (our Anthericaceae), but agrees with Asphodelaceae in several respects, on the basis of which we place it here. The white, somewhat *Anthericum*-like flowers have hairy filaments (Fig. 84I) and the thickly melaniferous seeds (HUBER 1969) have an elaiosome formed from the hilum. The locules, as in most Asphodeloideae, contain two ovules each. Anthraquinones (e.g. emodin) are reported from the leaves (HEGNAUER 1963; GIBBS 1974). Certain embryological details, however, agree better with the Anthericaceae.

Bulbine and related genera are likewise herbaceous with a single central inflorescence; their leaves are usually not succulent (but sometimes strongly so). The tepals are free from each other and yellow or rarely white. The inner layer of the aril contains lipids. *Bulbine* (c. 50) and *Bulbinella* (c. 15) occur in Southern Africa, the latter also in New Zealand, and the related, recently described *Jodriella* (3) occurs in tropical Africa (BAIJNATH 1978).

Kniphofia (70) in Africa, mostly in the southern parts, are acaulescent or rarely caulescent herbs of medium size, with rosulate, rarely distichous, linear leaves, sometimes with serrate margins. The inflorescences are more or less dense spikes, within which the flowers may vary in size and colour, the upper being often red and spreading or upright, the lower yellow and pendulous (hence the popular name, "Red-Hot Poker"). Rarely, the flowers are white or purple (see CODD 1968) and they may all be short and spreading, *K. breviflora* being conspicuously *Muscari*-like. Some species are grown as ornamentals, e.g. *K. triangularis, K. ensifolia* and various hybrids. *Kniphofia,* with its tubular, usually bright-coloured flowers largely pollinated by birds, is peripheral in subfamily Asphodeloideae and has generally been placed with *Aloë* and other genera of our Alooideae. As shown by BAIJNATH (1980) and CUTLER (personal communication), there are great differences in the anatomical construction of the leaves between *Kniphofia* and the Alooideae, and it seems most appropriate to place *Kniphofia* outside the latter subfamily.

Subfamily Alooideae

The members of this subfamily vary from minute plants with a rosette of succulent leaves, as in *Haworthia,* to giant trees branching pseudo-dichotomously, as with some species of *Aloë* (*A. dichotoma, A. bainesii*); the variable genus *Aloë* also contains small rosette herbs. Each plant often develops a number of inflorescences. As the shoot continues its growth sympodially the terminal inflorescences are pushed aside to a pseudo-lateral position.

The taxa of this subfamily are all conspicuously succulent-leaved. The leaves are usually spirally set, but distichous in species of *Aloë* as well as *Haworthia.* They vary in shape from linear or lanceolate to elliptic or triangular-conical and often possess lateral spines or teeth and frequently end as a sharp spine. The vascular bundles are present in a ring around the central ground parenchyma, which is not the case in the genera of the Asphodeloideae. A cap of aloine cells is present at the phloem pole of most vascular bundles of the leaf.

The aloine cells contain coloured secretions. In *Poelnizia,* several species of *Gasteria* and *Haworthia* and single species of *Aloë* the parenchyma cap (aloine cells) are replaced by sclerenchyma. The stomata are generally tetracytic.

The leaves are often perennial, dying off gradually. The flowers are more or less tubular and vary in colour from red, red and green or red and orange to white (as in *Haworthia*). The large-sized flowers are generally fleshy and bird-pollinated (which is also the case in *Kniphofia*). The perigone in *Haworthia* is two-lipped and thus distinctly zygomorphic. There are several to many ovules in each locule. The seeds are arillate.

The members of Alooideae produce anthraquinones.

The subfamily consists of six to seven genera with a markedly Southern African concentration.

Subfamily Alooideae is rather distinct, especially in its anatomical characters, and with the family concept adopted here may deserve that status. We assume that it is a monophyletic group of genera derived from some ancestral Asphodelaceae. The remaining Asphodelaceae (subfamily Asphodeloideae) are more varied and probably make up a paraphyletic group.

Aloë (330), ranges along the whole of Africa, including Madagascar, but is most concentrated in South Africa. They vary from modest herbs to veritable trees ("Kokerboom"). Species like *A. dichotoma* and *A. bainesii* in Namaqualand, western Cape, may attain a height of up to 7 m or more, having thick and seemingly dichotomously branched trunks. Other species have a trunk 1–5 m tall, like the common *A. ferox*. The leaves, which are very thick and fleshy, are sometimes distichous, but more often spirally set and may bear lateral spines. The carnose, often bright red outer tepals are fused into a tube. This is one of the genera with "aloine cells", mentioned above. The contents, rich in anthraquinones, are used against intestinal worms and as a cathartic. *A. ferox* is used for this purpose in South Africa and *A. vera* in the Mediterranean; *A. saponaria* in South Africa has a similar medical use. Many species are grown as ornamental leaf succulents, e.g. the small-sized *A. picta* and *A. variegata*.

Related to *Aloë* are the genera *Chamaealoë* (1), *Poelnizia* (1) and *Astroloba* (12), all in Southern Africa. – The species of *Lomatophyllum* (14), on Madagascar and the Mascarenes, have fleshy fruits.

Gasteria (50), likewise mainly South African, has a curved perigone with subglobose base; its leaves are strongly succulent and sometimes facetted. Several species are grown as greenhouse succulents. – *Haworthia* (ca. 150), differs from *Gasteria* in having a straight, apically two-lipped, rarely actinomorphic, and generally whitish, pink or red, perianth tube. The seeds are small. Many species are grown as ornamentals because of their imbricate, succulent or leathery leaves with smooth, denticulate or ciliate margins.

The common presence of anthraquinones, the lack of steroidal saponins, the simultaneous microsporogenesis, the different ovular morphology and the common presence of an aril are typical attributes of the Asphodelaceae. We have largely adopted the circumscription of SCHULZE (1975a).

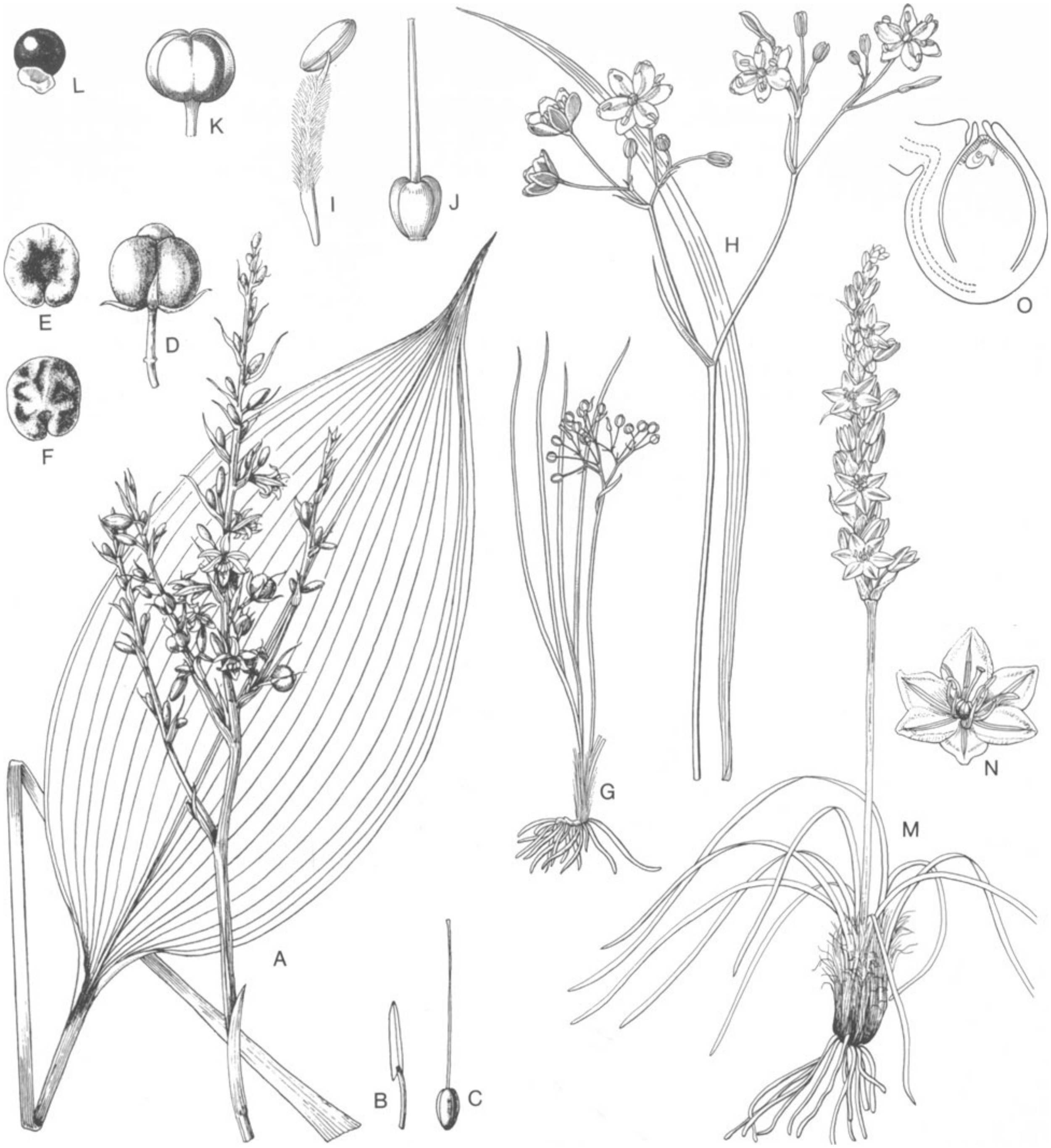
The great phenetic similarity between members of Asphodelaceae subfamily Asphodeloideae and certain Anthericaceae may cause practical problems. However, it is likely that the Asphodelaceae could be more closely related to other families which have simultaneous microsporogenesis, e.g. Hemerocallidaceae, Phormiaceae and Cyanastraceae.

Anthericaceae J.G. Agardh (1858) 33:620 (Figs. 84–86)

Rhizomatous herbs with most leaves concentrated in a basal rosette and with an erect, largely leafless aerial stem bearing a terminal inflorescence.

The leaves are reduced in certain Australian genera, where the scapes are the main assimilating parts. A woody trunk is never developed, and secondary thickening growth is lacking. The leaves are spirally set or rarely (for example, in *Caesia* and *Sowerbaea*) distichous. They are flat and dorsiventral, sometimes terete or triangular, generally linear, sheathing at the base, mostly inconspicuously parallel-veined and rarely scleromorphic, rigid or succulent but then not to the same extent as in Asphodelaceae. Ligule-like structures are present at the top of the leaf sheath in *Sowerbaea.* The stomata are anomocytic. Oxalate raphides are widely distributed in the family. Vessels are surprisingly often present in the stems (e.g. in taxa of *Anthericum, Arthropodium, Caesia, Johnsonia* and *Tricoryne*), where they have scalariform or rarely simple perforation plates.

The inflorescences are simple or compound racemes, spikes or panicles, sometimes condensed into dense heads or clusters (e.g. in some "Johnsonieae").



The flowers are hypogynous, trimerous and generally actinomorphic and bisexual. They are often jointed to a "pericladium". The tepals are 3+3, free from each other or basally connate into a tube; the two whorls may be similar or slightly different in size and shape. The tepal colour is white (to rose-coloured), yellow (*Tricoryne*), or blue or bluish violet (the last-mentioned colours being absent in Asphodelaceae). Zygomorphy af-

Fig. 84. Anthericaceae (**A–F**, **M–O**) and Asphodelaceae (**G–L**). **A–F** *Chlorophytum orchidastrum*. **A** Inflorescence and leaf. **B** Stamen. **C** Pistil. **D** Capsule. **E–F** seed in different views. (HEPPER 1968). **G–L** *Simethis planifolia*. **G** Plant. **H** Leaf and inflorescence. **I** Stamen. **J** Pistil. **K** Capsule. **L** Seed with caruncle. (ROSS-CRAIG 1972). **M–N** *Eremocrinum albomarginatum*. **M** Plant. **N** Flower. (CRONQUIST et al. 1977). **O** *Anthericum ramosum*, campylotropous ovule. (STENAR 1925)

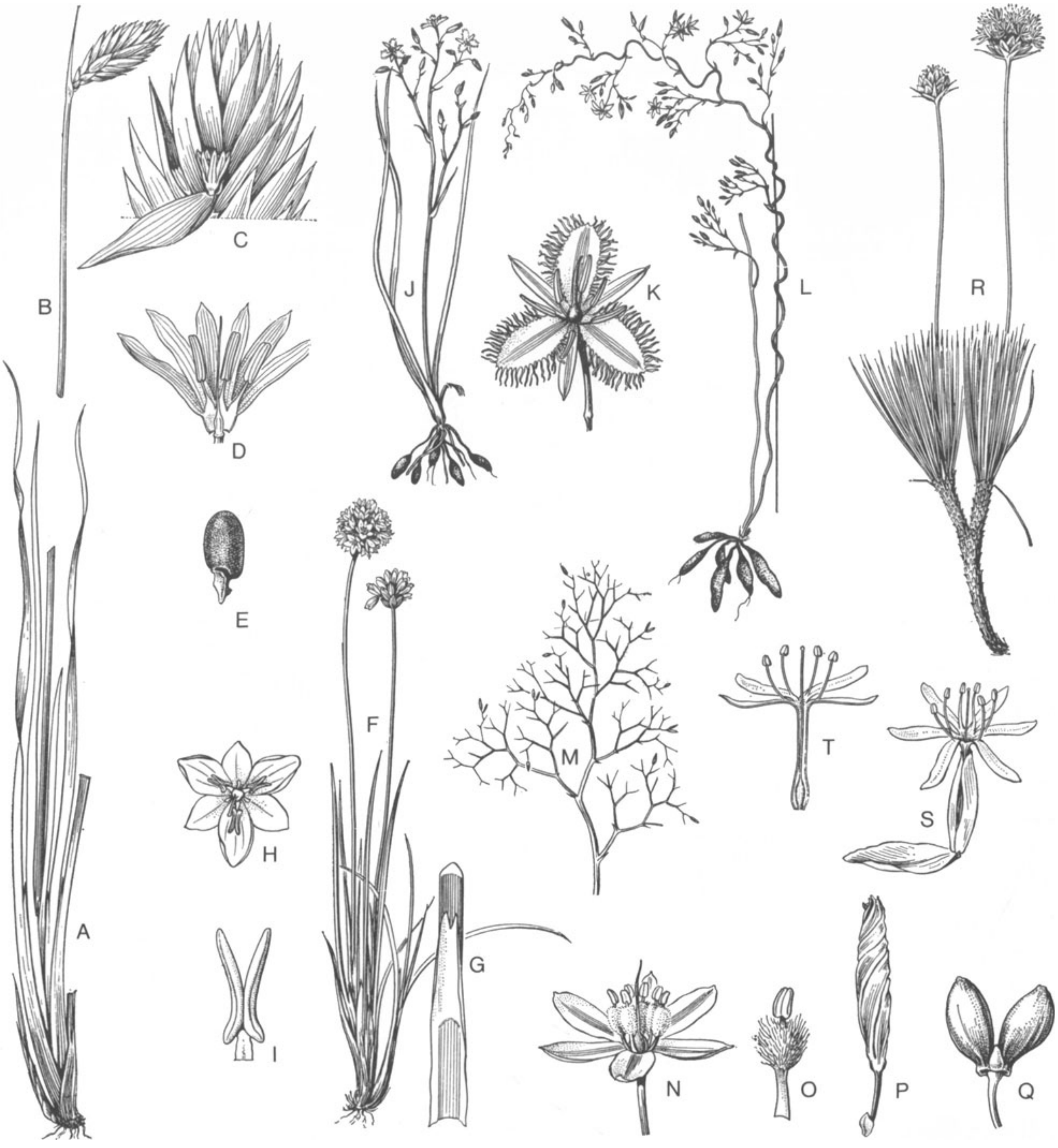


Fig. 85. Anthericaceae. Australian genera of the Johnsonia-Caesia groups. **A–E** *Johnsonia lupulina.* **A** Base of the plant. **B** Inflorescence, the flowers concealed between the bracts. **C** Bract bent away to show flower. **D** Flower, tepal tube spread open to show the three attached stamens and the pistil. **E** Seed. **F–I** *Sowerbaea juncea.* **F** Plant. **G** Ligule (ligules are very rare in the family). **H** Flower. **I** Anther, sagittate. **J–K** *Thysanotus tuberosus.* **J** Plant, note the swollen ends of some roots. **K** Flower. **L** *Thysanotus patersonii,* plant; the whole plant, as with *Bowiea* of Hyacinthaceae, consists mainly of a branched, scandent inflorescence. **M** *Thysanotus spiniger,* inflorescence, here much-branched, with rigid and straight branches. **N–Q** *Tricoryne elatior.* **N** Flower. **O** Stamen with hairy filament. **P** Spiralled withered flower. **Q** Fruit, here a schizocarp with two locules developed. **R–T** *Borya septentrionalis,* a somewhat dubious member of the family. **R** Branches, the leaves stiff and prickly. **S** Flower and bract. **T** Flower, longitudinal section. (All from TAKHTAJAN 1982)

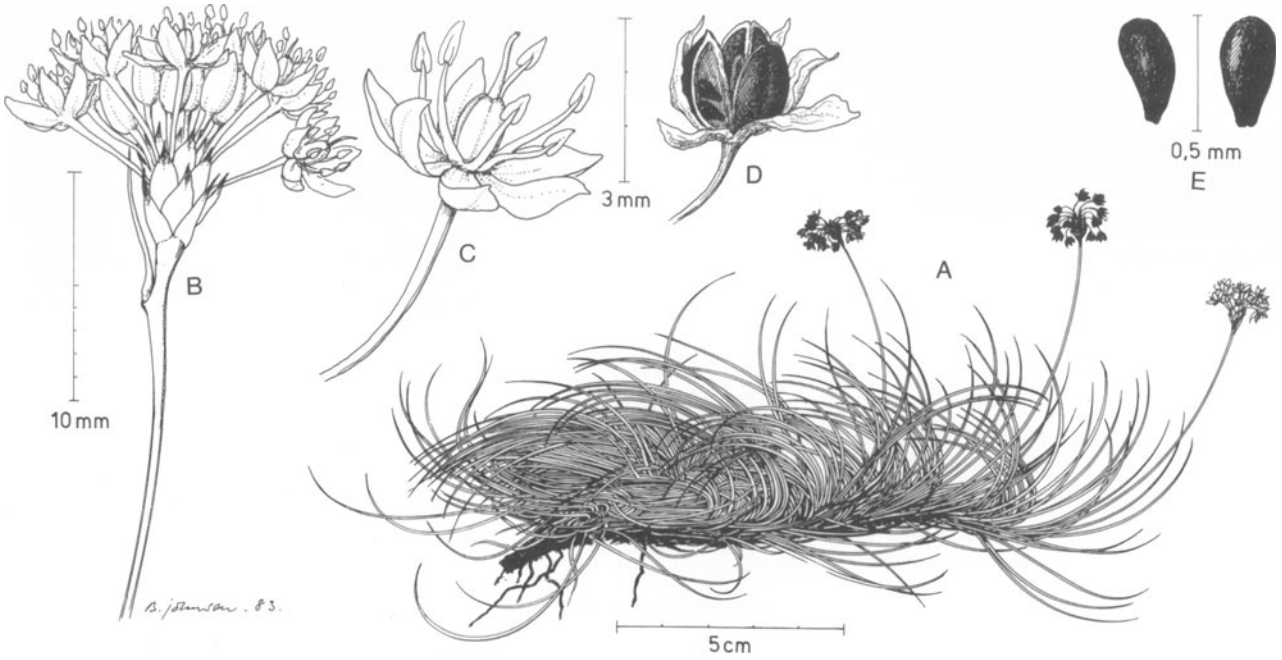


Fig. 86. Anthericaceae. *Alania endlicheri,* a member of the heterogeneous Johnsonia group. **A** Part of plant. **B** Inflorescence. **C** Flower. **D** Opening capsule. **E** Seeds; note that in this genus they are black, covered with a phytomelan layer. (Orig. B. JOHNSEN)

fecting shape and size of the tepals occurs rarely in, for example, *Chlorophytum.*

The stamens are usually 3 + 3 in number, but are reduced to 3 in several genera (*Anemarrhena, Arnocrinum, Hensmania, Johnsonia, Sowerbaea, Stawellia,* and some species of *Thysanotus*). The filaments are free or basally connate (*Echeandia*), and are glabrous or sometimes hairy (*Arthropodium, Glyphosperma*), and the anthers are introrse and dorsifixed-epipeltate or more rarely basifixed, and dehisce longitudinally. Microsporogenesis, in contrast to the Asphodelaceae, at least in the taxa known, is usually successive (but simultaneous in *Tricoryne*), and the pollen grains are sulcate or rarely (*Arnocrinum, Johnsonia*) trichotomosulcate or tetrachotomosulcate, i.e. provided with a three- or four-lobed distal aperture, or otherwise, and are normally dispersed in the two-celled state.

The pistil is syncarpous, tricarpellary and trilocular, with septal nectaries at least in many of the genera. The style is simple, erect and apically trilobate or punctiform, and the stigma is usually of the Dry Type. The placentation is axile. Each locule contains from two to many, generally campylotropous, crassinucellate ovules, in which a parietal cell is cut off from the archesporial cell. Embryo sac formation conforms to the *Polygonum* Type, and endosperm formation is generally helobial.

The fruit is a loculicidal capsule. The seeds occasionally have a conspicuous elaiosome structure (in *Caesia, Hensmania, Johnsonia* and *Stawellia*). They are elongate, ovoid and often very sharply angled, and their outer epidermis is generally encrusted with phytomelan. The endosperm contains lipids and aleurone, and has a linear embryo which is usually shorter than the endosperm. The embryo is slightly curved in several genera (*Anthericum, Arthropodium, Dichopogon* and *Thysanotus*).

Chemistry. Steroidal saponins seem to be typical, while anthraquinones are lacking, in which respect this family differs from the Asphodelaceae. Chelidonic acid is widespread in the family. Cyanogenic compounds are known in *Chlorophytum.*

Distribution. The Anthericaceae are distributed over most parts of the world with the tribe Caesieae and the probably highly heterogeneous "tribe" Johnsonieae concentrated in Australia. Also in Australia are *Thysanotus* and a number of smaller genera, while the large genera *Chlorophytum* and *Anthericum* have wide, mainly tropical distributions.

Anthericum (excl. *Trachyandra;* ca. 65) has its centre in Africa but is represented also on other continents. It is chiefly tropical and characterized by linear leaves, three- to seven-nerved tepals, nearly basifixed anthers, and a rounded capsule with several seeds. *A. liliago* grows in sandy calcareous habitats in Europe. – *Chlorophytum* (ca. 80–100) is an even larger genus with a wide tropical distribution. It differs from *Anthericum* in having distinctly trilobate, triangular or three-winged capsules. *C. comosum* from Southern Africa propagates itself effectively by producing plantlets in the inflorescence. A form with variegated leaves is a common foliage ornamental.

Thysanotus (47), which is mainly Australian, is interesting in having unequal outer and inner tepals, which are generally violet, the inner ones conspicuously fringed with hairs. A similar genus, *Bottinaea* (1), occurs in Chile. *Caesia* (9) and some other genera, mainly in Australia, are probably rather closely related to *Thysanotus*. They have blue or violet tepals, which twist spirally after anthesis. They also have anatropous ovules, and rarely nutlets (*Corynotheca*) instead of capsules.

Johnsonia (3) and a few other genera (*Arnocrinum, Hensmania, Stawellia*) are rhizomatous perennials with *Juncus*-like scapes. They have compact, spicate inflorescences with the flowers subtended by bracts. The leaves are sometimes reduced and assimilation is then restricted to the scapes. The stamens may be reduced to three only. The seeds are black and reniform and have a white caruncle. Some genera, for example *Arnocrinum* (3), resemble *Caesia* in having blue, finally twisted tepals. Other Australian genera, *Laxmannia* and *Sowerbaea,* have umbellate inflorescences, filiform leaves that are triangular in transection, and black prismatic seeds without an elaiosome. They are dubiously closely related to the former (KEIGHERY, personal communication).

The great diversity of the genera hitherto referred to a single tribe, the Johnsonieae, has recently been pointed out by KEIGHERY (unpublished). Besides the genera mentioned above, a few more are frequently placed here, viz. the two, likewise mainly Australian, genera *Borya* (7) (Fig. 85R–T) and *Alania* (3) (Fig. 86), both subshrubs with narrow, scleromorphic, either short and prickly or almost grass-like leaves, tubular, syntepalous flowers, spicate inflorescences, small, rounded to ovate seeds, and mycorrhizal roots (KEIGHERY, personal communication). These are somewhat woody at the base, and we suspect that they are better placed in or near the Dasypogonaceae. The genus *Tricoryne* (6), in Australia, which has grass-like leaves, tepals that are spirally twisted after flowering, umbel-like inflorescences, simultaneous microsporogenesis, a schizocarp rather than a capsule, and pale, globose seeds, may be misplaced in Anthericaceae and needs further investigation.

Thus the Anthericaceae comprise a complex which is probably heterogeneous. Decisions must await further gross-morphological, anatomical, embryological and pollen-morphological studies, in which the different generic groups should be considered separately. None of the groups seems to come particularly close to the Asphodelaceae, although there are great similarities between species of *Anthericum* or *Chlorophytum* (Anthericaceae) and *Simethis* and species of *Asphodelus* (Asphodelaceae).

Aphyllanthaceae G.T. Burnett (1835) 1:1 (Fig. 87)

A relatively small herb with a short rhizome and leaves reduced to their sheaths only. Secondary thickening occurs in the rhizome (CHAKROUN and HÉBANT 1983). The inflorescences are terminal on green, assimilating scapes which are much longer than the leaf sheaths (cataphylls). Vessels are lacking in the stem but are present in the roots, where they have simple and scalariform perforation plates (TOMLINSON 1965b). Unsuberized rather large cells with raphide bundles occur in the cortex of the stem. The stomata are deeply sunken and of the anomocytic type. The outer and lateral walls of the epidermis of the scapes are thick and comprise most of the mechanical tissue and the scapes also have a thick cuticle.

The inflorescence is a small, compressed, spike-like cluster with 1 or 2 (-3) flowers and their imbricate, hyaline bracts. Each flower is enclosed by one or two free and five basally fused scales, indicating that the inflorescence is in fact compound and branched. It appears to possess one terminal and a few lateral flowers (= branches), thus representing a reduced panicle.

The flowers are hypogynous and bisexual. The tepals are 3 + 3 in number and are basally fused into a tube; the lobes are narrowly elliptic-oblong and blue. There are 3 + 3 stamens inserted in the mouth of the perigone tube. They have narrow, glabrous filaments and epipeltate, longitudinally dehiscent anthers. Microsporogenesis is successive. The pollen grains are spiraperturate and similar to those of *Lomandra endlicheri* (Dasypogonaceae) (TAKHTAJAN 1980) and have a finely spinulose surface.

The pistil is trilocular and has an erect style which is apically tribrachiate with Dry papillate stigmatic surfaces. The ovary has septal nectaries and is tri-

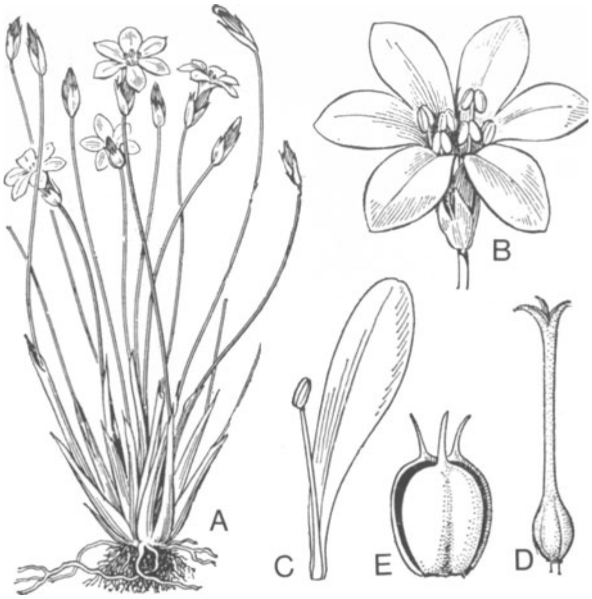


Fig. 87. Aphyllanthaceae. *Aphyllanthes monspeliensis.* **A** Plant. **B** Flower. **C** Tepal and attached stamen. **D** Pistil. **E** Capsule. (TAKHTAJAN 1982)

locular with each locule containing one anatropous ovule. Endosperm formation is helobial. The fruit is a loculicidal capsule, the seeds of which are slightly flattened and have a fairly thin outer epidermis thinly encrusted with phytomelan. The endosperm contains aleurone and lipids, and the embryo is straight and as long as the endosperm.

Chemistry. The rhizome contains steroidal saponins and the rhizome and leaves also contain wax alcohol.

Distribution. The single species, *Aphyllanthes monspeliensis,* is a west Mediterranean xerophyte growing on rocky hills. The reduction of the leaves and the scleromorphic, assimilating scapes are adaptations to the extreme climatic and edaphic conditions.

The relationships of *Aphyllanthes* are uncertain. The extraordinarily variable Anthericaceae in Australia, almost certainly a heterogeneous assemblage, include forms (*Caesia, Thysanotus*) with violet or blue flowers where the inflorescence is the assimilating part, but these genera deviate in various, different respects from *Aphyllanthes,* and the vast geographical distance makes any attempt to associate *Aphyllanthes* with any of them highly speculative and improbable. Lacking a better alternative we follow some previous taxonomists in recognizing Aphyllanthaceae as a distinct family. On the basis of the spiraperturate pollen grains Aphyllanthaceae is sometimes associated with Dasypogonaceae (see TAKHTAJAN 1980), but we consider this similarity the result of convergence.

Funkiaceae P. Horaninow (1834) 3:12 (Fig. 88)

Rhizomatous herbs or (*Hesperocallis*) basally woody plants with a short stem and bulb-like corm. The roots are often fleshy, although not fusiform. The leaves are spirally set, concentrated at the base or in *Hesperocallis* on the lower part of the stem, dorsiventral, linear, lanceolate or (within *Hosta*) even ovate to subcordate. The leaves are sheathing at the base and in some *Hosta* species the section between sheath and lamina is narrowed into a pseudopetiole. Further, the leaves are parallel-veined. The stomata are anomocytic. Oxalate raphides are known at least in the fruit wall of *Hosta.* Vessels are absent from the stem and leaves but are present in the roots (where they have scalariform perforation plates), at least in *Hosta.*

The inflorescence in all three genera is a simple raceme on a bracteate scape. The flowers are hypogynous and bisexual and may or may not be jointed to the pedicel. The tepals are fused into a cylindrical, campanulate, or funnel-shaped perigone with the six lobes of variable length and sometimes recurved. The perianth is actinomorphic or nearly so and blue, violet or white in colour.

There are 3+3 stamens inserted in the perigone tube, with mutually free, glabrous filaments, introrse anthers, the connective of which forms a tube over the filament tip. Anther dehiscence is longitudinal. The tapetum is secretory and microsporogenesis successive. The pollen grains are sulcate.

The pistil is syncarpous and three-locular, with a simple, filiform style with a minute, capitate or three-lobed stigma (*Hosta* having a Wet stigmatic surface). Placentation is axile and the ovules numerous and anatropous. The nucellus has a parietal tissue formed by a parietal cell cut off from the archesporial cell. Periclinal divisions occur in the nucellar epidermis except in *Leucocrinum.* A hypostase is formed (lacking in Hemerocallidaceae). Embryo sac formation conforms to the *Polygonum* Type, and endosperm formation, at least in *Hosta,* is helobial.

The fruit is an elongate to subglobose, loculicidal capsule with numerous seeds, which are fairly small, flattened or compressed and often elliptic.

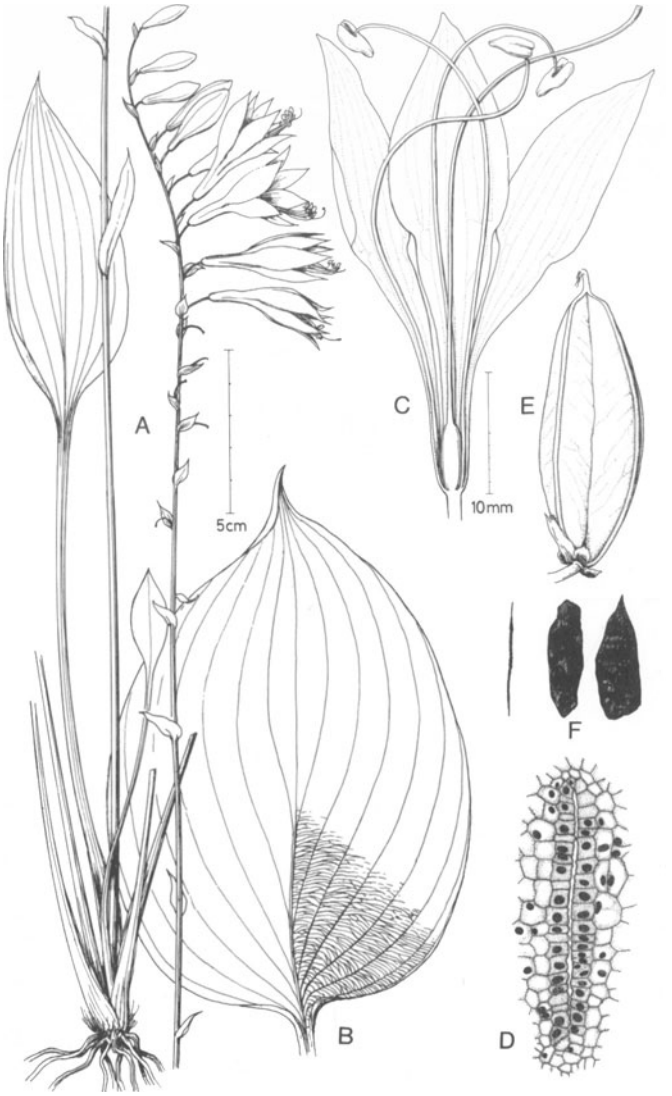


Fig. 88. Funkiaceae. **A** and **C.** *Hosta japonica.* **A** Plant, the basal parts and the inflorescence. **C** Flower, longitudinal section. **D** *Hosta* sp., septal nectary. (Weberling 1981). **B, E, F** *Hosta ventricosa.* **B** Leaf; note the minute, transverse and partly reticulate venation. **E** Capsule. **F** Seeds in different views. (Orig. B. Johnsen)

They have a thick, black coat of phytomelan. The outer integument is several layers thick, but all layers except the epidermis are strongly compressed, as is also the inner integument. The endosperm consists mainly of isodiametric thin-walled cells containing protein and fat. $n = 24.30$.

Distribution. While the largest genus, *Hosta,* is centred in China and Japan, *Hesperocallis* and *Leucocrinum* occur in Colorado, the former extending to southern California.

Hosta (ca. 10) has a scape with or without basal scale leaves. The leaves vary much in breadth and colour, and the flowers are situated in a one-sided, slightly nodding raceme. *Hosta* consists of shade plants. Several species and hybrids are grown as garden ornamentals, e.g. *H. caerulea, H. glauca, H. plantaginea* and *H. sieboldiana. Leucocrinum* (1) and *Hesperocallis* (1) occur in sandy valleys and in deserts, respectively. They are not particularly similar to *Hosta* nor to each other, but various shared features suggest relationships. *Leucocrinum* may prove more closely allied to Hemerocallidaceae (Cave 1964).

The position of Funkiaceae, like that of Hemerocallidaceae, is uncertain. Some details indicate that the family may be related to Agavaceae, this being supported most strongly by the karyotype of *Hosta* which agrees almost totally with that in Agavaceae. The chromosome number in *Hosta,* as in Agavaceae, is $n = 30$, but that in *Hesperocallis* $n = 24$. The serological investigations by Chupov and Kutiavina (1981) show affinity between *Hosta* and both the Agavaceae and *Camassia* of Hyacinthaceae.

Hyacinthaceae Batsch (1802) 40:900
(Figs. 89–91)

Mostly glabrous scapose perennial herbs with bulbs (except *Schoenolirion* and *Chlorogalum,* which have a rhizome). The bulbs generally have a membranous tunic and a number of free or coalescent bulb scales. The roots are sometimes thick and generally contractile. The leaves, concentrated at the base, are solitary to numerous, generally spirally set, flat and dorsiventral, and generally linear to linear-lanceolate, rarely elliptic to orbicular. Further, they are normally mesomorphic, sheathing at the base, non-petiolate and parallel-veined. The stomata are anomocytic. Crystal raphides contained in mucilage cells or canals are widely distributed in the family. Vessels are present in the roots only and have scalariform and/or simple perforation plates.

The leafless scape usually bears a simple or, more rarely, branched raceme or spike, its axis being elongate (in contrast to most Alliaceae). Rarely, however, as in *Massonia,* there is a head-like cluster of flowers. The inflorescence has few to many flowers and is generally bracteate, at least in the lower part.

The flowers are generally bisexual, hypogynous, trimerous and actinomorphic. The $3 + 3$ tepals are

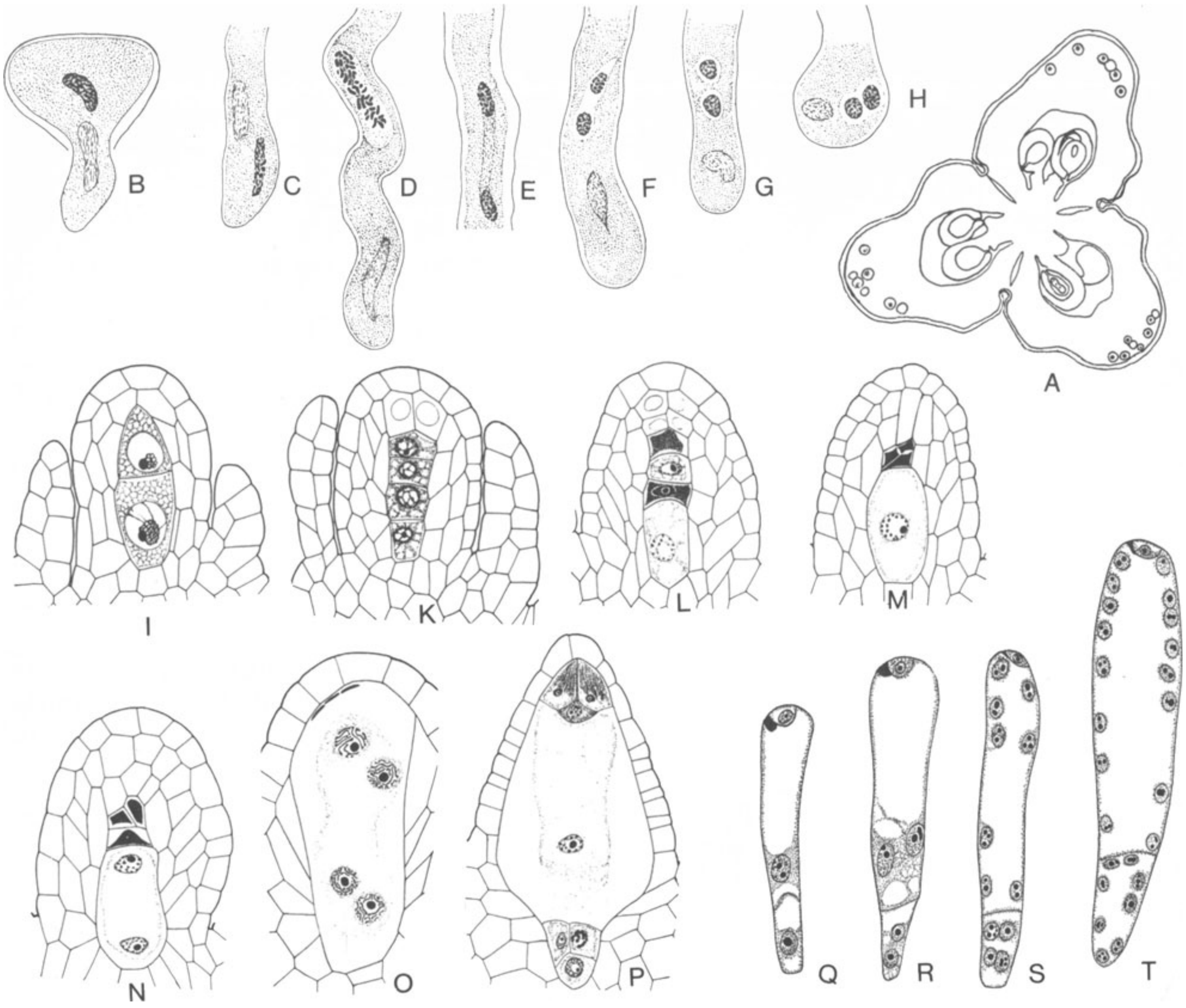


Fig. 89. Hyacinthaceae (**M–P**) and Asphodelaceae (**Q–T**). **A** *Albuca fastigiata,* ovary, transverse section. **B–H** *Muscari atlanticum* (=*racemosum*). **B** Pollen grain in the state of germination. **C–H** Pollen tube, with successive stages in division of the generative cell into two sperm cells, in **H** oriented at the tip of the pollen tube. (Wunderlich 1937). **I–P** *Urginea indica,* meiosis and formation of embryo sac (*Polygonum* Type), **I** after the first meiotic division, **K** with a linear megaspore tetrad, and showing at the top two cells of a parietal layer, **M–P** showing the chalazal megaspore developing into an 8-nucleate embryo sac. (Capoor 1937). **Q–T** *Eremurus himalaicus,* development of helobial endosperm. (Stenar 1928a)

free or more often connate, forming then a campanulate, urceolate or tubular perigone. The tepal colour varies considerably, being white, blue or violet, or more rarely yellow, red, brown or even nearly black. The tepals of the two whorls are generally similar in appearance, but may differ in size, shape and position (as in *Albuca*). In some cases the upper flowers are sterile and of different colour from the fertile, having only the function of attracting insects.

There are 3 + 3 stamens, inserted either at the base of the tepals or in the tepal tube. Their filaments, as in Alliaceae, are often broad and flat and in some genera each is produced into two lobes, one on either side of the anther (e.g. in species of *Chionodoxa, Ornithogalum, Eucomis*). In *Puschkinia* they even have appendages forming a "paracorolla". The anthers are introrse, "epipeltate" and dehisce longitudinally. The tapetum is glandular and microsporogenesis is of the Successive Type. The pollen grains are sulcate and two-celled, the generative nucleus being enclosed in an elongate, thin-walled cell often centrally located in the pollen grain (Wunderlich 1937).

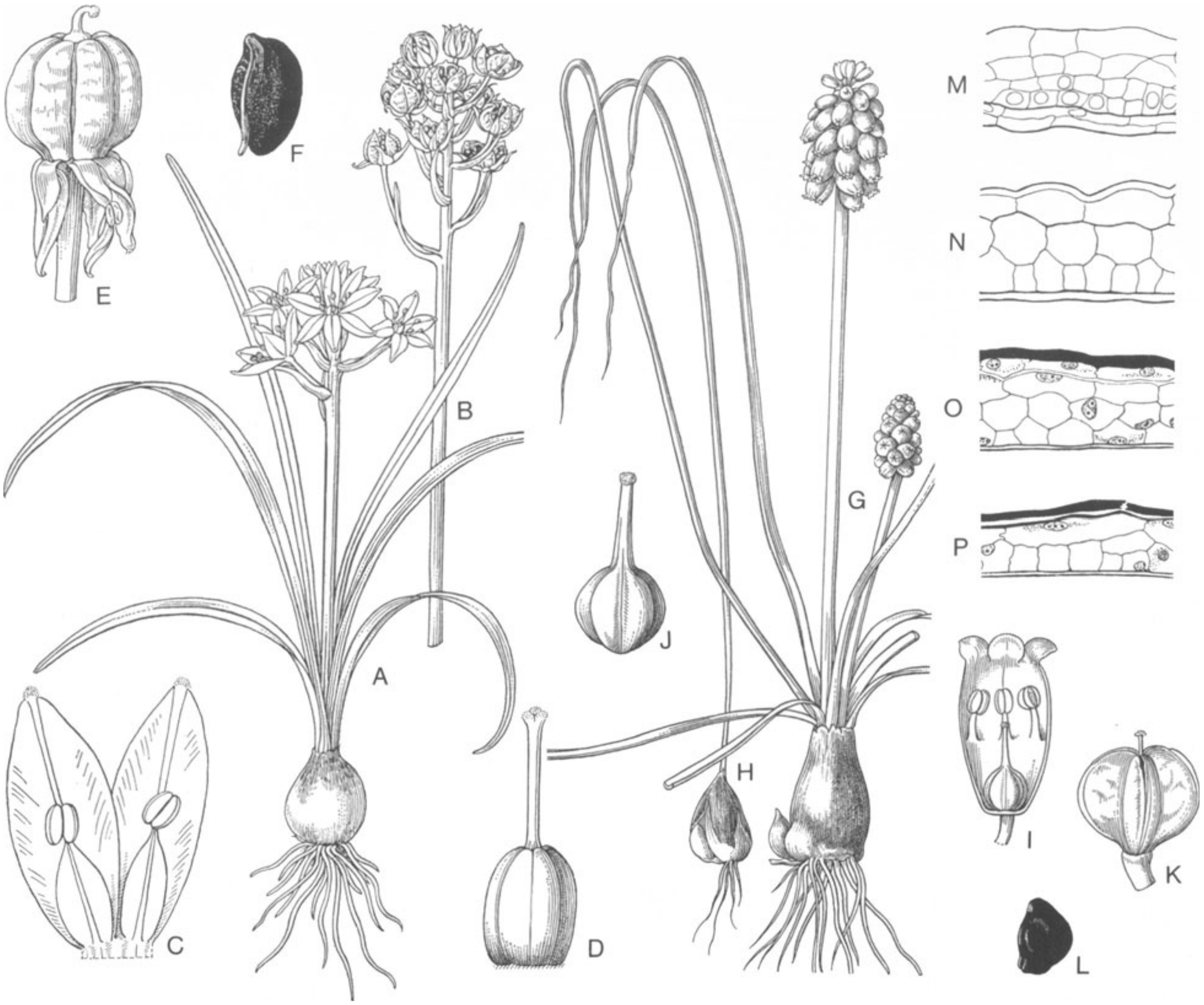


Fig. 90. Hyacinthaceae. **A–F** *Scilla verna*. **A** Flowering plant. **B** Infructescence. **C** Two tepals and opposite stamens. **D** Pistil. **E** Capsule. **F** Seed. **G–L** *Muscari atlanticum*. **G** Plant. **H** Young bulb with leaf. **I** Flower, longitudinal section. **J** Pistil. **K** Capsule. **L** Seed. (Ross-Craig 1972). **M–P** *Muscari atlanticum,* development of seed coat, **M–N** before and **O–P** after the development of the black phytomelan layer in the outer epidermis; the inner integument, which is two-layered in **M,** collapses and becomes a thin membrane. (Wunderlich 1937)

The pistil is tricarpellary and trilocular and has septal nectaries. Its style is simple, terminating in a punctiform or sometimes distinctly trilobate stigma with either a Wet or Dry papillate surface. The ovules are two to numerous in each locule, anatropous and with the axis straight or almost straight or, in a few genera, curved. They are crassinucellate, and a primary parietal cell is cut off from the archesporial cell and in addition the nucellar epidermis may divide periclinally to form further cell layers of a nucellar cap. Embryo sac formation conforms to the *Polygonum* or (rarely) *Scilla* or *Allium* Types, and endosperm formation is helobial or, more rarely, nuclear (nuclear in species of *Camassia, Hyacinthus, Scilla* and *Urginea*).

The fruit is a loculicidal capsule with, as a rule, two or more seeds per locule. The seeds are ovoid to pear-shaped and vary from rounded to strongly angular in transection; they may be small (1.2–2.0 mm), as in *Lachenalia* and *Massonia,* or large (5–8 mm), as in *Eucomis* or *Veltheimia.* The outer epidermis of the testa consists of several cell layers, and normally has a phytomelan crust, which is rather thick in *Massonia, Hyacinthoides* (*Endymion*) and *Hyacinthus,* but more often rather thin, and may even be lacking in *Chionodoxa, Puschkinia* and a few species of *Scilla,* where the outer epidermis collapses and forms an almost unsculptured yellowish brown layer. The innter integument forms a thin membrane, while the endosperm consists of cells with thin to rather thick and pitted walls and with contents of aleurone and fatty oils but usually no starch. Only exceptionally, as in one species of *Eucomis* and in *Scilla bifolia,* does the endosperm contain starch grains. The embryo is cylindrical or almost so, and straight or, in *Chlorogalum,* slightly curved.

Chemistry. Hyacinthaceae are characterized by producing steroidal saponins (often abundantly, as in the bulbs of *Albuca*) and chelidonic acid, which is known to occur in a number of genera. Salicylic acid occurs in the scape and bulb scales of *Hyacinthus*. The bulbs of *Urginea maritima* contain cardiotoxic glucosides (belonging to the so-called bufodienolides) and are therefore used as poison and in medicine. The bulbs of Hyacinthaceae contain fructans and also starch.

Parasites. Within the rust genus *Uromyces* one species, *U. muscari,* attacks species of *Muscari, Scilla, Dipcadi, Hyacinthus, Ornithogalum* and *Urginea,* all in Hyacinthaceae, but not members of other families. Another example of restricted fungal parasitism involves the smut genus *Ustilago.* Savile (1979) reports the following host genera in Asparagales: *Albuca, Bellevalia, Eucomis, Hyacinthus, Muscari, Ornithogalum, Urginea* and *Allium.* Of these genera all except *Allium* belong to Hyacinthaceae.

Distribution. The Hyacinthaceae are widely distributed, but most richly represented in Southern Africa and in a region from the Mediterranean to South-West Asia. They are apparently best adapted to a fluctuating moist-arid climate, withering down to the bulbs in the arid period.

Many genera provide widely cultivated mainly spring-flowering ornamentals.

There seem to be great difficulties in systematizing the genera. Some genera are pronouncedly peripheral in Hyacinthaceae and may merit the rank of one or two separate families. Included here are *Bowiea, Schizobasis, Chlorogalum* and *Schoenolirion,* which are also referred to Hyacinthaceae by Huber (1969) and seem to fit better here than with any other family. Some of these genera will briefly be discussed below.

Among the genera having *free or only basally fused tepals* are the following.

Ornithogalum (100) is an Old World genus richly represented in dry habitats, such as steppes and grassland from Southern Africa to Asia. The flowers are mostly white to greenish and as a rule have spreading tepals, flat filaments and rounded-ovoid seeds. The habit is most variable, from large herbs with racemose inflorescences to small, shortly scapose plants with few-flowered sometimes nearly umbel-like inflorescences. Several species are ornamentals, such as the commercially important *O. thyrsoides* from the Western Cape, South Africa, the "Chinkerinchee". Among the European species cultivated since the Middle Ages are *O. umbellatum* and *O. nutans.* Whereas some species are strongly poisonous, others such as the European *O. narbonensis* and *O. umbellatum* (bulbs) and the West European *O. pyrenaicum* (young shoots) are edible. – *Albuca* (50), centred in Southern Africa, has sparse racemes of *Galanthus*-like, white to yellow flowers, the inner tepals being erect to incurved and different from the outer which are more spreading. Some species are cultivated as ornamentals. – *Urginea* (50–100) is a variable genus of small and few-flowered to very large and multiflorous herbs, which ranges from South Africa and the Mediterranean eastwards to India. The free tepals of this genus are shed after flowering, and the seeds are angular. Best-known is *U. maritima,* a common species on coastal mountain slopes and shores in the Mediterranean. It has extremely poisonous bulbs containing the glucosides scillarin-A and -B. The red-bulbed varieties are used as rat poison; other forms provide heart medicines. – *Scilla* (80), in the Old World, is characterized by free white, blue or violet tepals and rather narrow filaments. The seeds are ovoid to globose and not strongly angular. Several species are grown as ornamentals. *S. sibirica,* indigenous in the Caucasus and southern Russia, is spring-flowering with few, nodding, campanulate bright blue flowers. *S. peruviana* from the Mediterranean, has a many-flowered raceme of long-pedicelled, violet flowers, with spreading tepals. The *S. bifolia* complex in southern and central Europe and western Asia has rather few-flowered unilateral racemes. – A related genus is *Hyacinthoides* (=*Endymion*) with three or four western European species (*H. hispanica* often cultivated), with lax racemes of nodding, light blue, campanulate flowers and bulbs with coalescent bulb scales (free in *Scilla*). – *Camassia* (4), indigenous to North America, is characterized by racemes of flowers with spreading, blue-violet or pale yellow tepals; some are cultivated for ornament. – To this group may also be referred the Southern African genus *Eucomis* (10), which is peculiar in having the inflorescence crowned by a fascicle of green leaves. The racemose inflorescence has greenish yellow to brown flowers.

Fig. 91. Hyacinthaceae. **A–B** *Schizobasis intricata.* **A** Plant, the leaves in the adult plant, as in *Bowiea,* are restricted to the bulb scales. **B** Flower. (KRAUSE 1930). **C–G** *Bowiea volubilis.* **C** Bulb. **D** Part of the intricately branched inflorescence. **E** Flower. **F** Pistil. **G** Style apex with stigma. (DYER 1941). **H–J** *Camassia quamash.* **H** Base of plant. **I** Upper part of inflorescence. **J** Two capsules. (HITCHCOCK et al. 1969)

Among the genera with *more or less connate tepals* are the following.

Chionodoxa (8), mostly in Asia Minor and *Puschkinia* (2), in the same region and eastwards, are *Scilla*-like genera with two basal leaves and bluish to white flowers with the tepals fused only basally. The stamens are joined to the mouth of the perigone tube; in the former genus they have free but flat filaments, while in *Puschkinia* they are fused into a tube. Both genera contain popular garden ornamentals like *C. sardensis* and *P. scilloides.* Detailed cytological studies in these genera and in *Scilla* by SPETA (1976) and GREILHUBER and SPETA (1976) show that morphological and cytological evidence is often contradictory and the conventional generic borderlines artificial. – *Hyacinthus* (3) is indigenous to South-Eastern Europe and Asia Minor. *H. orientalis,* with heavily fragrant flowers, is one of the most popular spring-time ornamentals. Various cultivars with white, yellowish, pink, crimson or blue flowers are cultivated commercially. Closely related to *Hyacinthus* are a number of genera such as *Hyacinthella* (11), *Brimeura* (2), and *Alrawia* (2). – *Bellevalia* (50) with a wide Old World distribution, and *Muscari* (incl. *Leopoldia,* 55), range from the Mediterranean as far as Caucasus and likewise contain a number of ornamentals. In *Muscari* the flowers are globose-urceolate with short tepal lobes; *M. botryoides* from the central Mediterranean and *M. armeniacum* from Asia Minor are frequently cultivated species. In *M. comosum* and other species, often treated in the genus *Leopoldia,* the uppermost flowers are sterile, closed and brightly coloured, while the fertile are dull in colour.

Dipcadi (55) ranges from South Africa to the Mediterranean. – *Lachenalia* (90) in South Africa is extremely variable in floral colour and often has a variegated scape and (one to five) variegated or spotted leaves. – Large mesomorphic leaves and a variegated scape characterize the likewise African genus *Veltheimia* (6). *Galtonia* (3) in South Africa are herbs with yellowish white, campanulate, pendulous flowers in an elongate raceme. *Galtonia candicans* and *Veltheimia viridifolia* are grown as ornamentals.

The South African genus *Schizobasis* (1) has a compound, twining inflorescence (Fig. 91 A–B).

Massonia (30) and some other Southern African genera have very short scapes and a densely compressed capitate or umbel-like inflorescence situated between two broad, sometimes orbicular leaves pressed against the ground. The habit of *Massonia* resembles that of some species of *Haemanthus* (Amaryllidaceae). The flowers have a tubular perianth, the lobes of which are sometimes reflexed. Their stamens have long, narrow filaments inserted in the floral tube.

Bowiea (1–3), in Southern to Central Africa, is a most peculiar plant which has a large bulb of thick green scales and filiform, quickly withering leaves (Fig. 91 C–G). The inflorescence is developed as a richly branched, herbaceous vine, with part of the branches transformed into tendrils. The flowers have six, equal, free, more or less reflexed, greenish tepals. The bulbs are poisonous.

The above grouping of the more important, "typical" genera of Hyacinthaceae is certainly artificial. Fusion of the tepals has undoubtedly occurred in several evolutionary lines within the family; in fact, *Chionodoxa* species can give rise to hybrids when crossed with members of the *Scilla bifolia* complex, and it has been proposed to include them in *Scilla,* whereas *Puschkinia* evidently has other affinities (SPETA 1976). Other divisions are based on whether the seeds are ovoid and rounded or sharply angular and flattened, and on the seed size. Chromosome structure can also be used in constructing a more phylogenetic classification in the family. Serological studies, finally, indicate other constellations, and suggest that neither *Camassia* nor *Bowiea* is very closely allied to the majority of the genera (CHUPOV and KUTIAVINA 1978, 1981).

Two genera that fall somewhat outside the ordinary variation pattern of the family and need to be reconsidered as regards their most appropriate position are *Schoenolirion* (4) and *Chlorogalum* (3) in North America, the former with rhizome, the latter species with a narrow bulb.

Alliaceae J.G. Agardh (1858) 30: ca. 720 (Figs. 92–94)

Perennial herbs with a bulb or a bulb-like corm, which has membranous or fibrous outer scales, or more rarely a rhizome (*Agapanthus* and *Tulbaghia*). The leaves are basally concentrated, but sometimes sheathing the scape for a considerable distance and therefore appearing cauline (as in *Allium scorodoprasum*). They are spirally set or distichous (at least in *Agapanthus*) and filiform-linear, lanceolate or rarely ovate. They may be flat, terete, fistulose or angular and are sheathing at the base, parallel-veined and rarely (as in *Allium ursinum*) constricted into a pseudopetiole between the sheath and a broad lamina. The stomata are anomocytic. Raphides are present in several genera but not, for example, in *Allium, Milla* and *Tulbaghia* (which contain allylic sulphides and other compounds, which are the source of the onion smell; see below).

The scape is terete (sometimes conspicuously fistulose) or angular and bears an umbel-like inflorescence of short- or long-pedicelled flowers. The inflorescence represents, at least in most cases, one or more contracted helicoid cymes. Rarely (as in

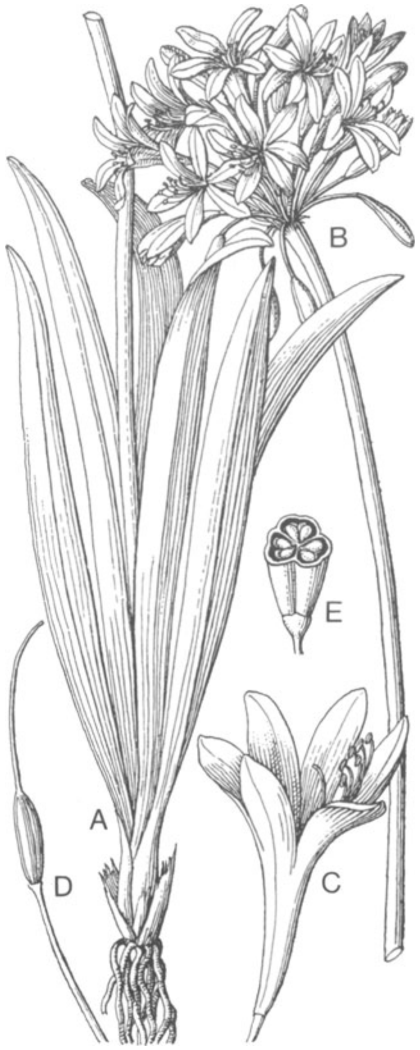


Fig. 92. Alliaceae. *Agapanthus umbellatus.* **A** Leaf rosette and the short rhizome, showing absence of bulb. **B** Scape with inflorescence. **C** Flower. **D** Young capsule. **E** Capsule, transverse section. (Krause 1930)

Milula) the inflorescence is cylindrical and spike-like.

The inflorescence is subtended by an involucre of (one,) two or more membranous spathal bracts, which may be free from each other and then usually spreading, or united at the base and then mostly erect and enclosing the buds, like a calyptra.

Articulation of the flowers with the pedicels occurs rarely. The flowers are trimerous, hypogynous, generally bisexual, and actinomorphic or (in most genera of the Gilliesioideae, for example) zygomorphic. The 3+3 tepals are free or often connate to form a campanulate or tubular perianth with erect, spreading or sometimes recurved lobes. The tepals are generally similar in the two whorls; they vary in colour from white to blue, violet, purple or even yellow. The functional stamens are 3+3 or sometimes 3 or 2, in the latter case (e.g. *Leucocoryne* and genera of the *Gilliesia* group) there are several staminodes. The filaments are inserted at the base of the tepals or in the perigone tube; they are more or less flat and those of the inner staminal whorl sometimes end with a tip on each side of the anther. The anthers are elongate (rarely short), epipeltate and introrse, and dehisce with longitudinal slits. The tapetum is secretory and microsporogenesis successive. The pollen grains are sulcate and two-celled when dispersed.

The pistil is tricarpellary and trilocular and has a single erect style with a trilobate or capitate stigma, which has a Dry or sometimes (*Bloomeria, Leucocoryne*) Wet papillate surface. Septal nectary grooves are present on the ovary. Each of the locules contains two to several ovules, which are campylotropous or less often anatropous, with a straight or curved axis. A parietal cell is generally *not* cut off from the archesporial cell, although this has been observed at least in *Agapanthus,* but the nucellar epidermis may divide periclinally to form a nucellar cap. Embryo sac formation seems to conform to the *Allium* Type, at least in *Allium* and *Leucocoryne,* but according to the *Polygonum* Type in *Nothoscordum, Muilla* and *Brodiaea.* Endosperm formation has been found to be nuclear in several species of *Allium* and *Brodiaea* but helobial in *Nothoscordum, Tulbaghia* and perhaps *Triteleia.*

The fruit is a loculicidal capsule with few to numerous seeds. These are sometimes rather small and ovoid or ellipsoidal to subglobose and rounded in transection (*Brodiaea, Triteleia* and related genera, having anatropous ovules), but more often triangular in transection and half-ovoid, half-globose or tetrahedral in shape. They are often larger where the ovules are campylotropous and the ovule axis curved 120 degrees (in *Allium, Nothoscordum, Muilla* and related genera) than when the ovules are anatropous. The testal epidermis is usually covered by a rather thick crust of phytomelan and consists of subisodiametric or slightly elongate cells. The inner layers of the testa, which is several-layered, are compressed or collapsed, as is the tegmen. Fatty oils and aleurone, but not starch, are deposited in the endosperm cells, which usually have rather thick, pitted walls. The embryo varies in length; it is usually more than half the length of the endosperm and becomes straight in the anatropous ovules, but more or less

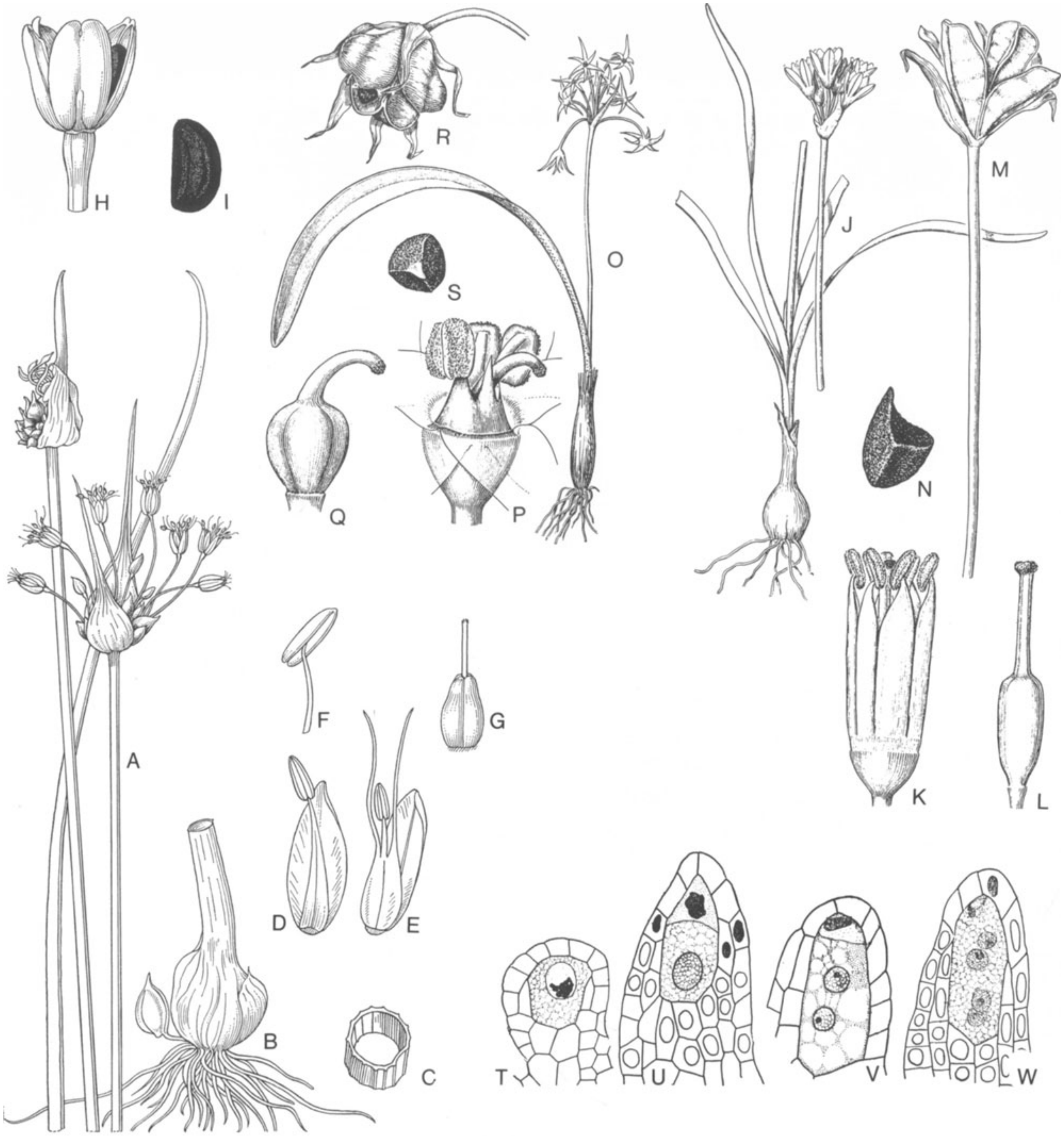


Fig. 93. Alliaceae. **A–I** *Allium vineale*. **A** Scape with inflorescences; note the bulbils at the base of the flowers. **B** Bulb. **C** Leaf, transverse section. **D** Tepal of outer whorl and the opposite stamen. **E** Tepal of inner whorl and the opposite stamen; note the long filamental lobes. **F** Anther and top of filament. **G** Pistil. **H** Capsule. **I** Seed. (Ross-Craig 1972). **J–N** *Nothoscordon inodorum*. **J** Plant. **K** Stamens and pistil. **L** Pistil. **M** Scape with capsule. **N** Seed. (Correa 1969). **O–S** *Solaria attenuata*. **O** Plant. **P** Androecium and gynoecium. **Q** Pistil. **R** Capsule. **S** Seed. (Correa 1969). **T–W** *Allium cepa*, early stages in development of embryo sac (*Allium* Type); note that the chalazal dyad (**V**) develops into the embryo sac. (After H.A. Jones and Emsweller 1936)

curved when the ovules are semi-campylotropous or campylotropous.

Chemistry. The family contains steroidal saponins with, for example, aigogenin (*Allium*), yuccagenin (*Agapanthus*) and agapanthagenin (*Agapanthus*) as sapogenins. Chelidonic acid is known to be present in several genera. While raphides are lacking in *Allium*, this genus possesses oxalate crystals in various other shapes (which may be characteristic of the species). Most or all species of *Allium* and *Tulbaghia,* and also, at least, species of *Ipheion, Androstephium, Leucocoryne, Milula* and *Tristagma,* contain sulphur compounds, such as allyl sulphides, propionaldehyde, propionthiol and vinyl disulphide, which participate in the essential oils causing the onion odour. The typical scent is released only when the tissues are wounded or during decay. The mechanism involved can be demonstrated by adding an enzyme, alliinase, to an amino acid, alliin, which is converted into the strongly "onion-scented", water-soluble compound allicin and other compounds. The bulb scales in *Allium* contain flavonoid compounds, e.g. quercetin, which is the reason for using onion scales in dyeing eggs. Finally, the thick bulb scales in *Allium* and other genera contain carbohydrates, in the form of inulin-like fructans but, at least in *Allium,* not starch.

Distribution. Alliaceae are widely distributed, especially the genus *Allium* itself. The other genera show characteristic distribution patterns: the subfamily Agapanthoideae is South African and, within the subfamily Allioideae, many smaller genera of the tribe Brodiaeeae (e.g. *Brodiaea* and *Milla*) are American (California, Mexico, Chile, etc.), while the subfamily Gilliesioideae has its centre in Chile in South America.

The subdivision of the family may be based on various characters, such as the underground parts (bulbs, tunicated corms, rhizomes), tepal characters (free or connate), stamen characters (filaments free or fused into a tube, narrow or broad and flat, with or without lateral tips), and ovule shape (anatropous or variably strongly campylotropous) which is also clearly connected with size and shape of the seeds. Besides, presence or absence of raphides and presence or absence of allyl compounds can be used, as well as chromosome characters and other details. A strong emphasis on embryology and seed characters may be the most acceptable approach, but for practical reasons the division here will follow more conventional lines.

Subfamily Agapanthoideae

This subfamily consists of only two genera. Both are rhizomatous, sometimes large, herbs with flat leaves and umbel-like inflorescences with two spathe-bracts, enclosing the floral buds. The pedicels are not articulate, the tepals are basally connate, and the ovules are half-campylotropous and develop into relatively large (4–11 mm), angular seeds provided with a wing at the funicular end. Their phytomelan crust is thinner than in most other Alliaceae. The two genera may not be particularly closely allied.

Agapanthus (7) (Fig. 92), in Southern Africa, are large, flat-leaved, saponin-rich herbs with many-flowered inflorescences of deep to light blue (rarely white) flowers without corona or stamen appendages. Embryo sac formation seems to be of the *Polygonum* Type. Crystal raphides occur in this genus, while allyl sulphides and similar compounds are lacking. Some species, e.g. *A. praecox, A. africanus* and *A. campanulatus,* are grown as ornamentals.

Tulbaghia (24, Vosa 1975) has its centre in South Africa and is characterized by the fewer-flowered "umbels" with violet (*T. fragrans*) or more often dull-coloured, green, brown or white tepals. These are alike in shape and fused basally into an urceolate or cylindrical tube. Three or six conspicuous, fleshy filamental "corona lobes" are present in the mouth of the perianth tube opposite the inner tepal lobes. The filaments are adnate for most of their length to the tepal tube, the subsessile anthers being inserted at different levels of the corona. Crystal raphides are lacking, and "onion-smelling" sulphur compounds are present in this genus. *T. fragrans* is grown for ornament.

Subfamily Allioideae

Subfamily Allioideae consists of herbs with a bulb covered by membranous or fibrous-coated as well as fleshy scales or with a corm covered by a membranous or fibrous coat. In most features the subfamily conforms to the family description. It is the largest and most important part of the family and apart from *Allium* has a clearly American concentration. It may be divided into two tribes, the Brodiaeeae and the Allieae. These are rather distinct and may alternatively be treated as subfamilies.

Tribus Brodiaeeae

This consists of some ten genera with a corm covered by membranous or fibrous scales (Moore 1953). The scape bears an inflorescence subtended by three or more separate, spreading spathal bracts, which do not enclose the flower buds. The flowers are often articulate on their pedicel. They are actinomorphic and have 3+3 functional stamens or 3 stamens and 3 staminodes. The ovules are anatropous or rarely (*Muilla*) campylotropous,

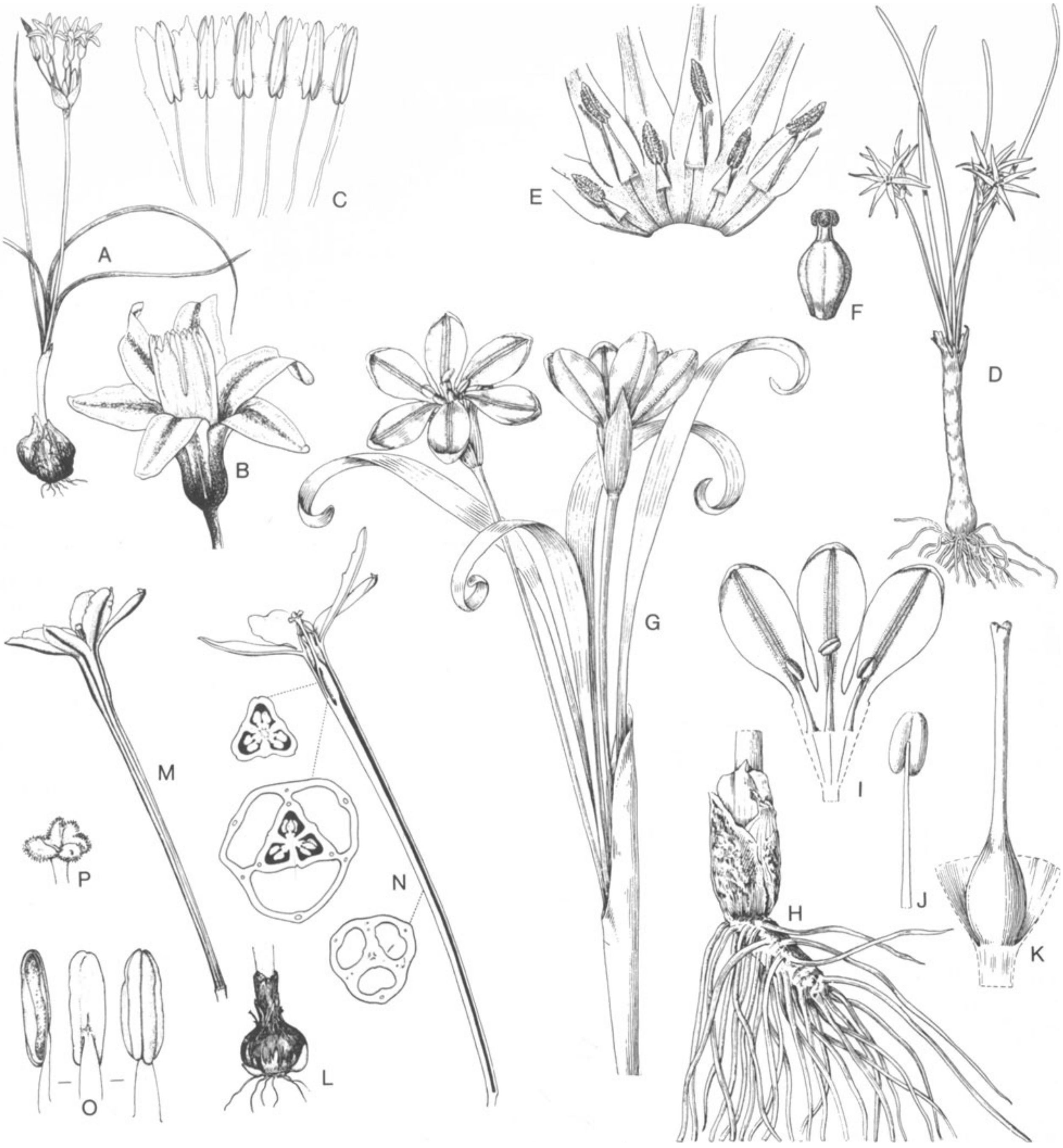


Fig. 94. Alliaceae. **A–C** *Androstephium breviflorum.* **A** Plant. **B** Flower. **C** Androecium, forming here a staminal tube. (Cronquist et al. 1977). **D–F** *Tristagma anemophilum.* **D** Plant. **E** Stamens, attached at their base to the perianth. **F** Pistil. (Correa 1969). **G–K** *Brodiaea circinnata.* **G** Inflorescences. **H** Rhizome, note that the bulb is here dissolved into an elongate rhizome; cf. *Scadoxus* in Fig. 95. **I** Half of the perianth with attached stamens. **J** Stamen. **K** Pistil. (Sandwith 1937). **L–P** *Milla magnifica.* **L** Corm. **M** Flower. **N** Flower in longitudinal section, showing also transverse sections at three levels. **O** Stamen in different views. **P** Style apex with stigmatic lobes. (Moore 1953)

having generally a straight axis, and developing into rather small, ovoid to subglobose rounded seeds. The phytomelan crust is thick. All the genera occur in America and most of them in North America.

Brodiaea (10) (Fig. 94G–K), *Dichellostemma* (6) and *Triteleia* (16) have tubular flowers. They contain some ornamentals, e.g. *Triteleia laxa* with blue flowers and *Dichellostemma ida-maia* with tubular, cigar-shaped, red and yellow flowers. – *Leucocoryne* (14), mainly in Chile, and two other genera have three functional stamens only. *L. alliacea* is often cultivated as an ornamental.

Some related genera, among them *Milla* (16), have parallel tunic fibres, covering a corm (in most genera the fibres are reticulate), a long-stipitate ovary, and a narrow-tubular perianth. The stipe may be connate to the tube by three lateral flanges. With respect to ovules and seeds these genera, like *Leucocoryne,* seem to be intermediate between the Brodiaeeae and Allieae. *Milla,* with its geographic centre in Mexico, has white or blue tepals.

Tribus Allieae

Tribus Allieae consists of seven genera which are truly bulbous plants with membranous or fibrous tunics covering a number of thick bulb scales. The leaves are very variable, being flat or terete, and sometimes falsely cauline (see the family description above). Two hyaline bracts subtend the inflorescence. These are normally more or less fused and enclose the young inflorescence. The flowers are not articulate on the pedicel. Their tepals are free or connate and variously coloured, but often violet. The stamens are 3+3 in number. The ovules are campylotropous and have a strongly curved axis. The unwinged seeds in this group of genera deviate conspicuously from those in the typical Brodiaeeae in being broad and triangular, but as in that tribe they have a thick phytomelan crust. The embryo is more or less curved. While *Allium* is widely distributed, the other, smaller genera are all centred in South America.

Among them is *Nothoscordum* (18), mainly in America. It has connate tepals and helobial endosperm formation. *N. fragrans* is a white-flowered species introduced in the Old World. – *Tristagma* (5) in Chile has flowers superficially reminiscent of those in *Tulbaghia.* – *Ipheion* (25) *uniflorum,* with a uniflorous scape, is indigenous in Argentina and Uruguay, but is widely cultivated.

Allium (incl. *Nectaroscordum*; ca. 550) is the largest genus in the family and is mainly distributed in the Northern Hemisphere. More than 110 species occur in Europe, most of them around the Mediterranean; other centres are in Asia and North America. The genus is characterized by having bulbs enclosed in membranous rather than fibrous scales, free or almost free tepals and often a subgynobasic style and by producing allylic sulphides and similar sulphur-containing compounds. Some species of *Allium* have true ligules, and another peculiarity is the occurrence in the genus of laticifers. The genus is richly represented in regions that are seasonally dry. It is divisible into many sections according to colour of the perianth and stamens, leaf characters (position and shape, whether terete, fistulose, flat or keeled, etc.) transection and thickness of the scape, and occurrence of nectariferous pores. In many species bulbils are developed in the inflorescence between the flowers. These serve as an effective means of vegetative propagation, especially in taxa with poor seed-setting.

Some species are cultivated as ornamentals, e.g. *A. christophii, A. karataviense, A. rosenbachianum* and *A. aflatunense,* all with stellate, violet flowers in globose heads, the former three from Turkestan, the last mentioned from Central Asia. *A. flavum* and *A. moly* from Turkey and South-Western Europe respectively are yellow-flowered, and *A. narcissiflorum* and *A. siculum* from the Alps and Southern Europe respectively, have pendulous, campanulate, reddish to brown flowers. *A. carinatum* with smaller, nodding flowers, is native in South-Eastern Europe. *A. cyathophorum* var. *farreri,* with purple flowers, and *A. cyaneum,* with blue, both from China, are dwarf ornamentals.

Several species are economically important. *A. sativum,* "Garlic", indigenous from Southern Europe to Central Asia, is grown for its white bulbs that are used to flavour meat and other food. The oil extracted from them, oil of garlic, is used in medicine and for flavouring food. It is rich in allyl-propyl disulphide and diallyl disulphide which with the enzymes released on bruising the tissues give a strong scent. – More widely used and milder are the diverse sorts of *A. cepa,* "Onion", which are cultivated throughout the world and are eaten raw in salads or roasted, boiled or fried with various kinds of food. The juice is mildly antiseptic. The species is grown in various varieties and forms. Var. *bulbiferum,* "Top Onion", produces rather large bulblets in the inflorescence. – *A. ascalonicum,* "Shallot", probably indigenous in western Asia, is grown as a garden vegetable and mostly used pickled. – *A. schoenoprasum,* "Chive", growing wild in Eurasia, for example on rocky habitats in the Baltic, is grown for its terete leaves used as sandwich salad. – *A. porrum,* "Leek", indigenous in the Mediterranean, is widely cultivated for the mildly flavoured bulb and leaf bases used in cooking. – Also other species, such as *A. ampeloprasum, A. chinense, A. fistulosum, A. ledebourianum* and *A. odorum* are cultivated for their bulbs or leaves.

Subfamily Gilliesioideae

Subfamily Gilliesioideae perhaps represents the most "advanced" of the subfamilies. It consists of about nine small genera, all in South America and most of them confined to Chile. They are small, bulbous herbs with a few basal, linear leaves and mostly few-flowered inflorescences subtended by two unequal, spathal bracts. The tepals are free or slightly fused and more or less unequal, sometimes by fusion appearing five or three in number. Adaxial appendages are often present inside and at the base of the tepals. The filaments are basally widened and fused into a staminal tube or cup. Three or four of the stamens may be transformed into staminodes, only the upper two or three then being fertile.

In a few genera, each with but one or two species, the flowers lack extrastaminal scales, e.g. in *Solaria* (2; Fig. 93 O–S) in Chile. Such scales are present in some other genera, among them *Gilliesia* (3), which has unequal tepals and a synandrium with only three functional anthers. *G. graminifolia* is sometimes grown as an ornamental.

The taxonomic position of Alliaceae has been variously interpreted. Some botanists include the Alliaceae in Amaryllidaceae, (HUTCHINSON 1934, 1973) or regard them as closely related to this family on the basis of similarities in many morphological characters, but this is not unequivocally supported by chemical characters, as the Amaryllidaceae lack saponins and possess unique alkaloids.

Another family which may be more closely allied to Alliaceae than Amaryllidaceae is Hyacinthaceae. Most characters found in Alliaceae are met with in this family although its inflorescence is racemose and a parietal cell is cut off in the nucellus, a condition rare in Alliaceae. Finally, as is pointed out in particular by HUBER (1969), there are several interesting similarities between the Alliaceae and some generic groups in the Anthericaceae, such as the occurrence (at least in certain cases) in both families of articulated pedicels, of campylotropous ovules, of a thick phytomelan crust on the seed, of helobial endosperm formation and of similar chemistry (as regards saponins and crystal raphides).

Alliaceae may not be such a homogeneous family as is generally assumed. Important features such as endosperm formation, raphides, underground parts and articulated or non-articulated pedicel are quite variable. An analysis of the variation in the family is obviously needed.

Amaryllidaceae Jaume St. Hilaire (1805) 50:860 (Figs. 95–97)

Perennial or biennial herbs with subterranean bulbs with thick, fleshy bulb scales, only rarely without a typical bulb and with a rhizome, as in *Scadoxus* and *Clivia*. The roots are contractile and in all cases known have vessels with scalariform perforation plates (in contrast to the frequently more advanced, simply perforated vessels in the roots of Alliaceae). The basal stem is herbaceous, short, sympodially branching, generally with distichous, basally concentrated leaves. The inflorescence-bearing scapes are terminal (as in Hemerocallidaceae, Hyacinthaceae and Alliaceae), but through sympodial branching may appear to be lateral.

The leaves are generally flat and dorsiventral, linear to almost orbicular, sheathing at the base, parallel-veined (veins often indistinct), mostly glabrous, and provided with anomocytic stomata and mucilage-filled cells or elongate sacs with raphides.

The usually glabrous scapes bear an umbel-like inflorescence comprising one to several helicoid cymes, the axes of which are suppressed. The inflorescence is subtended by from two to eight involucral scales which are free or basally connate. The flowers are not articulate on the pedicel. They are always epigynous, trimerous and bisexual and in most cases actinomorphic or weakly zygomorphic (strongly so in *Sprekelia*). The tepals are generally similar in the two whorls and vary from free to connate into a longer or shorter tube. Their colour may be white, yellow, purple or red, but not blue (violet in *Grittonia*). A perigonal corona structure, "paraperigone", forming a ring or tube is present in *Narcissus* (incl. *Tapeinanthus*; see under tribus Narcisseae).

The stamens are 3+3 in number (rarely 3 in *Zephyra* and up to 18 in *Gethyllis*). Their filaments are narrow or flat and inserted at the base of the tepals or in the tepal tube. In several genera a lateral, stipule-like, subulate appendage is present distally on the filament on each side of the anther (as in some genera of Alliaceae and Hyacinthaceae). The filaments may even be expanded and connate at the base to form a staminal "corona" structure, as in *Pancratium, Hymenocallis* and related genera. The anthers are epipeltate or perhaps basifixed in some genera (*Hessea, Leucocrinum, Galanthus*). They are generally elongate, longitudinally dehiscent or rarely (in *Galanthus, Leucojum* and *Lapiedra*) opening by apical pores. The tapetum is secretory (except, perhaps, in *Galanthus*, where it is reported to become amoeboid at an early stage); microsporogenesis is successive. The pollen grains are sulcate in most genera, but bisulculate in the tribe Amaryllideae, and are normally dispersed in the two-celled stage.

The ovary is inferior, tricarpellary, trilocular and provided with more or less distinct septal nectar grooves (except in Galantheae, where the nectar may be secreted from the distal part of the inner tepals). The style is simple with a punctiform, capitate or trilobate stigmatic apex, generally with a

Dry, papillate surface (more rarely Wet, e.g. in *Sprekelia*). The locules generally contain several to many, centrally inserted, anatropous or nearly anatropous (but never campylotropous), ovules, with two integuments or more rarely one and occasionally none. The ovules are crassinucellate and a primary parietal cell is probably cut off from the archesporial cell in most genera, but not in taxa studied of *Crinum, Eucharis, Narcissus* and some other genera, where the archesporial cell functions directly as the megaspore mother cell. Embryo sac formation generally conforms to the *Polygonum* Type but to the *Allium* Type at least in species of *Crinum* and, perhaps, *Pancratium*. The endosperm formation is nuclear or helobial, each type being found in several genera, and possibly of taxonomic interest within the family (see below).

The fruit in most genera is a capsule, but baccate, indehiscent fruits occur for example in *Chloanthus, Clivia, Cryptostephanus, Gethyllis* and *Haemanthus*. The seeds are highly variable: in European-centred genera, like *Galanthus, Leucojum* and *Narcissus,* they are mostly globose, ellipsoidal or ovoid, while in most of the primarily extra-European genera they tend to be more or less flattened. Exceptions are the species where the seeds do not enter a dehydrated stage but remain water-rich (75–92%; other seeds contain but 12–25% water) and germinate directly upon maturation. Such taxa are found, for example, in *Amaryllis, Boophane, Clivia, Haemanthus, Hymenocallis* and *Nerine;* the seeds in these cases are disseminated when the embryo is still quite small or are sometimes "viviparous".

The raphe sometimes develops a crest or wing, and an elaiosome is formed in the chalazal region in *Galanthus* and *Leucojum*. In the dehydrated seeds, the seed coat largely agrees with that in Alliaceae and Hyacinthaceae: the outer integument consists of several cell layers and its epidermis is covered with a mostly thin phytomelan crust. This, however, is lacking more often in Amaryllidaceae than in Hyacinthaceae, for example in species of *Leucojum, Galanthus* and *Sternbergia,* and in particular in water-rich seeds of some tropical and South African genera, especially in the tribe Amaryllideae. The subepidermal layers of the outer integument are mostly strongly compressed and those of the inner integument are collapsed into a thin film. The endosperm cells contain aleurone and fatty oils and in the terete seeds also cellulose (stored in the cell walls). Starch is frequently present, but in small amounts. The embryo is straight or slightly curved, cylindrical or in the flat seeds somewhat compressed, and generally more than half as long as the endosperm.

The water-rich seeds, on the other hand, are large, globose to ovoid, often green and lacking a phytomelan crust. The endosperm is richly developed and starch is the most important nutrient compound; it is also present in the integument(s), especially in the single integument of the seeds in some Amaryllideae (*Amaryllis, Boophane, Brunsvigia, Nerine*). In the ategmic (i.e. naked) seeds of some species of *Crinum* the nucellar remnants, endosperm and embryo make up the whole seed; the embryo is then large and green and may contain as much as 92% water.

Chemistry. Amaryllidaceae are easily characterized chemically. Steroidal saponins as well as allyl sulphides and similar compounds are probably lacking throughout, whereas particular alkaloids, not known to occur in other plants, are constantly present. Among the specific ("amaryllis") alkaloids are lycorin, belladin, haemanthanin, homolyrin, lycorenin, galanthanin, crinin and tazettin (WILDMAN 1968). About a hundred such bases are known which are considered to be biogenetically related. According to HEGNAUER (1963) an over-production of the amino acid tyrosine, which is the chief component in these alkaloids, has led to their biosynthesis. Chelidonic acid is widely distributed in Amaryllidaceae. The bulbs are rich in carbohydrates and also contain organic acids and soluble nitrogenous compounds. Calcium oxalate is found mainly in the form of raphide bundles, which are concentrated in mucilage-rich cells or sacs.

Distribution. The Amaryllidaceae are widely distributed. They are richly represented in the tropics and have pronounced centres in South Africa and, but less so, in Andean South America. Other groups have their centre in the Mediterranean. Groups of genera supposed to be phylogenetically related often have a particular geographic concentration.

Taxonomy. The family may be divided according to whether

1. the filaments are filiform or strongly modified, sometimes fused to form a coronal tube,
2. the pollen grains are sulcate or bisulculate,
3. the spathe bracts are two or more in number,
4. the style is strumose or not,
5. the integuments are single or double,
6. the fruit is a capsule or berry,
7. the anthers dehisce longitudinally or by apical pores,

8. the bulb coat is fibrous or not when torn,
9. the scape is hollow or not, and
10. the flowers are actinomorphic or zygomorphic.

There have been various attempts to divide the family into natural generic groups. The present division is a simplified version of some of the recent ones (by Pax and Hoffman 1930; Traub 1957, 1970; D. and U. Müller-Doblies 1978).

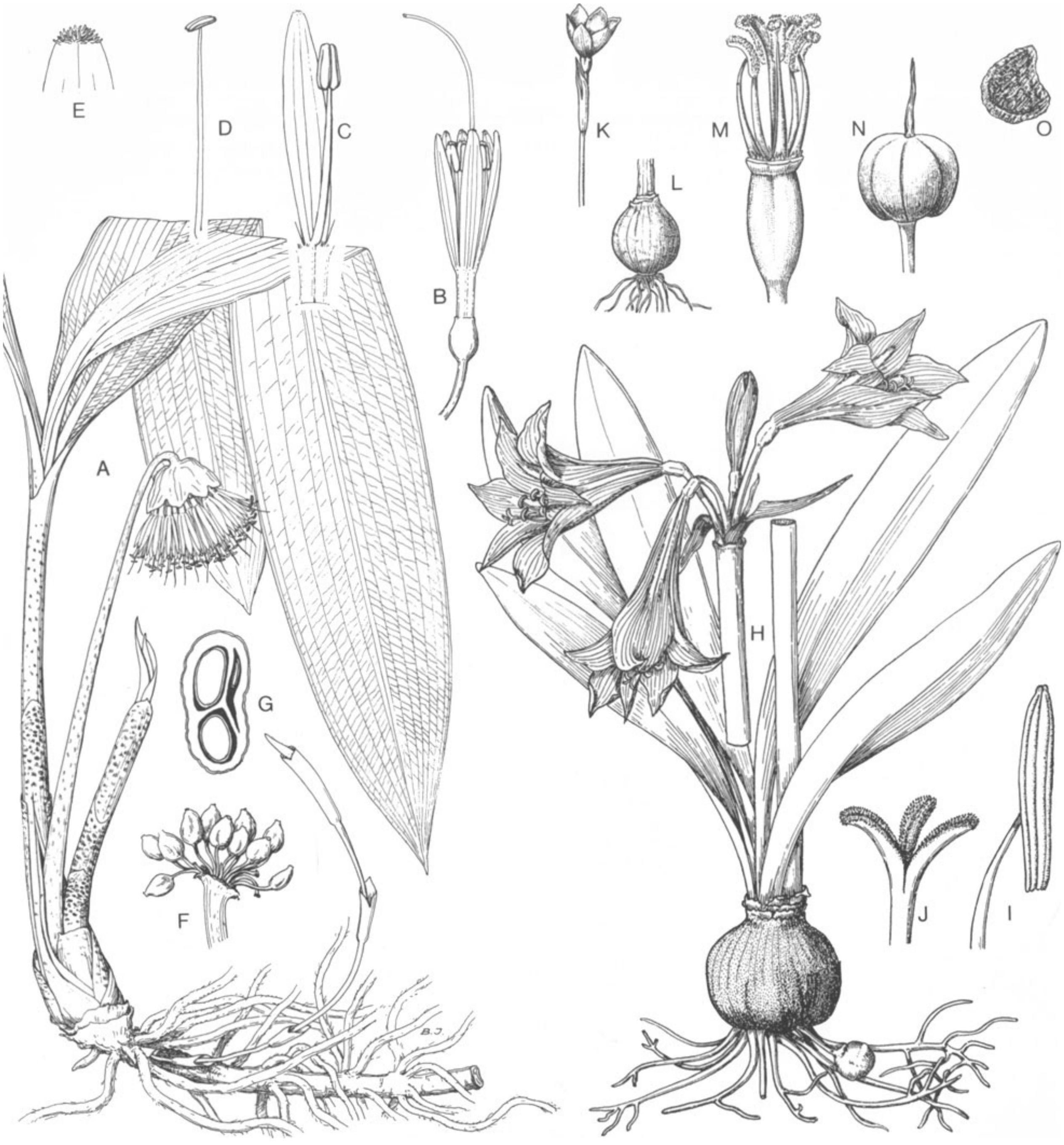


Fig. 95. Amaryllidaceae. **A–G** *Scadoxus nutans*. **A** Flowering plant; note the rhizome. **B** Flower. **C** Perianth segment and opposite stamen. **D** Stamen. **E** Apex of perianth segment. **F** Infructescence (berries). **G** Berry, transverse section. (Friis and Björnstad 1971). **H–J** *Hippeastrum rutilum*. **H** Plant. **I** Anther. **J** Style apex with stigmatic lobes. (Cabrera, 1968). **K–O** *Zephyranthes filifolia*. **K** Unifloral inflorescence. **L** Bulb. **M** Androecium and gynoecium. **N** Capsule. **O** Seed. (Correa 1969)

Tribus Haemantheae

Tribus Haemantheae consists of about six genera and has its centre of variation in Southern Africa. They usually have quite a big bulb, but this is replaced by a rhizome and thick sheathing leaf bases in *Scadoxus* (10), which has a more tropical distribution. The scape is solid or sometimes hollow (variable within *Cyrtanthus*), and bears an inflorescence of from one to many flowers. The spathal bracts vary from two to eight and are free or basally fused. The perigone is generally long and tubular, funnel-shaped or cylindrical and sometimes slightly zygomorphic. The six filaments generally lack distal tips or appendages and are not fused into a cup. They are usually inserted in the perigonal tube. The pollen grains are consistently sulcate.

Within this group there is a variation from loculicidal capsules with black, phytomelan-encrusted seeds (as in *Cyrtanthus*), to baccate fruits with few or even solitary seeds, which are globose, water-rich and lack phytomelan (as in *Haemanthus*).

Haemanthus (40) is often considered to be a large genus but many of the species seem to be local colour variants. The leaves are distichous and vary from rather narrow and erect to elliptic or circular and pressed against the ground (as in *Massonia* of Hyacinthaceae). The scape is generally broad and flattened, and often spotted. The spathal bracts are wide, often more than two in number, and sometimes fleshy. In some species they are bright red and serve as the main attraction, while the flowers are small, numerous and often very densely clustered. The locules are one- or two-ovuled and the fruit is a berry with globose, water-rich seeds. The genus is conspicuous in the Cape flora, and several species appear abundantly after veld fires. Especially forms of *H. coccineus* are often grown as ornamentals. The genus is well-known by cytologists for its large chromosomes (BJÖRNSTAD and FRIIS 1972). – *Scadoxus* (10) (Fig. 95A–E), from Arabia to Southern Africa, grows in shady forest habitats; the species have a loose bulb, with a distinct rhizomatous part or, more often, an elongate rhizome, and leaves that are not distichous.

Cyrtanthus (incl. *Vallota* and *Anoiganthus;* 48) is mainly South African. Most species have narrow red, yellow, pink or white tubular flowers. The ovary contains rather numerous ovules and the fruit is a loculical capsule with flat, ovate to oblong seeds with a wing at the micropylar end. *C. purpureus* (the former genus *Vallota*), has *Amaryllis*-like flowers. This and several other species of *Cyrtanthus* ("Kaffir Lilies") are grown as ornamentals.

Clivia (4) consists of rather large herbs without a typical bulb. They have several distichously arranged leaves and their tepals are fused only basally to form a funnel-shaped perigone, orange-red in colour. There are five to six ovules in each locule. The fruit, unlike that in *Cyrtanthus,* is a globose berry with one to few globose, water-rich seeds. *Clivia miniata* is commonly cultivated.

Possibly related to the Haemantheae, or to the Amaryllideae (below), is the genus (*Gethyllis*) (10) which has a short scape with a single spathal bract, a single flower with up to 18 stamens and a succulent fruit. Another possibly related genus is *Apodolirion* (6). Both of these genera are South African.

Tribus Amaryllideae

Tribus Amaryllideae consists of about ten genera and has a pronounced centre in the winter rainfall area of Southern Africa, although the genus *Crinum* has a pantropical distribution (see below). The tribe consists of small to large-sized herbs with well-developed bulbs. When bulb coats and leaves are torn apart minute fibres become visible (except in secondarily cartilaginous leaf coats). The leaves vary from narrow and linear (sometimes coiled or undulate) to broad, and the scape is always solid. The inflorescence consists of one to many flowers and is always subtended by two free spathal bracts. The flowers are actinomorphic or, the larger funnel-shaped ones in particular, slightly zygomorphic. The perianth tube varies from short to long and from broad and funnel-shaped or campanulate to narrowly tubular. The filaments generally lack appendages and never cohere into a tube; nor is there a perigonal corona. The most distinctive characteristic of this tribe is that the pollen grains are *bisulculate.* The style is slender or in some genera (e.g. *Strumaria*) swollen and triquetrous at the base; the stigma is trilobate or capitate. An embryological peculiarity is that the ovules, at least in several of the genera, are unitegmic, and in at least one species of *Crinum* there is no integument at all. The fruit has a dry pericarp and is either indehiscent or bursts open irregularly or loculicidally. The single integument in the seed is generally green and, like the endosperm, is rich in starch grains. In *Nerine* its epidermis even has stomata! These seeds are rich in water and do not have a true resting period.

Brunsvigia (20) consists of rather large herbs, the flowering scape of which is often developed much

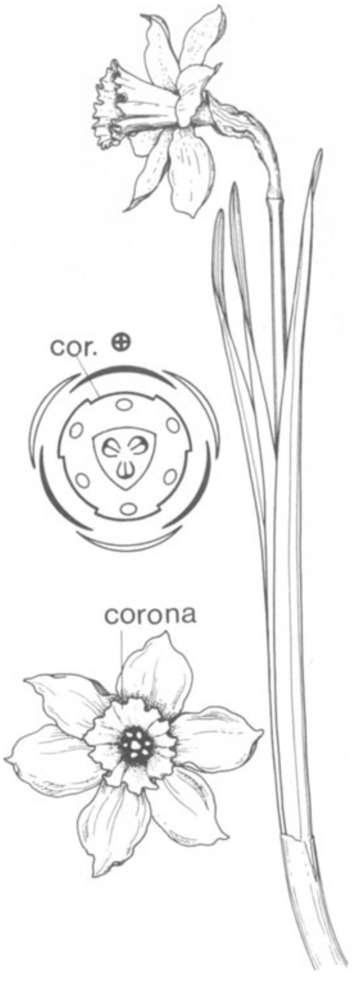


Fig. 96. Amaryllidaceae. *Narcissus pseudonarcissus.* Plant, floral diagram and flower with coronal structure. (Larsen 1973a)

earlier than the two to numerous distichous leaves. The locules of the ovary contain rather few ovules. The development of the globose infructescence is characteristic; its pedicels enlarge, then it dries up, separates from the stem and rolls around driven by the wind. The capsules are inflated and turbinate and the seeds are green and may germinate in situ. *B. josephinae* is sometimes grown as an ornamental. – While *Brunsvigia* has up to ca. 30-flowered "umbels", *Boophane* (5) may have a hundred flowers, but otherwise resembles the former genus in most features. – *Nerine* (ca. 30) has almost free tepals which are often undulate and usually pink to crimson. *N. sarniensis,* the "Guernsey Lily", *N. bowdenii, N. curvifolia* and other species are important in horticulture. – A few related genera are *Strumaria* (10), *Hessea* (10) and *Carpolyza* (1), all restricted to the dry regions of South Africa. They are small herbs with bulbs covered by fibrous tunics and have small, white to pink flowers with short or no perianth tube; the seeds are soft and fleshy as in the other genera of this group. *Strumaria* and *Hessea* are closely related; both having a strumose style and a globose fruit (Goldblatt 1977a).

Amaryllis (1) belladonna, the "Cape Belladonna", is a somewhat *Crinum*-like or *Hippeastrum*-like, fairly large herb with large, pink, campanulate flowers. It is indigenous in the south-western part of the Cape Province, but is now a widely cultivated ornamental. There has long been a nomenclatural confusion between this genus and the American genus *Hippeastrum,* the latter having frequently been called "Amaryllis" (Traub and Moldenke 1949; Tjaden 1981). The nomenclature seemed to be settled (Dandy and Fosberg 1954; etc.), but Traub recently (1983) has considered *Amaryllis* to be typified by a species of *Hippeastrum.*

Crinum (130) consists of herbs which may reach considerable dimensions and may have a falsely leafy stem (resulting from the scape being enclosed by leaf sheaths as in *Musa*). In some species prolonged (basal) growth of the leaves results in their tips trailing on the ground. The flowers are generally large and have a long white, rose or crimson perigone tube in which the filaments are inserted, and the fruits are capsules with fleshy seeds. The ovules are generally unitegmic or occasionally ategmic, in which case the seeds consist mainly of the endosperm and embryo. *Crinum* is widely distributed in the tropics and warm temperate regions. It contains many tall species, a number of which are cultivated, e.g. the Indomalaysian *C. amabile,* the tropical Asiatic *C. latifolium* and *C. asiaticum,* the Himalayan *C. amoenum,* the American *C. americanum* and *C. erubescens,* the South African *C. bulbispermum* and *C. campanulatum,* the West African *C. laurentii* and *C. nutans* and the Australian *C. pedunculatum.*

Tribus Hippeastreae

Tribus Hippeastreae consists of about ten genera with a pronouncedly American distribution. They represent herbs of various dimensions with tunicated bulbs which do not expose any fibres when torn apart. The leaves are linear and flat, and the scape generally hollow. The inflorescence is subtended by an involucre of two or four spathal bracts which may be free from each other (as in *Hippeastrum* and some related genera) or, more often, fused into a tube (as in *Zephyranthes* and several related genera). The flowers may be solitary or rather numerous in the inflorescence, and are actinomorphic or often zygomorphic (as, in particular, in *Sprekelia*). The tepals are almost free or more often fused into a tube, while a "paraperigone" is mostly lacking or, when present, inconspicuous. The filaments are often of different lengths. The anthers dehisce longitudinally and the pollen grains are sulcate. The style is not thickened and the locules have few to several, bitegmic ovules. The fruit is a loculicidal capsule with seeds that are generally flat, dry, encrusted with phytomelan, and often winged.

Hippeastrum (55–75) (Fig. 95H–J) is American, ranging from the West Indies and Mexico to Argentina. It consists of often large herbs with distichous flat leaves and scapes with two free spathal bracts. The large, mostly purple or red flowers are funnel-shaped and slightly zygomorphic. The tepals are free or basally connate, and the filaments are unequally long and more or less upcurved. The application of the name "*Amaryllis*" to this genus, here (dubiously) considered incorrect, persists in horticultural circles. Numerous species are grown as ornamentals, e.g. *H. advenum, H. bifidum, H. elegans, H. puniceum, H. reginae* and *H. striatum*. – *Rhodophiala* (30), in South America, consists of species having slender scapes with a few-flowered pseudo-umbel of funnel-shaped, variously coloured, flowers. The flowers may have a "paraperigone" of scales or bristles at the base of the tepals.

Zephyranthes (ca. 60) is distributed from Chile to far up into North America. It has narrow, linear leaves and a slender, short scape with a unifloral inflorescence subtended by a tubular involucre of spathal bracts. The flower is actinomorphic, erect or suberect and funnel-shaped, with a short tube. A "paraperigone" of bristles or scales may be present. The capsules have locules with few, flat, black seeds. Ornamental species include *Z. atamasco, Z. bifolia, Z. brasiliensis, Z. candida, Z. smallii* and *Z. tubiflora*. *Sprekelia* (1) *formosissima*, in Mexico to Central South America, is extraordinary in having a single-flowered scape with a strongly zygomorphic, firm, red flower with spreading tepals, the lower three of which enclose the long filaments and style. The flower is strongly adapted to bird pollination. The seeds are D-shaped, narrowly winged and black.

Tribus Lycorideae

Tribus Lycorideae differs from the preceding mainly in having a compact (not hollow) scape, and in being Asiatic in distribution. – *Lycoris* (17), distributed from Burma to Korea and Japan, has a somewhat *Nerine*-like appearance, but the capsular fruits have round, smooth, black seeds. It may represent a rather primitive element in the family. A "paraperigone" is sometimes present in the form of small scales at the throat of the tepal tube. – Related is *Ungernia* (8) in central Asia.

Tribus Stenomesseae

Tribus Stenomesseae (incl. Eustephieae), like the following tribe, is South American. It includes ca. 14 genera. In this group the leaves, which are sometimes petiolate, vary from thin to fleshy, as in *Rauhia*. The scape is solid and the flowers mostly yellow or red and often pendulous (in many cases exhibiting the syndrome of ornithogamy). Their stamens are often fused basally into a staminal cup; in other genera they are free but variously appendiculate. The filaments may be callous at the base and their appendices may even be petaloid. The filaments are sometimes long and declinate. The fruit is capsular and the seeds are black, and often flat, either D-shaped and winged or oblique and unwinged.

Stenomesson (20), ranging between northern Chile and Ecuador, generally has pendulous flowers and a well-developed staminal cup. – *Chlidanthus* (2), from Mexico to Bolivia, has flowers with a long tepal tube. The filaments of the outer staminal whorl are short and inserted in the mouth of the perigone tube, while those of the inner whorl are longer and inserted basally in the tube.

Phaedranassa (6), which ranges from Andean Peru to Costa Rica, has petiolate leaves. – The tubular flowers of *Eustephia* (4), in Peru and Argentina, have free filaments with tooth-like appendages inserted in the perigone tube.

Tribus Eucharideae

Tribus Eucharideae, with about five genera, is likewise mainly American (*Eurycles* excepted). The staminal filaments in this group, as in some of the following, are either laterally dilated and fused into a basal cup or supplied with basal appendages. In this tribe the seeds are generally large, globose and fleshy, but in contrast to the Amaryllideae, with similar seeds, the fruit is a loculicidal capsule. The flowers vary in colour, from being white and *Pancratium*-like to red-and-yellow as in the Narcisseae.

Eucharis (20) in Central America and northern South America, has a short perigone tube dilated at some distance from the base. The filaments, inserted on the margin of the perigone tube, are basally indistinctly appendiculate and narrow. The flowers are white or slightly yellowish, as in the related genus *Hymenocallis* (55), which ranges from the temperate South-Eastern U.S.A. to Northern South America. In *Hymenocallis,* the filaments are basally fused into a cup of varying appearance. *Eucharis* and *Hymenocallis* include several species widely cultivated as ornamentals, e.g. *Eucharis grandiflora* and *E. candida,* and *Hymenocallis narcissiflora, H. macleana, H. vargasii, H. longipetala* and *H. expansa.*

Tribus Pancratieae

Tribus Pancratieae consists of four Old World genera only, ranging from South Africa to Macaronesia and the Mediterranean Region and further eastwards into tropical Asia. They are large to small herbs with linear or linear-lorate leaves and inflorescences with one to several generally white flowers. The perigone is basally tubular and funnel-shaped with spreading segments. The six stamens are either fused basally into a staminal cup with narrow filaments continuing above, or free and with lateral basal appendages. A capitate stigma terminates the style. The fruit is capsular and the seeds dry, black, turgid and angled or spherical.

Pancratium (20) ranges from the Canary Islands through the Mediterranean Region to Asia. The Mediterranean *P. maritimum* and *P. illyricum* are grown as ornamentals. – *Vagaria* (1), in Asia Minor, has free stamens with basal appendages.

Tribus Narcisseae

Tribus Narcisseae consists of small to medium-sized herbs with linear leaves and a solid scape bearing an inflorescence of one to several (rarely numerous) flowers. Its spathal bracts are basally fused into a tube. The flowers are actinomorphic and have six equal tepals. Inside this a "paraperigone" or "corona" is generally present, which varies from a dentate, rudimentary cup to a large, broadening and sometimes undulate tube. The anthers dehisce longitudinally and the pollen grains are sulcate. The ovary is trilocular, with several bitegmic ovules in each locule. The fruit is a capsule with globose to angular, dry and black seeds.

Narcissus (27) has a typically West-Mediterranean distribution and is here taken to include *Tapeinanthus* (= *N. humilis*) in Spain-Morocco, which has a reduced paraperigone. The colours of the tepals usually vary in the genus from white to bright yellow and the paraperigone from white or light yellow to orange or orange-red.

Narcissus is extremely variable in Spain and Portugal, where most species occur. Most are spring-flowering, but a few, namely *N. viridiflorus* (which is indeed green-flowered), *N. humilis* (see above), *N. serotinus* and *N. elegans* flower in the autumn. Several of the spring-flowering taxa have been subject to intensive breeding and are important garden ornamentals. They include the variable *N. tazetta* ("Tazettas"), indigenous in central Mediterranean, *N. poeticus* ("Poet's Narcissus"), indigenous in regions from Spain to Greece, and *N. pseudonarcissus* ("Daffodil") (Fig. 96). *N. poeticus* and *N. tazetta* have a short paraperigone, coloured reddish orange and yellow respectively, while in *N. pseudonarcissus* the paraperigone is large, yellow and undulate. A variable small-sized species complex is centred on the West-Mediterranean species *N. bulbocodium* which, relative to the perigone, has a large paraperigone. This and the likewise small-sized, western *N. cyclamineus,* with reflexed tepals, are often cultivated in gardens.

Sternbergia (5), ranging from the Mediterranean to Iran, though lacking a paraperigone, perhaps belongs here.

Tribus Galantheae

Tribus Galantheae might be united with the Narcisseae, but may be distinguished in terms of the anthers dehiscing by pores instead of slits. The tribe includes two or three genera with a Mediterranean-Western Asiatic distribution.

These consist of small to moderate-sized herbs with tunicated bulbs and sessile, lorate leaves, which are from broadly linear to almost filiform. The scape is cylindrical or compressed, solid or hollow, and bears one or few, usually pendent, flowers subtended by one or two partly green spathal leaves. The tepals are free or basally fused and are white, often with green or yellow spots. Usually the anthers open by apical pores. The pollen grains are sulcate. The pistil is trilocular and has several bitegmic ovules in each locule. It devel-

Fig. 97. Amaryllidaceae. *Galanthus nivalis*. **A** Flowering plants and bulb. **B** Leaf, transverse section. **C** Flower, longitudinal section. **D** Tepals of the inner whorl, outer and inner surface. **E** Stamen, longitudinally poricidal dehiscence. **F** Fruit. **G** Seed, with terminal appendages. (Ross-Craig 1972)

ops into a capsule with turgid, subglobose or ellipsoidal, pale or black seeds.

Galanthus (5) ranges from Mediterranean Europe to Asia Minor and the Caucasus. Some species are polymorphic and up to 13 species are often recognized. The scape is normally one-flowered and the bract single but two-ribbed. The tepals are unequal, the inner being short, truncate, notched and convolute. The flower is white but the inner tepals have one or two green blotches externally and green striation within. All the species are early-spring flowering, but the widespread *G. nivalis* has autumn-flowering forms. *G. nivalis* and other species, "Snowdrops" (Fig. 97), are very common garden ornamentals in cool-temperate regions.

Leucojum (8), ranging from Portugal to Crimea and Armenia, has one- to five-flowered inflorescences with one or two spathal leaves. The flowers are campanulate. The tepals are almost equal and have green or yellow tips. The subglobose, black or brown seeds may or may not have a crest-like appendage. This genus also includes mostly spring-flowering ornamentals, such as *L. vernum* and *L. aestivum* but *L. autumnale,* a slender herb, flowers in the autumn.

The Amaryllidaceae form one of the climax groups in the Asparagales. They are probably most closely allied to Alliaceae and Hyacinthaceae and share with them the bulb, the leafless scape, the normally phytomelan-coated seeds and various other attributes. They are definitely not closely related to the Hypoxidaceae, the Agavaceae (subfam. Agavoideae), the Haemodoraceae or the Alstroemeriaceae, with which they have formerly been united on the basis of the shared epigynous flowers.

Order Melanthiales

Two Families: Melanthiaceae and Campynemaceae.

Perennial or rarely annual herbs with short or long rhizomes, rarely corm-like, and exceptionally with a bulb-like base although without nutrient bulb-scales. The plants are rarely woody in the basal part. The roots are fibrous and generally provided with vessels that have scalariform perforation plates, whereas vessels are absent in stems and leaves. Vessels are completely lacking in one or two wholly chlorophyll-deficient genera. The aerial stem varies from being leafy to comprising a leafless scape and a basal rosette.

The leaves are usually spirally set but sometimes distichous. They are dorsiventral, often more or less flat, in some genera ensiform and *Iris*-like. The leaves are sheathing at the base, linear, lanceolate or rarely ovate, except in the achlorophyllous taxa, where they are scale-like; occasionally tapering at the base and nearly pseudopetiolate. Ligules occur rarely (*Pleea*). Cells containing crystal raphides occur in most genera.

The inflorescences are simple or compound racemes or spikes or rarely panicles; the flowers are bracteate or ebracteate, bisexual or very rarely unisexual, hypogynous, half-epigynous or epigynous (Campynemaceae), trimerous, and generally actinomorphic, being zygomorphic only in *Chionographis*.

The perigone consists of 3+3 tepals, which are free from each other or sometimes slightly connate basally or occasionally forming a campanulate or tubular perigone (in the hemi-epigynous taxa). It is generally inconspicuous, white, pale yellow, brown to purple or, rarely, bright yellow (*Narthecium*). It is fused to the basal parts of the ovary in a few genera. The tepals are generally similar in the two whorls and in some genera have basal nectaries. Spotted patterns and spurs are usually lacking.

The stamens are usually 3+3 but in *Pleea* up to 9 or 12. The filaments are free from each other; in *Narthecium* they are provided with spreading hairs. The anthers are basifixed or dorsifixed-hypopeltate, generally extrorse but sometimes introrse (a combination thereof in *Campynemanthe*), and dehisce longitudinally. The tapetum is secretory (Fig. 98W). Microsporogenesis is successive or rarely (*Tofieldia*) simultaneous. The pollen grains are generally sulcate, but are sometimes bisulculate (Tofieldieae) or tetraforaminate (Chionographideae). The exine surface is generally reticulate, rarely spinulose. The pollen grains are dispersed in the two-celled state; the generative cell is small, narrow and peripheral in the pollen grain.

The pistil is tricarpellary and trilocular or rarely unilocular (at least in *Campynema*). In most genera the stylodia are separate. Sometimes the locules are free in their upper part, and in the Petrosavieae and in *Harperocallis* the three carpels are separate nearly to their base (El-Hamidi 1952). An apically tribrachiate style occurs in *Aletris,* but some genera, such as *Tofieldia,* have a single style and a capitate stigma. The stigmatic surface is Dry in *Veratrum*. Septal nectaries are often lacking but occur in several genera (e.g. *Petrosavia, Protolirion, Tofieldia, Zigadenus)*. The locules contain two to numerous ovules, which are crassinucellate and anatropous or rarely (*Petrosavia*) campylotropous. A parietal cell is cut off from the archesporial cell (Fig. 98C) and forms a parietal tissue. Embryo sac formation follows the *Polygonum* Type (Fig. 98I–L), and endosperm formation where known is helobial (Fig. 98N–O) (a difference from all Liliales) (Stenar 1925, 1928b; Eunus 1951).

The fruit is generally a capsule or rarely (where the carpels are almost separate) consists of three follicles which open up along their inner suture. The capsules are loculicidal (most Aletreae and Metanarthecieae) or septicidal (*Clara, Hewardia* and *Pleea*), but *Tofieldia* and the Veratreae have carpels free in the apical parts; their capsules open ventricidally from the apex towards the base and along the central parts. Arils and fleshy caruncles are lacking. The seeds are generally rounded and isodiametric in transection, always elliptic, elongated longitudinally but not conspicuously flattened, and rarely longitudinally striate (*Aletris*). However, they are generally provided with wings or terminal appendages. The seeds are winged all around in *Melanthium* and *Veratrum*. Terminal appendages are of considerable length in some genera, for example, in *Narthecium* and *Tofieldia,* and the chalazal one is usually longer than the micropylar. The testal part of the seed coat has few, sometimes only two, cell layers; the epidermal cells are elongate and colourless, either well-preserved or collapsed. The testa lacks phytomelan (a difference from nearly all capsular Asparagales) as well as phlobaphene. The tegminal part of the seed coat is thin and collapsed, red-brown or yellowish; only rarely are its cells retained, though flattened (*Narthecium*). The endosperm usually consists of thin-walled, frequently isodiametric cells containing aleurone and fatty oils and sometimes traces of starch, the latter in the form of rounded grains. More often than in Liliales is the embryo small; it is ovoid or globose ($^1/_7$–$^1/_9$ of the length of the endosperm though sometimes considerably longer).

Chromosome Numbers. There is no single clear basic chromosome number in the order: x may be 8 or 11 (*Veratrum*), 12 (*Chionographis*), 13 (*Narthecium, Metanarthecium, Aletris*), 15 (*Tofieldia, Xerophyllum*), or 17 (*Helonias, Heloniopsis*), suggesting an aneuploid series.

Chemistry. Among chemical characteristics should be mentioned the common presence of raphides (in both families). Steroidal saponins are known to occur in many genera; those of *Narthecium* are thought to cause liver disease (icterus) in non-pigmented sheep (HEGNAUER 1963). Alkaloids derived from steroidal precursors such as cholestanol as well as those of the C-nor-D-homo Type (SEIGLER 1977) are found in several genera in the Veratreae. Thus, roots of *Veratrum* contain toxic alkaloids (veratramin, jervin and allied compounds). Also the alkaloids of the seeds of *Schoenocaulon* (= *Sabadilla*) have medical use; dissolved in acetic acid they are frequently used as insecticides.

Parasites. It is interesting to note that two related species of the rust genus *Puccinia* (section *Caricinae*) attack genera of this order only, viz. species of *Amianthium, Schoenocaulon, Veratrum, Xerophyllum* and *Zigadenus* (HOLM 1966), which further indicates that these genera form a biogenetically related group as regards proteins and/or other compounds.

Distribution. Melanthiaceae is a mainly Northern Hemisphere family distributed over Eurasia and Northern America with a few genera extending to South America. The members are mainly temperate to boreal (rarely alpine or tropical), and grow in forests, marshes, meadows, etc. Two genera (*Petrosavia* and *Protolirion*) are achlorophyllous, sometimes quite whitish, forest floor plants occurring in South-Eastern Asia and on Borneo, and on the Malay Peninsula, respectively. In contrast, Campynemaceae occur in the Southern Hemisphere, *Campynema* in Tasmania and *Campynemanthe* in New Caledonia.

Taxonomy, Relationships. The treatment of these families in a separate order is the logical consequence of their combination of attributes. They lack the features typical of each of the Asparagales, Liliales and Burmanniales.

Thus they differ from the Asparagales in that the seeds are not phytomelaniferous (although the fruits are capsular), the tepals are inconspicuous, the stylodial branches are generally separate and the embryo is small.

Unlike the Liliales endosperm formation is helobial and septal nectaries may be lacking; the tepals are less conspicuous and rarely spotted as is characteristic of the Liliales. Raphides are generally present.

The Melanthiales might seem to be more closely allied to the Burmanniales, but the tenuinucellate ovules (where also no parietal cell is formed) and diminutive seeds that characterize Burmanniales make a technical separation easy. Also, the vast majority of Burmanniales are achlorophyllous plants. The Burmanniales share some embryological and seed attributes with Philydrales (HAMANN, personal communication), and we hesitate to associate them intimately with Melanthiaceae.

AMBROSE (1980), who studied the Melanthiaceae from a cladistic point of view, questioned that the family is monophyletic. Its members are variable in a number of characters which are generally constant in other liliifloran families. Further evidence as regards the host specificity of particular *Puccinia* species such as pointed out by HOLM (1966) may become important in this connection.

Key to the Families

1. Flowers hypogynous or half-epigynous . . . . **Melanthiaceae**
1. Flowers epigynous . . . . . . **Campynemaceae**

Melanthiaceae Batsch (1802) 25:150 (Figs. 98–100)

Description as for the order, above, but flowers not epigynous and placentation never parietal.

It is possible that a division of Melanthiaceae into three or four families would better reflect the variation in the group. For example, Petrosaviaceae has already received recognition. Division of the family into tribes has been proposed in earlier treatments (e.g. KRAUSE 1930; HUTCHINSON 1934, 1959, 1973).

The family has been dispersed among a number of tribes, generally placed in Liliaceae s. lat. in previous literature. In BENTHAM and HOOKER (1883) its genera were placed mainly in the tribes Narthecieae and Veratreae; in KRAUSE (1930) under the tribes Tofieldieae, Petrosavieae, Helonieae, Hewardieae, Veratreae and Aletreae, and in HUTCHINSON (1973) under the tribes Narthecieae,

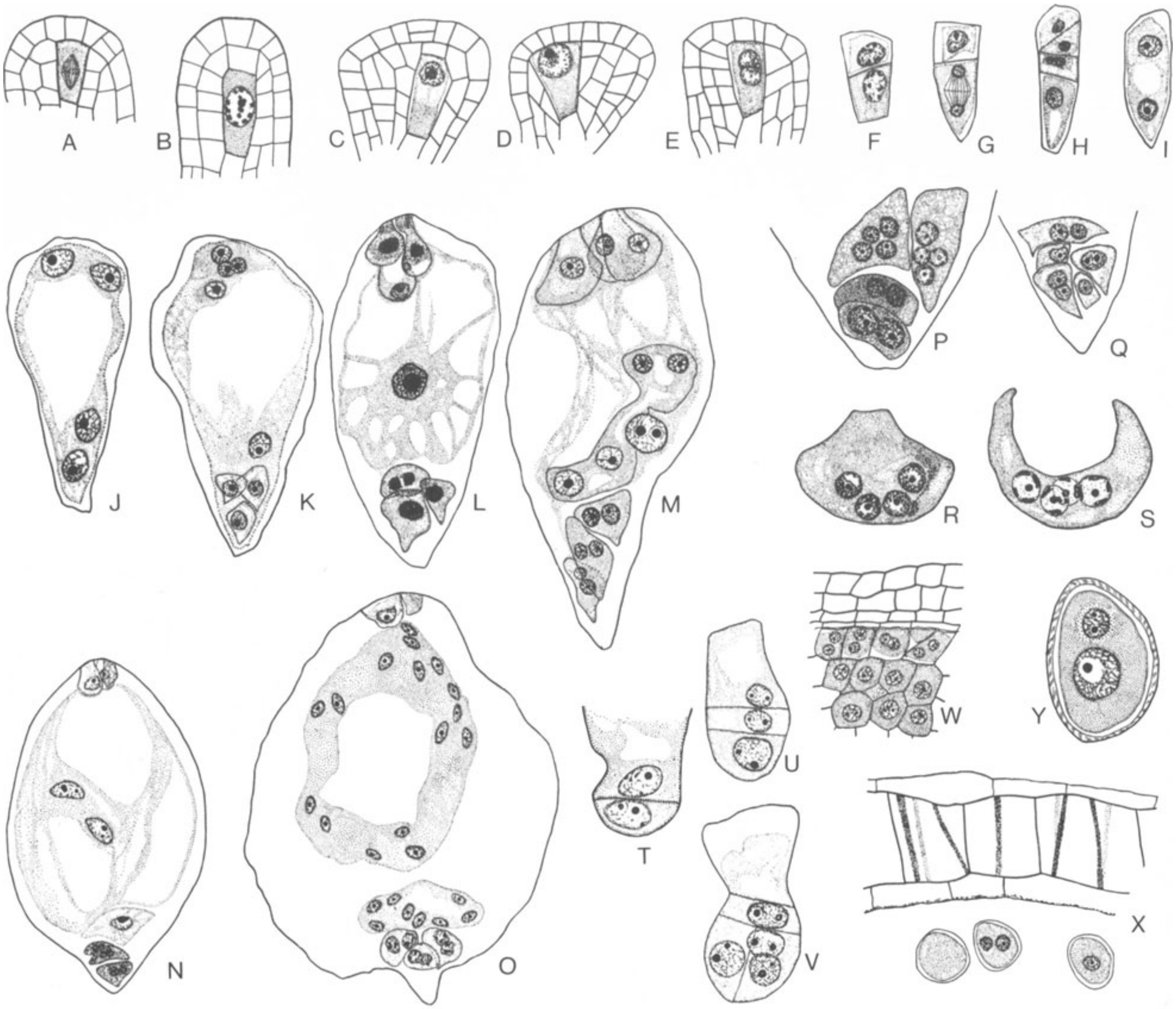


Fig. 98. Melanthiaceae. *Amianthium muscaetoxicum,* embryological details. **A–L** development with (**B–C**) and without (**D–E**) formation of parietal cell, meiosis (**F–H**), and embryo sac formation (**I–L**), with the polar nuclei having fused in **L. M** Two embryo sacs in the same nucellus, one mature and one in the 4-nucleate stage. **N–O** Endosperm formation and development, according to the Helobial Type. **P–Q** Increase in nucleus number in antipodal cells and increase also in number of antipodal cells. **R–S** Antipodal cells assuming peculiar shapes (resembling chalazal chambers). **T–V** Development of the early embryo. **W** Anther, sectioned to show tapetum and archesporial cells (both dark). **X** Endothecium (with spiral wall thickenings) and nearly mature pollen grains. **Y** Pollen grain. (Eunus 1951)

Helonieae and Veratreae and in the family Petrosaviaceae. Recently, Ambrose (1975, 1980) has investigated their variation to test their possible homogeneity, in which he utilized numerical methods (Ambrose 1980), finding rather different constellations of genera.

We shall try here to present a division of the family taking into account data from the available sources.

Tribus Petrosavieae

Tribus Petrosavieae consists of two saprophytic, achlorophyllous genera, *Petrosavia* (1) and *Protolirion* (3) (Fig. 99), which grow in rain forests in Eastern Asia, Malaya and Borneo. They are small, vesselless herbs with thin rhizomes and scaly leaves. The flowers are almost hypogynous, having

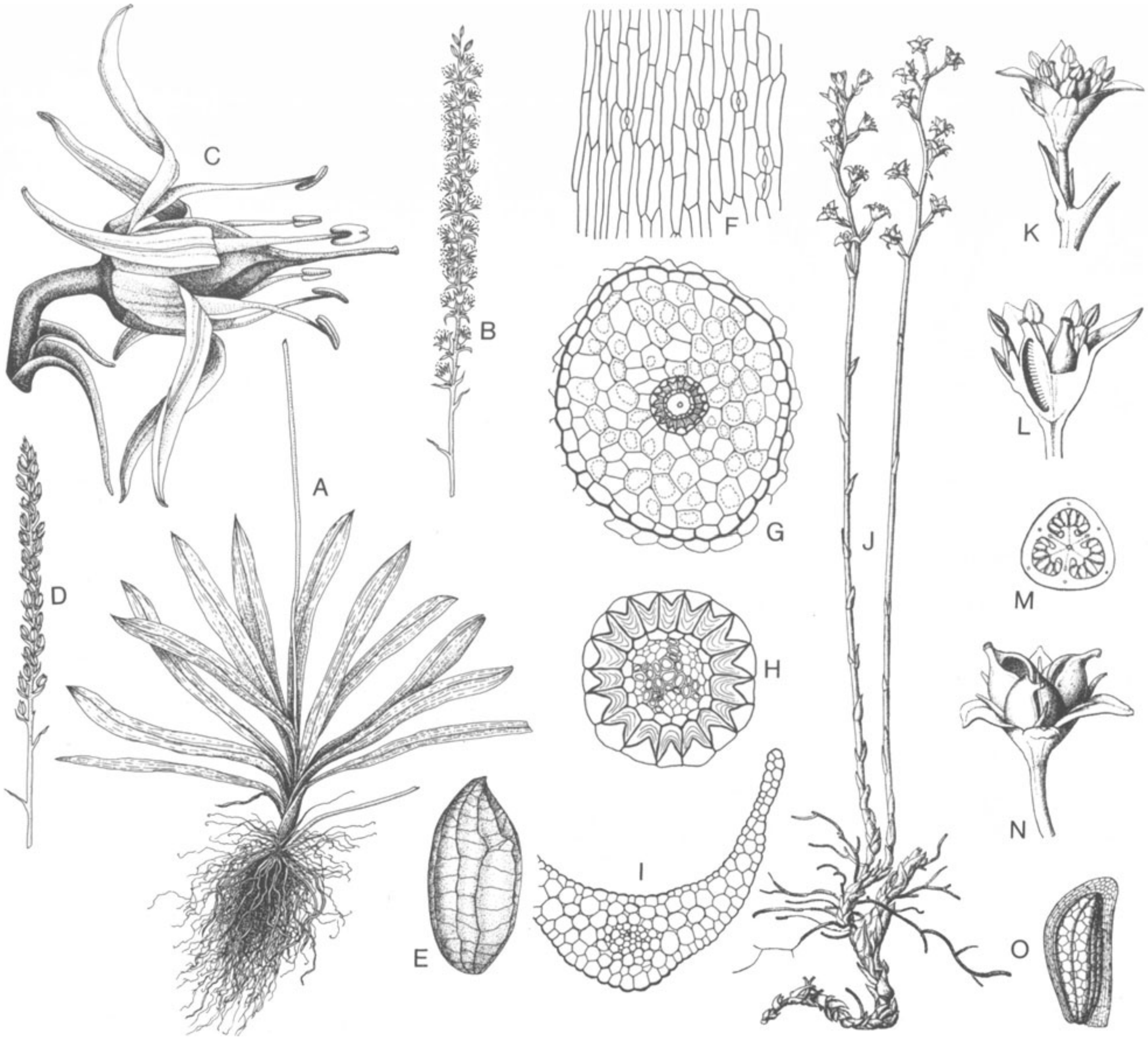


Fig. 99. Melanthiaceae. **A–E** *Metanarthecium luteoviride*. **A–B** Plant. **C** Flower. **D** Infructescence. **E** Seed; note that this is not black. (UTECH 1978b). **F–I** *Petrosavia stellaris*. **F** Stomata. **G** Stem, transverse section. **H** Stele. **I** Scale-leaf, transverse section. (STANT 1970). **J–O** *Protolirion sakuraii*. **J** Plant. **K** Flower. **L** Same, longitudinal section. **M** Ovary, transverse section. **N** Trifolliculus. **O** Seed. (KRAUSE 1930)

only basally fused carpels which mature into follicles. Septal nectaries are present. The pollen grains are sulcate to inaperturate. – These genera have an anatomy very much like that in Triuridales. Their carpels, largely free, have been taken as an indication that these genera form a very primitive group of Liliiflorae.

Tribus Melanthieae

This tribe consists of large or medium-sized herbs with bulb-like bases (*Amianthium, Stenanthium, Zigadenus* spp., *Schoenocaulon,* etc.) or often short, thick rhizomes (*Melanthium, Veratrum*). The leaves are variable, from narrow and grass-like to broad, lanceolate-ovate and prominently veined (as in *Veratrum*). The stems end in a spike, raceme or panicle which is sometimes compound and extensive. The flowers are mostly white to dark purple, and the stamens bear cordate to reniform anthers dehiscing extrorsely. The pollen grains are sulcate. Each carpel of the pistil ends in a separate stylodium. The carpels open ventricidally and their seeds are larger than in the following groups. In the seed coat the outer integument is retained (not collapsed as in most other genera). The plants are rich in alkaloids. Among the genera in this group may be mentioned *Schoenocaulon, Stenanthium, Amianthium* and *Melanthium,* restricted to America, and *Zigadenus* and *Veratrum* which occur in Eurasia as well.

Schoenocaulon (= *Sabadilla;* 10) ranges from Florida to Peru. It consists of tough herbs with a bulb-like corm, grass-like leaves and dense-flowered spikes with partly unisexual flowers. The seeds of *S. officinale,* in mountain meadows of Guatemala and Venezuela, are used to produce an insecticide (see above). – *Zigadenus* (15) occurs from Siberia to North America and in Mexico. Its tepals are basally adnate to the ovary and bear basal nectar glands. *Z. elegans* is the most widespread species. Some species are grown as ornamentals.

Melanthium (5) is a North American genus. Like *Veratrum* it is rhizomatous and has a pubescent inflorescence. The leaves are, however, narrow and the tepals clawed. *M. virginicum* is grown as an ornamental. – *Veratrum* (45) is the largest genus in the family and has a wide distribution in the Northern Hemisphere. The plants grow in meadows. They are mostly large herbs, which may reach a height of 2 m or more and have prominently veined leaves. The flowers vary from white or pale greenish to dark purple. The pistil has separate stylodia; its ovary develops into a sometimes inflated septicidal capsule. Several species, like the Eurasiatic *V. album* and *V. nigrum,* the Japanese *V. mackenii,* and the American *V. californicum, V. insolitum* and *V. viride* are grown as ornamentals. *V. album* is grown for the subterranean parts, which contain alkaloids (see above) and are used in medicine as a sedative and cardio-vascular depressant. – *Stenanthium* (5) in North America, has polygamous flowers and tepals basally fused to the ovary. It is a bulbous plant with linear or lanceolate leaves.

Tribus Narthecieae

Tribus Narthecieae consists of a number of genera with short, tuberculate rhizomes and erect herbaceous, leafy stems with terminal spikes or racemes. The stamens are mostly extrorse and the pollen grains are sulcate. Nectaries are found at the tepal bases, and septal nectaries are lacking. The carpels are either apically separate to form free stylodial branches or completely fused and forming a single style, as in *Heloniopsis, Nietneria, Narthecium* and *Metanarthecium.* In *Aletris* and *Nietneria* the perianth is adnate to the ovary for about half its length. The capsules are mostly loculicidal, and the seeds small, generally with a collapsed outer integument; terminal appendages are present or absent. Saponins and oxalate raphides are present but no alkaloids are known in this tribe.

Helonias (1) *bullata* is a herb up to 80 cm, occurring in swampy regions in Atlantic North America and sometimes grown as an ornamental. The tepals are purplish and spreading, the anthers blue. – *Heloniopsis* (4), in Korea, Japan and Taiwan, has campanulate, carmine-red flowers; *H. orientalis* is often grown as an ornamental. – *Aletris* (10) in Eastern Asia, Indomalaysia and North America, has grass-like leaves and yellow or white, connate tepals. The dried underground parts of *A. farinosa,* "Colic Root", in eastern North America, are used by the Indians as a diuretic, and against colic. – *Metanarthecium* (5) (Fig. 99A–E) occurs, in subalpine meadows in Japan and Formosa. – *Nietneria* (1), in the mountains of Guayana, has stiff somewhat falcate leaves. – *Narthecium* (8) in Eurasia as well as North America grows in marshy places. In AMBROSE's (1980) study it was shown to be the genus most closely similar to *Nietneria,* but it has a number of singular features. It is a herb with creeping rhizomes forming clones of plants with crowded, ensiform, *Iris*-like leaves. The erect stems are basally leafy and bear racemes of yellow, stellate flowers with hairy filaments and introrse anthers. The seeds are pale and have long terminal appendages. In contrast to the other genera, the tegmen does not collapse but consists of distinct cells with lemon-yellow contents. *Narthecium ossifragum* (Fig. 100A–E) is a common subatlantic herb growing in acid bogs in western Europe. – Also *Lophiola* (2) in Atlantic North America seems to belong in this group of genera (AMBROSE 1980).

Tribus Tofieldieae

This consists of two genera, *Tofieldia* (17) (Fig. 100F–K), a North temperate and arctic genus growing in moist alpine to cold-temperate habitats. In this genus should perhaps be included *Pleea* (1) *tenuifolia* (UTECH 1978b), a marsh plant in Southern U.S.A. Closely allied is also *Harperocallis* (1), in Florida. These genera are relatively small herbs with creeping rhizomes, distichous, often unifacial leaves and small, often whitish flowers with a non-caducous perigone. *Tofieldia* has 3+3 or (*Pleea*) 6+3, or even 6+6, stamens with introrse, subbasifixed anthers. Microsporogenesis

Fig. 100. Melanthiaceae. **A–E** *Narthecium ossifragum*. **A** Plant. **B** Dehiscing capsule. **C** Tepal and opposite stamen; note the pubescent filament. **D** Ovary. **E** Seed with long, terminal appendages. **F–K** *Tofieldia pusilla*. **F** Plant, to the *left* in fruiting stage. **G** Flower. **H** Stamen. **I** Pistil. **J** Capsule. **K** Seeds. (**A–K** Ross-Craig 1972). **L–P** *Xerophyllum tenax*. **L–M** Plant. **N** Inflorescence. **O** Flower. **P** Fruit. (**L** and **P** Hitchcock et al. 1969; **M–O** Takhtajan 1982)

at least in *Tofieldia* is simultaneous, and the pollen grains are bisulculate. Septal nectaries are known in *Tofieldia*. The carpels are usually free in the apical part, with free stylodia or in some species of *Tofieldia* with a tribrachiate style. In *Harperocallis* the carpels are free almost to the base. The capsules are ventricidal to septicidal, and the seeds are small and have terminal appendages. Oxalate raphides are lacking, at least in *Tofieldia*.

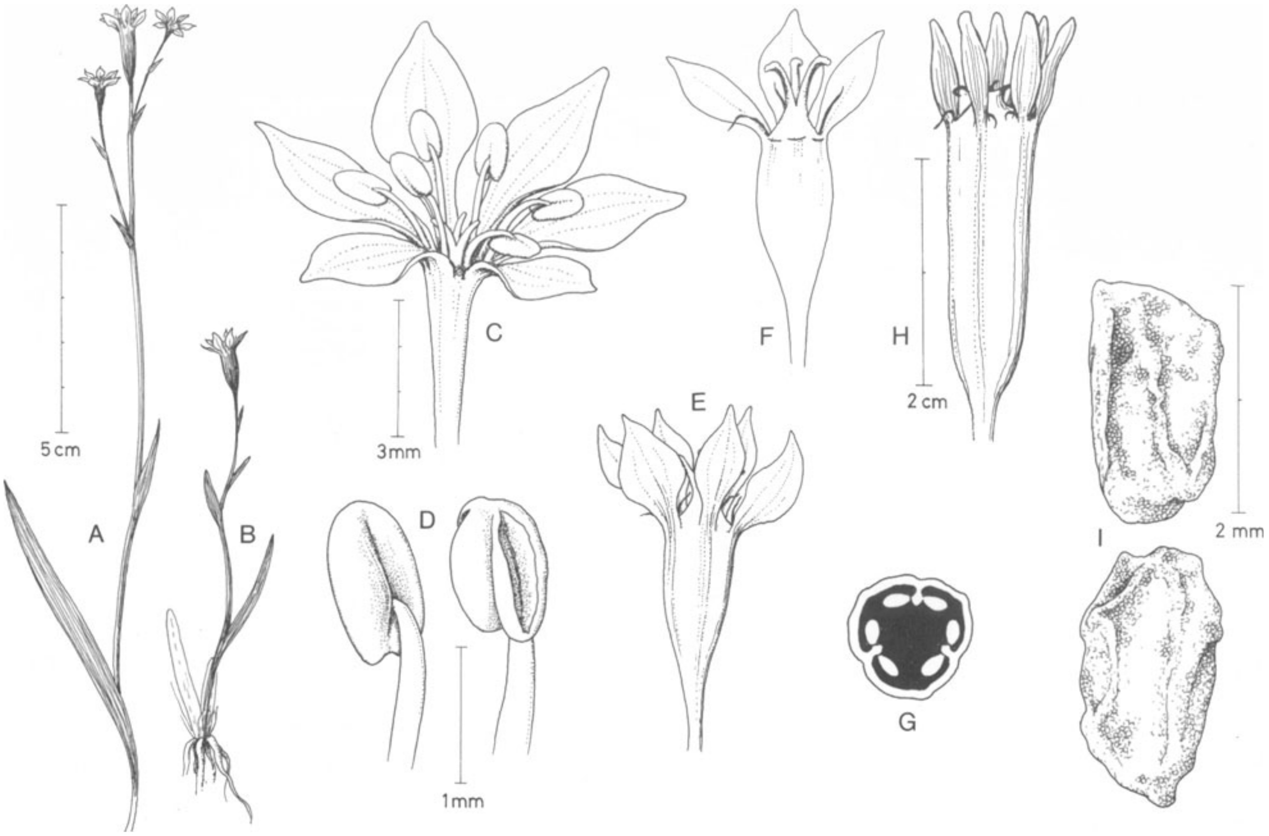


Fig. 101. Campynemaceae. *Campynema linearis*. **A–B** Plants. **C** Flower; note the hypopeltate stamens. **D** Anther, different views. **E–F** Flower, late stage. **G** Ovary, transverse section. **H** Fruit with persistent tepals and filaments. **I** Seeds, pale in colour. (Orig. B. JOHNSEN)

Tribus Chionographideae

Tribus Chionographideae consists of two distinct genera with small-seeded loculicidal capsules. The plants have short, thick rhizomes and agree in most respects with the Aletrideae but have pollen grains with four round apertures and show advancement in other respects: *Chionographis* having zygomorphic flowers, the three or four tepals directed basewards being much reduced in size compared to the two or three upper, and *Chamaelirium* having unisexual flowers (the plants are dioecious). Both genera are small, *Chionographis* (2) is found in moist places in Japan, and *Chamaelirium* (1) in Atlantic North America.

Tribus Xerophylleae

This consists of the genus *Xerophyllum* (Fig. 100L–P) only, a stiff erect herb with a tuberous rhizome and numerous densely situated, dorsiventral, grass-like, tough leaves with coarse margins. The flowers are numerous and situated in a pyramidal to cylindrical spike. The pollen grains are sulcate. The fruit is a loculicidal capsule with numerous small seeds with terminal transparent appendages. – *Xerophyllum* (3) occurs in North America; the leaves of *X. tenax* are used for making baskets.

Campynemaceae Dumortier (1829) 2:3
(Fig. 101)

Small, erect, glabrous, terrestrial herbs with a very short rhizome from which radiate fairly thick adventitious roots. The leaves are linear, sheathing, parallel-veined and glabrous; they are few in number and either they are restricted to the base or there may be one or two smaller ones on the cauline stem. Raphides are present (GOLDBLATT, personal communication). The inflorescence is a few-flowered panicle or a solitary flower (*Campynema*) or a several-flowered pseudo-umbel (*Campynemanthe*). Lateral flowers are subtended by a bract and have a rather long pedicel with dorsal prophyll.

The flowers are glabrous, actinomorphic, epigynous or hemiepigynous, bisexual and hexamerous with a six-veined ovary. The 3+3 tepals are all similar, being ovate or broadly lanceolate, free from each other and inserted near or somewhat below the top of the ovary. They are pale and sometimes distinctly dotted-striated. In at least *Campynema* they persist as a crown near the top of the ovary until the fruit is nearly ripe.

The stamens are 3+3, inserted at the base of the tepals. They have slender filaments and tetrasporangiate, longitudinally dehiscent anthers. In *Campynema* the anthers are sagittate and dorsifixed and all six are extrorse; in *Campynemanthe* they are basifixed, the outer being larger and extrorse, the inner smaller and introrse.

The tapetum in *Campynema* is secretory with multinucleate tapetal cells (DUTT 1970). Microsporogenesis in this genus is successive, and the pollen grains are sulcate and dispersed in the two-celled stage.

The carpels above the level of insertion of the tepals and stamens in *Campynema* are nearly separate or at least have wholly separate stylodia (Fig. 101 F), whereas in *Campynemanthe* they are fused into a single apically trilobate style. The ovary in *Campynema* is unilocular (described as trilocular by DUTT 1970) with parietal placentae; that in *Campynemanthe* is trilocular.

The following embryological data refer to *Campynema* and are taken from DUTT (1970).

The ovules are numerous, anatropous and weakly crassinucellate. The micropyle is formed by the inner integument alone. A parietal cell cut off from the primary archesporial cell divides anticlinally and its derivatives then divide periclinally to form a parietal tissue. Embryo sac formation follows the *Polygonum* Type. The endosperm formation is not known.

The fruit is a cylindrical, six-ribbed capsule (? pyxis) with numerous seeds. The capsule of *Campynemanthe* may open by a lid (PAX and HOFFMANN 1930). The seeds are irregular, ovoid-angular, folded and pale; in *Campynema* they are about 2 mm long.

The chromosome number and chemistry are unknown.

Campynema (1) (Fig. 101) occurs in Tasmania and *Campynemanthe* (2) in New Caledonia. Both genera occur in mountainous regions, sometimes growing in humus in forests.

The family needs further study, but is almost certainly closely allied to the Melanthiaceae as well as to the Burmanniales. It should not be associated with Iridaceae or related families in Liliales, where raphides are lacking.

Order Burmanniales

Three Families: Burmanniaceae, Thismiaceae and Corsiaceae.

Annual or perennial herbs, generally achlorophyllous, saprophytic (white, yellowish or reddish) or more rarely chlorophyllous and autotrophic, all with mycorrhiza. The perennial autotrophic taxa grow from an elongate or sometimes tuberous rhizome; in the achlorophyllous taxa adventitious roots generally radiate from the base of the vertical stem. The leaves are alternate or spirally set, dorsiventral, exstipulate, sheathing at the base and parallel-veined. In the chlorophyllous taxa they are linear and sometimes long and grass-like, and generally concentrated mainly on the basal part of the stem; in the achlorophyllous taxa they are small and scale-like. Vessels are present in the roots, at least in many Burmanniaceae, but otherwise may be completely lacking. Sometimes they are present in the stem, namely in autotrophic species of *Burmannia,* rarely also in the leaves, having then scalariform perforation plates. Laticifers and silica bodies are lacking; raphides are present, at least in some Thismiaceae; they are perhaps lacking in Burmanniaceae. The stomata are anomocytic.

The inflorescences are sometimes unifloral, with a terminal and regular or a pseudo-terminal and zygomorphic (Corsiaceae) flower; but in most Burmanniaceae they consist of one or more (often two) rhipidia, which are sometimes condensed in a head-like cluster; in Thismiaceae, it seems, the inflorescence is racemose.

The flowers are usually actinomorphic, rarely bilabiate and weakly to strongly, zygomorphic. They are half-epigynous to epigynous and trimerous, generally with two whorls of tepals which are more or less connate, sometimes into a campanulate, cylindrical or urceolate tube. The lobes of the two whorls may be equal or the outer either smaller or larger than the inner. The difference is often considerable and sometimes the inner lobes are totally absent. The perigone lobes are variously shaped and are sometimes filiform and jointed, and sometimes connate at the tips. In Corsiaceae one of the tepals is wide, while the others are narrow. The tepals are generally pale blue or white. There are no perigonal nectaries.

The stamens are 3+3 or 3 in number; in the latter case they are opposite the inner whorl of tepals. They are usually inserted in the perianth tube on very short filaments, but in Corsiaceae they are free from the perianth and inserted at the top of the ovary and have longer filaments. In Thismiaceae the filaments are connate in several genera. Anther attachment is varied and the connective is often broad, forked or appendiculate. The tapetum is probably glandular but in *Sciaphila* (Thismiaceae) it has been reported to be plasmodial (WIRTZ 1910). Microsporogenesis is successive. The pollen grains, which are free from each other, are either provided with one rounded aperture (i.e. they are ulcerate) or lack distinct apertures; two to three thin aperturoid areas may also be present; in Corsiaceae and in *Apteria* of Burmanniaceae they are, however, sulcate. They are dispersed in the two- or three-celled stage.

The ovary is trilocular or, more often, unilocular, with axile and parietal placentae respectively. The style is filiform or short and stout and is apically simple or tribrachiate. A variety of gynoecial nectaries, which may be classified as septal nectaries in a wide sense, but which in the unilocular forms are located on top of the ovary, are present in the order. The ovules are numerous, small, anatropous, bitegmic and tenuinucellate. A parietal cell is probably never cut off from the archesporial cell. Embryo sac formation follows the *Polygonum* Type or (in some *Burmannia* species) the *Allium* Type, and endosperm formation is helobial (a record of cellular endosperm needs to be verified). The small primary chalazal chamber becomes haustorial and 2-(-6)-nucleate (RAMASWAMY 1970), and the primary micropylar chamber becomes coenocytic and finally cellular (DAVIS 1966). The embryo is exceedingly small and undifferentiated; its growth may be arrested at the four-celled to ten-celled stage. The fruit is usually capsular and dehisces irregularly or by a transverse slit, rarely by valves. The seeds, which are numerous and diminutive, may be slightly twisted and have a sculptured testa.

Shortly before maturation the endosperm may still be rich in starch grains, but in the ripe seeds the endosperm lacks starch (HAMANN, personal communication).

Chemistry. Possibly, saponins are present judging from the haemolytic effect of root and stem extracts.

Distribution. Burmanniales are pantropical, distributed in both the Old and the New World. The smaller genera of Burmanniaceae are most richly represented in South America, the Thismiaceae are centred in Brazil and the Indonesian region, and Corsiaceae with its two genera occurs in Chile, eastern Australia and New Guinea. The saprophytic species grow among decaying leaves on the shady floor of tropical rain forests, etc., while the autotrophic species of *Burmannia* grow in damp fields, grassland and swampy coastal forests.

Relationships. The group is somewhat controversial with regard to its position and circumscription. The closest relatives are perhaps the Melanthiales, in which Campynemaceae takes an intermediate position between the orders. Burmanniaceae and Thismiaceae are undoubtedly closely related and are regarded by JONKER (1938) and others as one family, while Corsiaceae is more dubiously related to these families.

There is obviously much convergence in evolution of achlorophyllous plants (cf. the similarities between taxa of Geosiridaceae, Triuridaceae, Melanthiaceae-Petrosavieae, some Orchidaceae). The extrorse stamens may suggest relationships with Liliales. Until the embryology (e.g. endosperm formation), nectary conditions and other details of the Corsiaceae are clarified, the present position of this family can only be considered provisional.

The occasional occurrence of vessels, and the habit of the autotrophic members, in combination with epigyny and a tendency to produce numerous small seeds may suggest a common origin between Burmanniales and Orchidaceae and related families. However, these characteristics have probably evolved by convergence.

An alternative interpretation of the relations is that the Burmanniales are related to the Philydraceae. With this family they have in common the presence of vessels in stems and leaves (autotrophic species of Burmanniaceae are considered), occasional presence of oxalate raphides, helobial endosperm formation, starch-containing endosperm (however, in Burmanniales only in the unripe seeds), and the twisted seeds.

Key to the Families

1. Functional stamens 3; inflorescence cymose . . . . **Burmanniaceae**
1. Functional stamens usually 6; inflorescence racemose 2
2. Flowers actinomorphic; stamens attached to the perianth lobes; anthers introrse . . . . **Thismiaceae**
2. Flowers zygomorphic; stamens free from the perianth lobes; anthers extrorse . . . . **Corsiaceae**

Burmanniaceae Blume (1827) 9:100 (Figs. 102 and 103 A–F)

Autotrophic herbs, small or rarely up to 75 cm tall, with linear, dorsiventral, sometimes grass-like leaves *or* small, brownish or pale, saprophytic herbs with short bracteal leaves. Oxalate raphides are possibly lacking. Vessels with scalariform perforation plates are present in stems and leaves of some of the autotrophic taxa. The flowers are situated in cymose inflorescences, often in double-rhipidia, or few or solitary on the end of the stem.

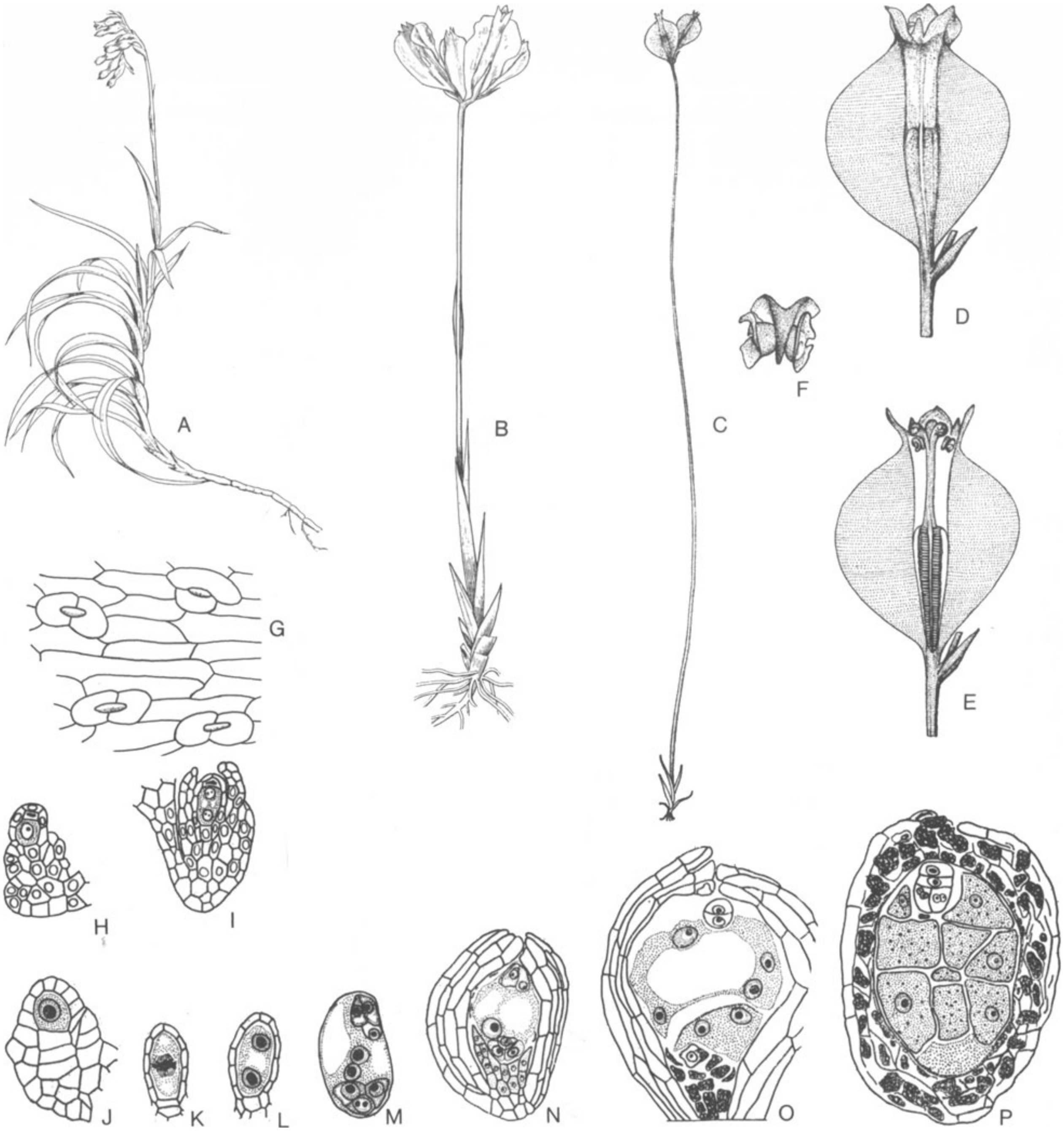
The perigone is generally actinomorphic, syntepalous and cylindrical, trigonous-obconical or funnel-shaped, with a straight or rarely curved tube, and often fairly short lobes. The inner perianth lobes in *Burmannia* are smaller than the outer or are totally absent; in the other genera there are six, usually subequal lobes. The flowers of *Burmannia* have three crests or prominent and often broad wings running from the base of the ovary right up to the perianth lobes.

There are only three stamens, and these are placed opposite the inner tepals (thereby differing from those in Iridaceae and Geosiridaceae, where the stamens alternate with the inner tepals). The filaments are short and inserted in the perianth tube. The anthers have a thick and broad, sometimes transversely considerably extended connective with laterally dehiscent thecae. The pollen grains are sulcate (*Apteria*), ulcerate or inaperturate.

The ovary is not totally inferior, but the perigone tube is situated on its upper part. The ovary in *Burmannia* and *Campylosiphon* is trilocular with axile placentation, but is otherwise unilocular with three parietal placentae, which may emerge centrally at the ovary base. Nectaries are of the septal type or situated on top of the ovary or dispersed on the sides of the ovary (RÜBSAMEN 1983). The style is apically divided into three distinct branches, each of which bears a stigmatic surface. The capsule dehisces irregularly or by three lateral slits. The seeds are small and mostly have the testa extended into a long wing at each end, as in many orchids, but differ from these in having endosperm.

Distribution. The family is widely distributed in the tropics and subtropics. Most of the small genera occur in South America, whereas *Burmannia* has its centre in Asia and Australia.

Burmannia (60) (Fig. 102) is mainly Asiatic-Indonesian-Australian, but has some species also in the Americas, where they range as far north as Carolina. It consists of both chlorophyllous plants



with relatively long, linear, often recurved leaves, and achlorophyllous saprophytes, sometimes only 2–6 cm tall. The perianth tube is straight, generally provided with three prominent wings (see above), and blue, white or yellow in colour. Among the green, chlorophyllous species may be mentioned *B. disticha,* from Ceylon to Eastern Australia, which may be up to 75 cm tall, *B. longifolia* in the Indomalesian region, *B. azurea,* from Burma to the Philippines, with sky-blue flowers, and *B.*

Fig. 102. Burmanniaceae. **A** *Burmannia longifolia,* habit. **B** *B. coelestis,* habit. (**A** and **B** from JONKER 1948). **C–F** *B. madagascariensis.* **C** Habit. **D** Flower. **E** Same, longitudinal section. **F** The sessile anther. (GEERINCK 1970). **G** *B. candida,* stomata. (SOLEREDER and MEYER 1930). **H–I** *B. candida,* ovule in different stages, **I** showing a binucleate embryo sac. (ERNST and BERNARD 1912). **J–P** *B. coelestis,* development of embryo sac (**J–N**), endosperm (**O**) and seed (**P**). Note the hypostase (**N**), the helobial endosperm formation (**O**), and the copious endosperm of the minute seed (**P**). (RAMASWAMY 1967)

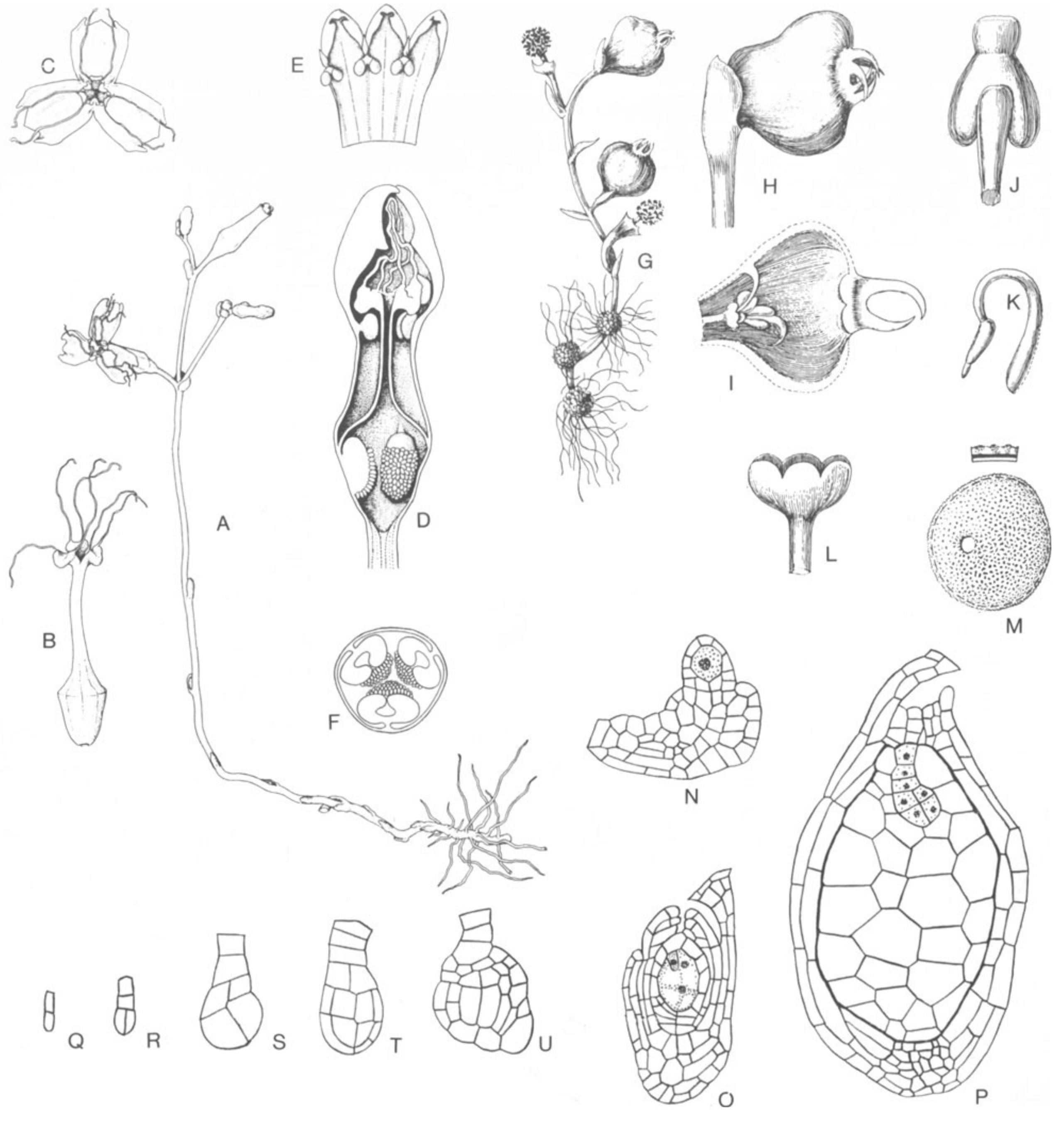


Fig. 103. Burmanniaceae (**A–F**) and Thismiaceae (**G–U**). **A–F** *Gymnosiphon longistylus.* **A** Plant. **B** Flower, lateral view. **C** Flower, front view. **D** Flower, longitudinal section. **E** Perianth with anthers attached between lobes. **F** Ovary, transverse section. (Mangenot and Deviller 1965). **G–L** *Afrothismia pachyantha.* **G** Plant. **H** Flower, lateral view. **I** Flower, longitudinal section (ovary not included). **J–K** Stamen in different views. **L** Style apex and stigma. (Hepper 1968). **M** *Afrothismia winkleri,* pollen grain. (Erdtman 1952). **N–U** *Thismia rodwayi,* embryological details. **N–O** Developing ovule. **P** Unripe seed with young embryo. **Q–U** Embryo development. (Campbell 1968)

flava, in Brazil, with yellow flowers. – *Campylosiphon* (1), in tropical South America, is an achlorophyllous herb, with a few-flowered paniculate inflorescence. The flowers have a curved, unwinged perigone tube, and a trilocular ovary.

A number of other small genera, most species of which occur in tropical America, have a unilocular ovary. These genera all lack chlorophyll. The largest of these is *Gymnosiphon* (30) (Fig. 103A–F), distributed in South America, Africa and Eastern Asia.

Thismiaceae J.G. Agardh (1858) 6:35 (Fig. 103G–P)

Achlorophyllous, often slightly succulent herbs with scale-like leaves and solitary or few flowers terminally (? or pseudo-terminally) on an erect stem or laterally, sometimes subsessile from near the base. The rhizome is sometimes branched and coral-like. Where there are several flowers, the inflorescence is a bracteate raceme. The flowers have an urceolate to campanulate, sometimes zygomorphic perianth tube which may be delimited upwards by a distinct margin or diaphragm. The perianth lobes, six in number, are equal or unequal. In the latter case the inner lobes are generally longer and narrower than the outer. Sometimes the inner perianth lobes are linear and geniculate (as in *Afrothismia*), sometimes linear, curved, swollen apically or fused with each other to form a "mitre" with holes or appendages, often forming quite bizarre configurations.

There are six or rarely three stamens. They are inserted in the perianth tube, often descending, and have an enlarged connective, which may contribute to the filling up of the entrance of the perianth tube. In *Sarcosiphon, Scaphiophora* and *Thismia* the stamens are fused with each other into a collar. The thecae are separate from each other, as in Burmanniaceae, but dehisce introrsely. The pollen grains, at least in some genera, are ulcerate. After flowering the perianth tube is shed from the ovary by a circumscissile slit.

The ovary is always unilocular, and has a mostly short, persistent style which is apically trilobate. There are three parietal placentae. The embryological conditions agree largely with those in Burmanniaceae. The capsule is thick-walled and generally opens apically.

Distribution. Thismiaceae is a disjunctive family occurring in South-east Asia, Africa, America (mainly Brazil), Australia and New Zealand.

Taxonomy. The genera are often very incompletely known, certain species having been collected only once or a few times, and the herbarium specimens are generally in unsatisfactory condition. There are certain problems as regards the recognition of the smaller genera. These are distinguished partly on the basis of the shape of the perianth lobes.

The largest genus, *Thismia* (25), is divisible into several sections distributed in South America (mainly Brazil) as well as Indomalesia, Australia and New Zealand, with one species in the USA. – Other bizarre genera are *Triscyphus* (1) in Brazil and *Geomitra* (1) on Borneo. – *Oxygyne* (1), in the Cameroons, unlike the other genera, has only three stamens, and so may be a link with Burmanniaceae, although this is dubious. – *Afrothismia* (2; Fig. 103G–M) occurs in Western Africa.

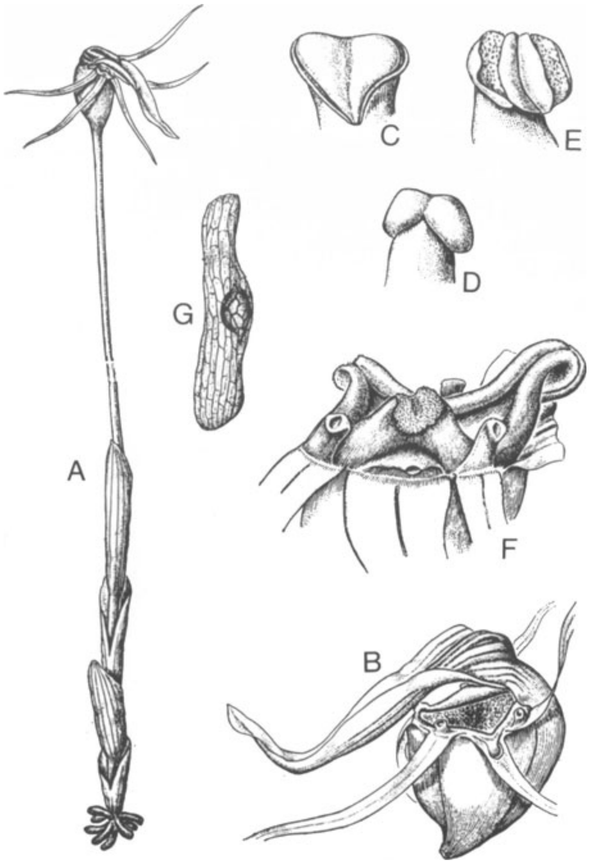


Fig. 104. Corsiaceae. *Arachnites uniflora.* **A** Plant. **B** Flower. **C–E** Anther in different views (it is extrorse). **F** Stylar region of female flower, fruit stage. **G** Seed. (Correa 1969)

Corsiaceae Beccari (1878) 2:9 (Fig. 104)

Rhizomatous saprophytes with scale-like leaves and solitary flowers on an erect stem. The flowers are epigynous, bisexual or unisexual, and strongly zygomorphic, one of the six perianth segments, the posterior of the outer whorl, being large and brightly coloured, while the other five are linear-filiform. There are six stamens with extrorse, longitudinally dehiscent anthers and short but distinct filaments, which are free from the perianth. The pollen grains are free, and sulcate, having a rather elliptic aperture.

The pistil is unilocular, with three far-intrusive, bifurcate placentae; the style is short, thick and apically trilobate. The fruit is a capsule opening by three vertical valves, and the seeds are numerous and very small, with the reticulate testa produced into a wing at each end.

Corsiaceae consists of *Corsia* (8) in New Guinea and eastern Australia, a genus with bisexual flowers and an elongate capsule, and *Arachnites* (1) in Chile, with unisexual flowers and a globose capsule. In *Corsia* the posterior tepal is erect and ovate and the other tepals are pendulous, whereas in *Arachnites* the posterior tepal is lanceolate and curved over the entrance of the perianth tube, while the others are spreading.

Order Liliales

Ten Families: Alstroemeriaceae, Colchicaceae, Uvulariaceae, Calochortaceae, Liliaceae, Geosiridaceae, Iridaceae, Apostasiaceae, Cypripediaceae and Orchidaceae.

Perennial herbs, rarely woody and with secondary thickening growth (some genera of Iridaceae). The roots are slender or in some Alstroemeriaceae and Orchidaceae inflated and nutrient-storing. The root hairs are developed from epidermal cells of the same size as other epidermal cells or sometimes (within Orchidaceae) from short-cells. A multiple velamen is present in the roots of many Orchidaceae and Cypripediaceae and, for example, in *Lilium* of Liliaceae, but is generally lacking in the other families of the order. The roots have vessels with scalariform or simple perforation plates. Mycorrhizas are widespread, and probably universal in Orchidaceae and related families, sometimes in combination with lack of chlorophyll.

The subterranean parts of the stem are developed as rhizomes or corms or take part in forming bulbs. The rhizomes vary in appearance especially in the mycorrhizal plants. Corms are widespread in Iridaceae and Colchicaceae; they are generally covered with fibrous or membranous tunics. Bulbs occur in Liliaceae, Calochortaceae and a few Iridaceae, and vary greatly in the number and shape of the bulb scales.

Most taxa have erect stems with cauline leaves, rosette plants with leafless scapes being rare outside Cypripediaceae and Orchidaceae. Herbaceous much-branched vines occur in Colchicaceae (e.g. *Gloriosa*), Alstroemeriaceae (*Bomarea*) and Orchidaceae (e.g. *Vanilla*). Succulent stems (pseudobulbs) and leaves are common in Orchidaceae but rare in other families. Vessels are present in the stems of Alstroemeriaceae, Uvulariaceae and of some Orchidaceae, where they have scalariform perforation plates, and of Apostasiaceae, where they may also have simple perforations, but they are only rarely present in the other families (e.g. *Sisyrinchium* of Iridaceae).

The leaves are distichous, spirally set, or rarely subopposite (some Orchidaceae) or verticillate (some Liliaceae). They are generally filiform, linear, lanceolate or ovate, and have a sheathing base. Sometimes the leaf lamina is constricted towards the base into a pseudo-petiole. Whereas the leaves are generally bifacial and flat or canaliculate, they are unifacial-ensiform in most Iridaceae and in certain orchids (several groups). In Alstroemeriaceae the leaf lamina is generally inverted. The veins are parallel or arching and apically converging; when the leaves are broad (as in *Tricyrtis, Disporum,* certain orchids) a minor reticulate venation may be present between the main veins. Vessels are normally lacking in the leaves (present only in some orchids and in *Sisyrinchium* of Iridaceae and then having scalariform perforation plates). The stomata are anomocytic except in Orchidaceae and Cypripediaceae, where the stomatal conditions are highly variable and partly characteristic for the subgroups (see further under Orchidaceae). Silica bodies are lacking except in a number of genera of Apostasiaceae, Cypripediaceae and Orchidaceae. Raphides are lacking in all families except Alstroemeriaceae, Apostasiaceae, Cypripediaceae and Orchidaceae, where they are abundant and in Uvulariaceae, where they occur very rarely (GOLDBLATT, personal communication). Unicellular or uniseriate hairs are scattered in the order. Laticifers are lacking.

The inflorescence is terminal or (e.g. in some Orchidaceae) lateral. It is generally not situated on a leafless scape from ground level, except in some Cypripediaceae and many Orchidaceae. It constitutes a raceme or a thyrse or is composed of one or more generally monochasial cymes. There is no articulation between the flower and its pedicel, nor is a typical "pericladium" developed.

The flowers are bisexual or rarely unisexual, trimerous, hypogynous or frequently epigynous, actinomorphic or weakly to (often) very strongly zygomorphic, and vary from minute to large and conspicuous. They are pollinated by various kinds of insects or rarely by birds.

As in Asparagales, the tepals are generally 3+3 in number and may or may not be equal in the two whorls. Unlike most Asparagales and many Melanthiales, the tepals generally have perigonal nectaries, although their function may be substituted by osmophores. An exception is Iridaceae subfamily Ixioideae, which has septal nectaries (see the discussion under Iridaceae). Nectariferous spurs or sacs are sometimes present at the base of one, three or more of the tepals. In Cypripediaceae and Orchidaceae, where the flowers are strongly zygomorphic and generally resupinated, the inner median tepal, then directed downwards, is generally developed as a more or less conspicuous *labellum,* which may be provided with a spur (see further under these families). The tepals vary from inconspicuous to very large and showy and in some taxa of nearly all families have variegated, checkered, drop-like, radially striate or transversely figured colour patterns, which are otherwise very rare in monocotyledons.

The stamens are 3+3, 3, 2 or 1 in number; when they are three in number they usually represent the outer whorl (Iridaceae, Geosiridaceae), when two they belong to the inner whorl (Cypripediaceae, Apostasiaceae pro parte) and when solitary the stamen belongs to the outer whorl (Orchidaceae). The filaments are generally narrow and without lateral appendages or apical lobes; they are more or less connate in some Iridaceae, in Calochortaceae and rarely in Colchicaceae (*Sandersonia*). In Apostasiaceae, Cypripediaceae and Orchidaceae, there are only one to three stamens, but sometimes rudimentary staminodes, and these are more or less intimately fused with the style into a gynostemium, the details of which are described under each family. The anthers are basifixed or (as in many Liliaceae) dorsifixed-epipeltate or the connective may form a tube around the tip of the filament, making the anthers falsely basifixed. The anthers are extrorse in most families, but introrse in others, e.g. in Apostasiaceae, Cypripediaceae and Orchidaceae. Anther dehiscence is longitudinal. The endothecial thickenings are of the Spiral Type or, in certain Orchidaceae, of the Girdle Type. The tapetum is secretory, and microsporogenesis is simultaneous in Iridaceae, Apostasiaceae, Cypripediaceae and Orchidaceae but successive in other families investigated.

The pollen grains are dispersed separately or, in most Orchidaceae, in tetrads which in addition cohere in so-called massulae or in pollinia (which comprise all the pollen tetrads of each microsporangium or of each theca). The different specializations and mechanisms connected with pollen transfer in Orchidaceae are described under this family. The pollen grains are sulcate in most families, but in the majority of the Orchidaceae the exine is thin and the pollen grains thus have no distinct aperture. Bisulculate, ulcerate, foraminate and spiraperturate pollen grains are restricted to isolated genera or species. The pollen grains are dispersed in the two-celled stage.

The pistil is tricarpellary and trilocular in most families but unilocular in nearly all Orchidaceae and some Cypripediaceae and Alstroemeriaceae. The carpel apices sometimes extend into separate stylodia, as in most Colchicaceae, but are generally fused at least basally (STERLING 1975, 1977), forming one style which is often tribrachiate or trilobate at the apex (the complicated structures in Orchidaceae are described separately). The stigmatic surface is Dry in Iridaceae, Calochortaceae and part of Colchicaceae and Liliaceae, Wet in all Orchidaceae studied and in Alstroemeriaceae, Trilliaceae and some Colchicaceae and Liliaceae. Placentation is axile in the taxa with trilocular ovaries and parietal in those with unilocular ovaries. The ovules are generally numerous and in Apostasiaceae, Cypripediaceae, Orchidaceae and Geosiridaceae extremely numerous. They are nearly always anatropous (weakly campylotropous in some Colchicaceae) and bitegmic; they are crassinucellate (Iridaceae), weakly crassinucellate or often tenuinucellate (Apostasiaceae, Cypripediaceae, Orchidaceae, etc.). A parietal cell (and parietal tissue) is developed only in the Iridaceae. Embryo sac formation generally conforms to the *Polygonum* Type or, in Liliaceae, to the *Fritillaria* Type, and in Cypripediaceae and a few Orchidaceae, to the *Allium* Type. Endosperm formation is constantly of the Nuclear Type, but a conspicuous feature in Cypripediaceae and Orchidaceae (and presumably also in the Apostasiaceae) is that endosperm formation is arrested in the very earliest stage and often does not take place at all; fusion of polar nuclei (or the central nucleus) with one sperm nucleus may not take place or, if it does, the primary endosperm nucleus may not divide or may divide only twice (in *Vanilla* up to four times). Embryogeny is of the Asterad or Onagrad Type.

The fruits in nearly all Liliales are loculicidal or septicidal capsules, or the rupture is between six ribs, as in many Orchidaceae, for example. Berries occur in some Alstroemeriaceae, in one or two genera referred here to Uvulariaceae (*Disporum, Clintonia*) and in a few orchids. Loculicidal capsules predominate in the Iridaceae, Liliaceae and Alstroemeriaceae, septicidal ones in Calochortaceae and Uvulariaceae and in most Colchicaceae.

The seeds are disc-shaped, angular, ellipsoidal or elongate, and often (in particular in Orchidaceae) have wings or flattened processes at both ends. In Orchidaceae and related families the seeds are diminutive and occur in enormous number (see under those families). Aril-like structures occur in some Iridaceae (*Iris* sect. *Regelia, Pseudoregelia* and *Oncocyclus*) and caruncles are found in certain other groups, developed from the chalazal region or from the raphe or hilum (*Erythronium, Gagea, Uvularia, Colchicum, Hermodactylus, Patersonia*). The testal layers of the seed coat in the unripe seeds often temporarily store starch, which has disappeared in the ripe seeds. The testal layers of the seed coat are always retained and sometimes form a sarcotesta, and the epidermis is never encrusted with phytomelan (though black in *Dietes* of Iridaceae and *Vanilla* of Orchidaceae); its inner epidermis is sometimes developed as a lipid layer. Also the tegmen is generally retained as a cell layer, and is not as completely collapsed as in Asparagales. The endosperm where it occurs (i.e. in all taxa except Apostasiaceae, Cypripediaceae and Orchidaceae) consists of cells with thick or thin pitted walls; the cells store aleurone and lipids. Starch grains are normally lacking, though rarely present in small amounts. The embryo is generally straight and rather well developed (about two thirds of the endosperm length or more) though sometimes short. It is curved in some scattered genera.

Chemistry. In chemical characters the Liliales are characterized by the rather uneven occurrence of steroidal saponins except, at least, in the alkaloid-bearing Colchicaceae. Whereas raphides are absent from several families (see above), calcium oxalate is often present in Iridaceae as long prismatic bodies. Chelidonic acid is common in taxa of Colchicaceae and is known in some taxa of Iridaceae and Alstroemeriaceae. Specific alkaloids, totally different from those found in Amaryllidaceae, occur in most or all Colchicaceae, Calochortaceae and a few genera of Liliaceae and Iridaceae, and are largely different in these groups. Alkaloids are probably absent in Alstroemeriaceae, Iridaceae, most Liliaceae and Uvulariaceae. In the Colchicaceae, one molecule of phenylalanine and one of tyrosine unite to form a series of compounds including colchicine and androcymbine. *Fritillaria* of the Liliaceae and some genera of Iridaceae have alkaloids of similar structure. C-glycoflavones are common in Orchidaceae, where also a number of other flavonoids occur, although Liliales are otherwise rather poor in flavonoids.

Distribution. Liliales has a world-wide distribution. The largest family, Orchidaceae is also subcosmopolitan, having a tropical concentration, whereas the Apostasiaceae are found in Indomalaysia and tropical Australia and the Cypripediaceae over a great part of the Northern Hemisphere and also in South America. Iridaceae, the next largest family, has a southern distribution with a chief centre in Southern Africa. This is also largely the case with Colchicaceae, while Alstroemeriaceae is South American. Geosiridaceae is known from Madagascar. The other families have a Northern Hemisphere distribution, Liliaceae with its main centre in western to central Asia and Calochortaceae in the western U.S.A.

Relationships, Taxonomy. The Liliales have here been circumscribed largely as by HUBER (1969) with the addition of what is generally known as Orchidales (Apostasiaceae, Cypripediaceae, Orchidaceae), which we may call the orchid families. These have been included here on the basis, firstly, of the reasons presented on p. 95, which indicate that these families arose out of early lilialean ancestors with some features in common with each of Alstroemeriaceae and Uvulariaceae, and thus that the Liliales would become a paraphyletic group without them. We are convinced, however, that the former Orchidales comprise a monophyletic group.

Minor problems remain as regards the delimitation of Liliales. Thus at least Philesiaceae, here placed in Asparagales, might be better placed in Liliales near Alstromemeriaceae, as in DAHLGREN and RASMUSSEN (1983), and *Medeola,* here placed in Liliaceae, shows some resemblance to *Scoliopus* of Trilliaceae (Dioscoreales). These examples illustrate that more research is needed before the taxonomy can be stabilized.

Burmanniales, which was formerly associated with Orchidaceae in the wide sense, has been considered by us to be rather distantly related to it (see further on p. 95 and under Burmanniales), the similarities like epigyny, small seeds and frequent lack of chlorophyll being presumably conditions that have evolved independently in the two groups. A third, presumably independent, group with these attributes is the Geosiridaceae, which shares most features with Iridaceae.

Within the Liliales the Alstroemeriaceae, and the three families Apostasiaceae, Cypripediaceae and Orchidaceae, form a couple of possibly related groups. Uvulariaceae, Calochortaceae and Liliaceae, which also approach the few rhizomatous Colchicaceae, form another group, Iridaceae and Geosiridaceae approaching, to some extent, Uvulariaceae and Colchicaceae.

The Alstroemeriaceae and the orchid families often have vessels in the stems, they contain raphides, the flowers are epigynous, the anthers are introrse and the ovules lack parietal tissue. The Alstroemeriaceae are, however, not clearly related to the orchid families; some similarities may depend on convergence. The orchid families are advanced in further characteristics, such as stronger zygomorphy, loss of some stamens, development of a labellum, simultaneous microsporogenesis, reduction of endosperm or total loss of endosperm formation. Their enormous number of small seeds and specialized pollen-clump pollination in combination with mycorrhizal life have obviously been very favourable, partly in combination with epiphytic life, and Orchidaceae is now one of the two largest families of flowering plants (the other is Asteraceae).

Some families of terrestrial plants, mainly of the Northern Hemisphere, that lack raphides and have rather large and showy tepals, weakly crassinucellate or tenuinucellate ovules without parietal tissue form one familial group. Here belong Liliaceae and Calochortaceae, both with bulbs, and the former with *Fritillaria* Type embryo sac formation, and Uvulariaceae, with rhizomes. A few genera which have tended to be placed in other families, *Disporum, Clintonia* and *Kreysigia,* are here placed in Uvulariaceae. Colchicaceae, with corms and usually with typical kinds of alkaloids, approach the Uvulariaceae. The seeds are more or less distinctive in shape: flat and platelike, or transversely or longitudinally prolonged, and often with the outer epidermis colourless or with a water-soluble yellow pigment. The cotyledon is not coleoptile-like. The stigmatic surface is Dry or Wet. Alkaloids of various kinds, mainly from steroidal precursors, are sporadically present.

Finally, Iridaceae and Geosiridaceae may form another group approaching the Colchicaceae. These seem to form a stock that consists mainly of corm geophytes with a strong concentration in the Southern Hemisphere. Their seeds are mostly isodiametric, and neither flat nor provided with wings or appendages. The outer epidermis of the seed coat has straight radial walls. The inner integument retains its cellular character and generally contains the brownish pigment phlobaphene. In addition, embryo sac formation conforms to the *Polygonum* Type, the cotyledon often has a coleoptile-like appearance, the stigmatic surface is mostly Dry and oxalate raphides are lacking. Styloids are often present in Iridaceae. Alkaloids when present are of the colchicine type (see above).

Key to the Families

1\. Flowers hypogynous 2
1\. Flowers epigynous 6
2\. Plants bulbous 3
2\. Plants with rhizomes or corms 4
3\. Fruit septicidal (*Polygonum* Type embryo sac formation) . . . . . **Calochortaceae**
3\. Fruit loculicidal (*Fritillaria* Type embryo sac formation) . . . . **Liliaceae**
4\. Plants rhizomatous 5
4\. Plants with a corm . . . . **Colchicaceae**
5\. Leaves bifacial (dorsiventral) . . . . **Uvulariaceae**
5\. Leaves unifacial-ensiform . . **Iridaceae:***Isophysis*

6. Stamens 1 or 2, very rarely 3, filaments fused with the style into a gynostemium 7
6. Stamens 3 or 6, filaments not fused with the style 9
7. Anthers 2 or 3 8
7. Anther solitary . . . . **Orchidaceae**
8. Labellum large, sac-shaped . . . **Cypripediaceae**
8. Labellum not conspicuously different from the other tepals . . . **Apostasiaceae**
9. Stamens 6 . . . . **Alstroemeriaceae**
9. Stamens 3 10
10. Chlorophyllous plants generally with ensiform leaves . . . . **Iridaceae**
10. Achlorophyllous plants with scale-like leaves . . . . **Geosiridaceae**

Alstroemeriaceae Dumortier (1829) 4:160 (Fig. 105)

Erect or twining herbs with sympodial rhizomes. Certain of the roots are fusiform and modified to store nutrients and water. The roots have vessels with scalariform and sometimes simple perforation plates, and the stems have vessels with scalariform perforation plates. The stems of the vines may be up to 4 m long or more. The leaves are scattered on the stems and are linear to lanceolate, narrowing at the base and not sheathing. They are generally twisted at the base so that their morphologically lower side is turned upwards. The leaves are glabrous or in some species of *Bomarea* provided with unbranched simple hairs on the lower (morphologically upper) surface. Oxalate raphides are known in *Alstroemeria.*

The branches end in inflorescences which consist of helicoid cymes and are generally umbel-like; they are rarely unifloral. The flowers, which are generally subtended by relatively large, green and leaf-like bracts, are trimerous, epigynous, bisexual and actinomorphic or slightly zygomorphic. The mostly free tepals vary from nearly similar to conspicuously different in the two whorls, the outer being often shorter, of different colour and less variegated than the inner, which often bear a dotted or striate-dotted colour pattern. Their colour varies from orange to rose-coloured, purple or green. Nectaries are present near the base of two or all of the inner tepals. The ovary on the surface shows distinct decurrent borders of the outer tepals; likewise a circular "scar" around the top of the fruit is left after the shedding of the perigone.

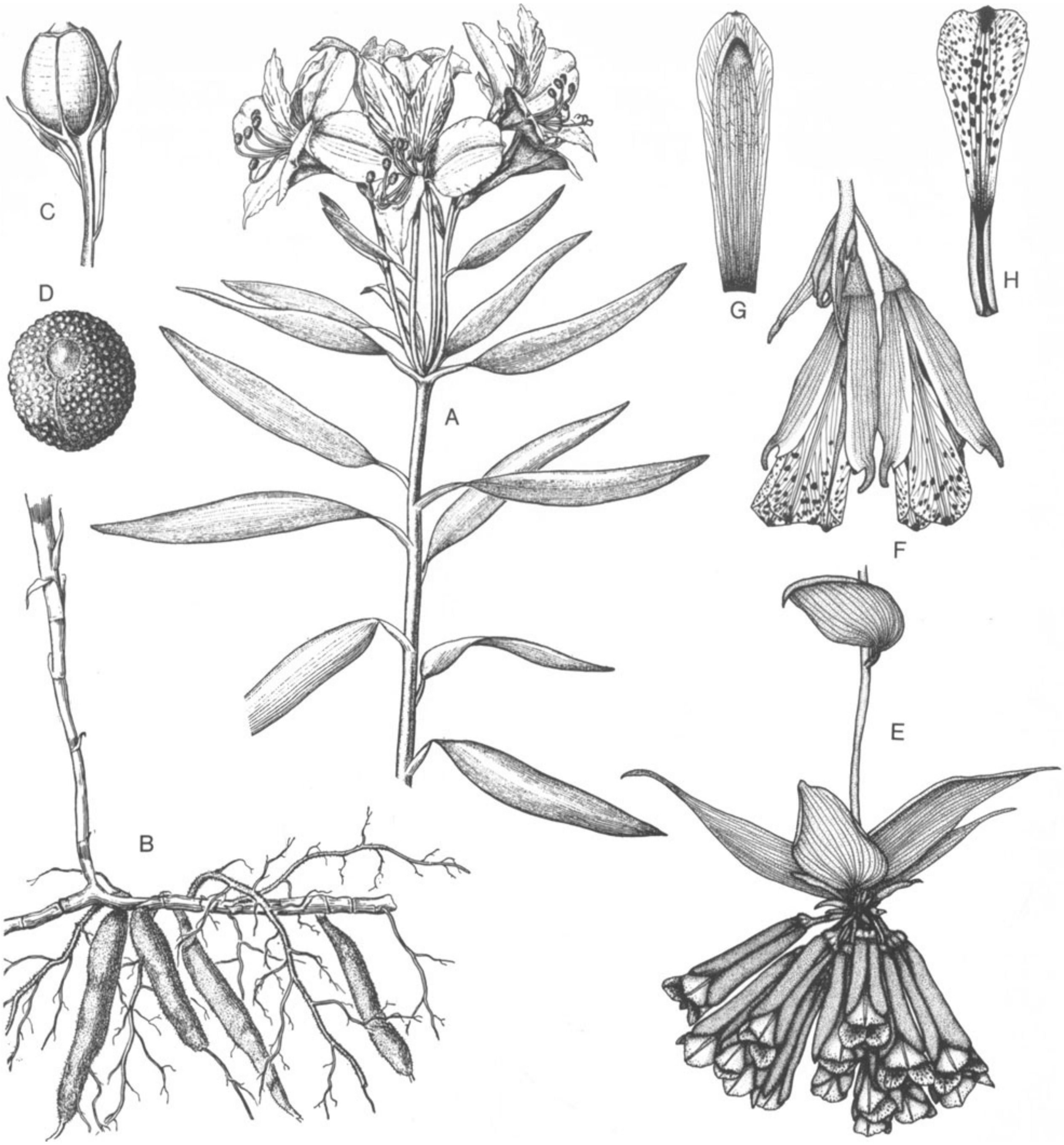
There are 3+3 stamens which have narrow filaments and elongate pseudo-basifixed anthers. Dehiscence is introrse and longitudinal. Microsporogenesis is successive. The pollen grains are large and sulcate, usually plano-convex with the sulcus on the convex part of the grain. The pistil is trilocular or rarely unilocular and has a single style with three apical stigmatic branches, the stigmatic surface of which (at least in *Alstroemeria*) is of the Wet Type. Daumann (1970) reported septal nectaries for *Alstroemeria,* but this needs verification. The ovary contains numerous anatropous ovules on axile (*Alstroemeria, Bomarea*) or parietal (*Leontochir, Schickendantzia*) placentae. No parietal cell is cut off from the archesporial cell. Embryo sac formation conforms to the *Polygonum* Type.

The fruit is a capsule which is generally loculicidal; occasionally it is indehiscent or opens explosively. The seeds are globose or rounded-ellipsoidal. The outer integument of the seed coat in *Alstroemeria* is dry and consists of few to eight cell layers, but in *Bomarea* it is thick and multi-layered and forms a veritable sarcotesta with sparse starch grains. Cell differentiation in the outer integument is weak; the cells are colourless or contain a yellow pigment, and there are sparse subepidermal "bladder cells" in *Alstroemeria* containing oxalate raphides. The inner integument collapses into a thin membrane, while the endosperm cells have thick pitted walls and contain aleurone and fatty oils but no starch. The cylindrical embryo is about two thirds the length of the endosperm. When germinating, the seedling does not have a coleoptile-like cotyledon. The basic chromosome number is $x=8$ (*Alstroemeria*) or $x=9$ (*Bomarea*).

Chemistry. In chemical respects the family is characterized by its probable production of steroidal saponins, and its production of chelidonic acid, while alkaloids are lacking. The storage roots contain starch. In some of these respects Alstroemeriaceae is not very characteristic of the order. Alstroemeriaceae share with Liliaceae the occurrence of tuliposides (Slob et al. 1975).

Distribution. Alstroemeriaceae is restricted to South and Central America and has its centre in Andean South America.

Alstroemeria (60) consists of erect herbs of variable size, usually with relatively large, yellow, orange or reddish flowers which are often more or less zygomorphic, generally with striated inner tepals (especially the upper two) and upcurved filaments. The leaf blades are inverted. *A. aurantiaca,* "Peruvian Lily", and other species, mainly from Chile, are frequently grown as ornamentals. Several hybrids and breeding products have been pro-



duced. *A*. *pulchella* in Brazil reaches a height of 90 cm and has striking red-and-green flowers.

Bomarea (100) species are mostly vines with actinomorphic, frequently more or less tubular flowers having straight filaments. The outer tepals are generally much smaller than the inner, sometimes appearing sepaloid although not being green. The perigone is often salmon-red, and is sometimes green on the apical parts; the inner side of the

Fig. 105. Alstroemeriaceae. **A–D** *Alstroemeria aurantiaca*. **A** Upper part of flowering plant. **B** Rhizome with swollen roots. **C** Capsule. **D** Seed. (Correa 1969). **E–H** *Bomarea pardina*. **E** Pendulous inflorescence. **F** Two flowers. **G** Tepal of outer whorl. **H** Tepal of inner whorl. (Neuendorf 1977)

inner tepals generally has a variegated or spotted pattern. The inflorescence in some species, such as *B. cordei,* has long-pedicelled flowers. The storage roots of some species are edible and taste slightly similar to "Jerusalem Artichoke" (*Helianthus tuberosus*). Some species are grown as ornamentals, e.g. the orange-flowered *B. caldasii* from Ecuador.

While these two genera have flowers with a trilocular ovary, two small genera, *Leontochir* (1) in Chile and *Schickedantzia* (1), in Andean Argentina, have unilocular ovaries with parietal placentae. The former is a vine, the latter a small, erect herb.

Alstroemeriaceae has sometimes been included in Amaryllidaceae because of its epigynous, hexastaminate flowers in an umbel-like inflorescence, but is only distantly related to that family.

The possession of oxalate raphides and, most probably, of steroidal saponins and of the rhizomatous underground parts provide differences from the Liliaceae, Uvulariaceae and Calochortaceae, but most evidence points to a close alliance with these families and the orchids. The presence of septal nectaries in Alstroemeriaceae may represent a relic property.

Another possible affinity should be mentioned, namely with the Philesiaceae, where such characters as the climbing habit, twisted leaf blades, differentiation of the perigonal whorls, variegated tepal colour, perigonal nectaries and phytomelan-free seeds are found. Whether most or all of these result from convergent evolution is still uncertain.

Colchicaceae A. P. de Candolle in Lamarck & de Candolle (1805) 17:170 (Figs. 106–107)

Low or tall, erect or sometimes twining herbs, with a subterranean, starch-rich corm. In some genera (*Gloriosa, Littonia, Sandersonia*) the corm is stoloniferous. Such stolons or runners may form apical tuberculate corms from which buds are developed. Vessels are present in the fibrous roots only and have scalariform perforation plates.

The leaves may be few and basally concentrated, several on a short leafy stem, or numerous and scattered on a long, erect or climbing, sometimes branched, stem. They are dorsiventral, mostly linear or lanceolate, sessile, or rarely constricted into a pseudopetiole, sheathing at the base, parallel-veined and, rarely, cirrhose, ending in a tendril (as in *Gloriosa*). In those species of *Colchicum* which flower in autumn the leaves are developed after the flowers. Raphides are lacking.

The aerial stem is herbaceous and usually stiff and erect, sometimes climbing, ending in racemes (or monochasial systems) or rarely in a single flower.

The flowers are trimerous, actinomorphic, hypogynous and generally bisexual. The 3 + 3 tepals are more or less similar in size and shape: they are free from each other or basally connate, in *Colchicum* forming a long narrow basal tube. They vary much in size and are basally provided with nectaries. (*Colchicum* and *Androcymbium* lack perigonal, but have androecial, nectaries.) Tepal colour varies from white to purple, red or yellow, and sometimes it is variegated (as in species of *Colchicum*) or, more often, two-coloured, the base with a different colour from the rest.

The stamens are free from each other and have narrow or basally broad, glabrous filaments and mostly short, ovate, longitudinally dehiscent anthers; these are usually extrorse, but rarely latrorse or nearly introrse. Microsporogenesis is successive. The pollen grains are generally sulcate, but 2-, 3- or 4-foraminate and spiraperturate pollen grains occur in species of *Colchium* and *Androcymbium* (RADULESCU 1973b).

The pistil is trilocular and either has three totally free stylodia or a style which is tribrachiate at least in its upper part (STERLING 1975, 1977). The stigma is Dry or Wet. Each locule contains several to many anatropous (to weakly campylotropous) ovules on axile placentae. A parietal cell is not cut off from the archesporial cell, but in some genera (at least some Iphigenieae) the epidermal cells of the nucellus divide periclinally to form two or more layers. Embryo sac formation conforms to the *Polygonum* Type. Nucellar embryony occurs at least in *Colchicum*.

The fruit is capsular and dehisces according to various modes, usually septicidally but in some genera loculicidally. The seeds are generally globose, but ovoid in *Onixotis*. Appendages arising from the chalazal region occur in *Colchicum*. The testal part of the seed coat consists of few to many cell layers, which in the unripe seed contain starch. The outer epidermis is retained or compressed (to collapsed) and often contains the red-brown pigment phlobaphene. The tegmen is variably compressed, with or without the pigment phlobaphene or other yellowish red pigments. The endosperm generally contains somewhat thick-walled, pitted cells with aleurone and fatty oils, but no starch. A straight, relatively short, elongate or rarely subglobose embryo is enclosed in the endosperm. An important feature of this family, like Iridaceae,

Fig. 106. Colchicaceae. **A–G** *Androcymbium striatum.* **A** Flowering plant. **B** Flower. **C** Tepal and attached stamen. **D** Pistil. **E** Carpel, longitudinal section. **F** Fruit, wall partly removed to show seeds. **G** Seed. (Krause 1930). **H–K** *Ornithoglossum parviflorum.* **H** Habit. **I** Flower. **J** Tepal. **K** Stamen. (Nordenstam 1982). **L–P** *Iphigenia oliveri.* **L** Habit. **M** Flower. **N** Pistil, wall partly removed to show placentation. **O** Capsule. **P** Seed. (Krause 1930)

is that the seedling has a conspicuously coleoptile-like cotyledon. $x = 5, 7, 10, 11$ or 12 (in Colchiceae 7, 8, 9, 10, 11, 12, 19), 11 being perhaps the basic number.

Chemistry. The family is characterized by the absence of steroidal saponins and oxalate raphides. Chelidonic acid and alkaloid bases are present in most or all genera. The alkaloids represent colchicine and related compounds (Wildman and Pursey 1968) and are extremely poisonous (see further under the ordinal description). Starch is accumulated in the vegetative parts, e.g. in the corms.

Distribution. Colchicaceae has a pronounced centre in the summer rainfall regions of South Africa, but ranges through Africa to the Mediterranean end of western Asia, where the largest genus, *Colchium* (incl. *Merendera* and *Bulbocodium*), has its main distribution area. A few genera occur in Asia and a few others are found in Australia. *Iphigenia* and *Wurmbea* (incl. *Anguillaria*) are disjunct, occurring in South Africa and Australia (*Iphigenia* also in Tropical Asia and New Zealand).

The following division of Colchicaceae largely follows Nordenstam (1982).

Tribus Anguillarieae

Tribus Anguillarieae consists of erect, non-climbing herbs with a bulb-like corm and with sessile flowers in spicate bractless inflorescences. The flowers are generally small or medium-sized with white, brownish, purplish or violet tepals. The tepals are free or connate and the anthers extrorse

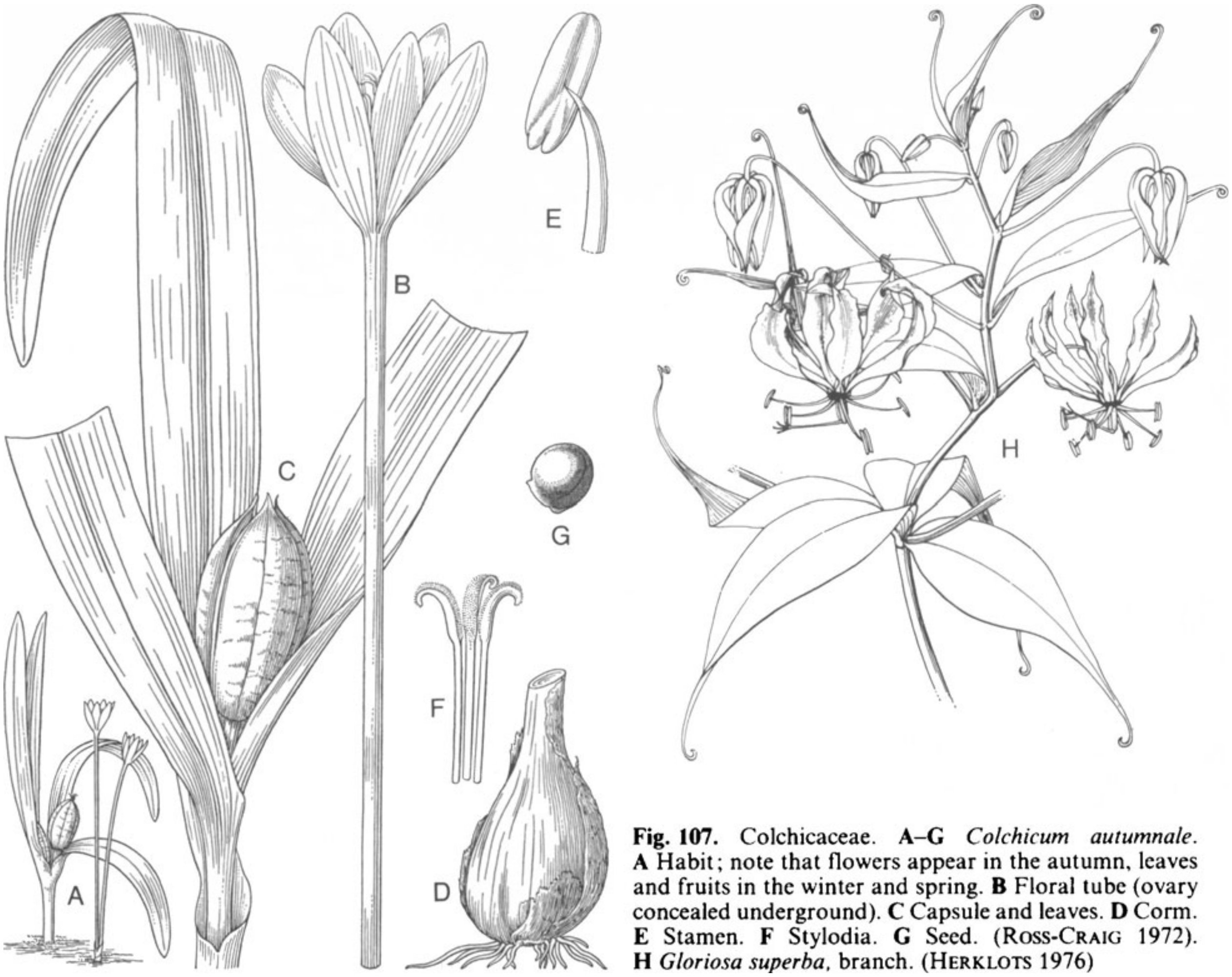


Fig. 107. Colchicaceae. **A–G** *Colchicum autumnale*. **A** Habit; note that flowers appear in the autumn, leaves and fruits in the winter and spring. **B** Floral tube (ovary concealed underground). **C** Capsule and leaves. **D** Corm. **E** Stamen. **F** Stylodia. **G** Seed. (Ross-Craig 1972). **H** *Gloriosa superba*, branch. (Herklots 1976)

or latrorse. The pollen grains are sulcate. The pistil has three fairly long stylodial branches. The capsules are septicidal or "endocidal" (*Neodregea, Onixotis, Wurmbea* pro parte) or loculicidal (*Wurmbea* pro parte). This group is largely South African, but occurs also in Australia.

Wurmbea (incl. *Anguillaria;* ca. 35) is a South African-Australian genus of hyacinthaceous habit with white, yellow, pink or more or less purple or brown-patterned, basally connate tepals (see MacFarlane 1980). – *Onixotis* (*Dipidax*) (ca. 4), has white or rose-coloured to purple-violet flowers; *O. triquetra,* a decorative meadow species, is sometimes grown as an ornamental.

Related to Anguillarieae is the genus *Baeometra* (1), in the Cape Province of South Africa, with a bracteate spike and with tepals tapering at the base and coloured yellow inside and red outside.

Tribus Iphigenieae

This consists of erect herbs, which either have a short aerial stem and basally concentrated leaves or an erect or twining stem on which the leaves are dispersed. The leaves are sometimes pointed or cirrhose. The underground part consists of a bulb-like corm, from which runners may be formed. The inflorescence is a bracteate raceme, and the bracts may be foliose (as in *Sandersonia, Littonia* and *Gloriosa*). The flowers vary from medium-sized to rather large and conspicuous, and have free, or more rarely fused tepals, which vary in colour from white to bright red, yellow or dark-violet or almost black. The style or stylodia are often abruptly bent at right angles to the ovarian axis. *Iphigenia* (6) (Fig. 106L–P) ranging from South Africa through India to Australia and New Zealand, comprises erect, non-climbing herbs with loculicidal capsules. The Southern African genera

Ornithoglossum (8) (Fig. 106H–K) (NORDENSTAM 1982) and *Hexacyrtis* (1) (WILLIAMSON 1983) are similar.

Gloriosa (6) (Fig. 107H) has a wide range from South Africa through Ethiopia to eastern Asia. It is a vine with branches up to 150 cm long, pendent flowers, yellow to bright or dark red or often bicoloured tepals and a style bent basally almost at right angles. *G. superba* and *G. rothschildiana* are frequently cultivated ornamentals. The corms are rich in colchicine and very poisonous. – Two other genera, *Littonia* (8) and *Sandersonia* (1), both African, belong to this tribe. They are twining or erect herbs and may have cirrhose leaves. In *Sandersonia* the tepals are fused to form a campanulate perigone.

Tribus Colchiceae

Tribus Colchiceae consists of two genera, *Androcymbium* and *Colchicum,* the latter of which is sometimes divided into several genera. The subterranean parts are tunicated bulb-like corms, and the flowers, which are solitary or few, are situated on a very short stem (actually axillary in a few-flowered spike), basally in the centre of the shoot; they are frequently developed before the green leaves and have long-clawed tepals, the claws being free or fused into a long tube. The anthers are latrorse. The pollen grains are variable: usually 2–4-foraminate, sometimes spiraperturate. There are three stylodia which are free or fused basally into a style. The pistil develops into a septicidal capsule. – *Colchicum* (incl. *Merendera, Synsiphon* and *Bulbocodium;* 65) (Fig. 107A–G) is centred in the Mediterranean Region and western Asia. It includes a number of chiefly autumn-flowering species, many superficially resembling species of *Crocus* (Iridaceae). The ovary is concealed above the corm in the underground part of the perigone, growing above ground at maturity. Many species are grown as ornamentals, including *C. autumnale, C. alpinum, C. cilicicum* and *C. speciosum.* The corms and seeds are rich in the toxic alkaloid colchicine, which is used in medicine. It is also used in plant breeding to induce polyploidy. The most frequently grown species for these purposes is *C. autumnale*. In the species sometimes treated as *Merendera* and *Bulbocodium,* the tepal claws are not fused as in the other species of *Colchicum.* – *Androcymbium* (40) (Fig. 106A–G), which ranges from South Africa to the Mediterranean, has densely clustered flowers enveloped by bracteal leaves.

Uvulariaceae C.S. Kunth (1843) 8:ca. 40 (Fig. 108)

Erect, medium-sized herbs up to ca. 1.5 m, with creeping rhizomes, and an erect aerial stem with few to numerous, well-developed lanceolate to ovate leaves scattered on the stem, the lower often not larger than those on the upper parts of the branches. Cataphylls are often present at the base of the aerial stem. The leaves are generally sessile (rarely shortly pseudopetiolate) acute to acuminate, basally cuneate, truncate, cordate or rarely amplexicaul, glabrous or hairy and with arching, converging main veins, and in some cases (*Tricyrtis,* some species of *Disporum*) with clearly reticulate venation between the main veins (Fig. 108C, K). Vessels with scalariform perforation plates, at least in *Tricyrtis* but perhaps in all genera, are present in the stems as well as in the roots. Raphides are usually lacking, but have been observed in *Disporum* and *Streptopus* associated with crystal sand (GOLDBLATT and HENRICH, personal communication).

The inflorescence is a generally few-flowered and sparse panicle (or thyrse), with cymose components (Fig. 108J) or a spike with solitary or paired axillary flowers. Green foliose leaves are generally present in the inflorescence. Recaulescence phenomena are often present in the inflorescence region.

The flowers are fairly small to medium-sized or rather conspicuous (*Tricyrtis*), bisexual, actinomorphic, hypogynous, and trimerous. They are white, pale yellow or more or less purple-spotted (*Tricyrtis*). The outer or all tepals often have a basal, nectariferous, swelling or sac, which may be globose and shiny, as in *Tricyrtis,* or a spur (in some species of *Disporum,* s.lat., Fig. 108G). The tepals are often suberect to slightly spreading, pointed and in some genera narrow and tapering. The stamens are 3+3 in number and have erect glabrous filaments, which are narrow, erect and sometimes connate basally, the anthers are dorsifixed-hypopeltate and extrorse and dehisce longitudinally. The pollen grains are sulcate and dispersed in the two-celled state.

The ovary is globose to ovoid, tricarpellary and trilocular, and has a tribrachiate style (STERLING 1977). There is great variation, even within the genus *Disporum* s.lat., in the relative length of the style: in some taxa the stylodial branches are free almost from the base, in others there is a style with three rather short apical lobes (Fig. 108D, E); sometimes the stylodial branches are spreading

Fig. 108. Uvulariaceae. **A–D** *Disporum* (*Prosartes*) *lanuginosa*. **A** Flowering branch. **B** Rhizome. **C** Leaf; note the reticulate venation. **D** Flower, 3 tepals and 3 stamens removed. **E–F** *Disporum* (s.str.) *smilacinum*. **E** Flower, 3 tepals and 3 stamens removed. **F** Tepal. **G–L** *Disporum* (s.str.) *calcaratum*. **G** Flower, 3 tepals and 3 stamens; note the extrorse anthers. **H** Tepal of outer whorl, with long nectariferous spur. **I** Stamen. **J–O** *Tricyrtis latifolia*. **J** Flowering branch; note the monochasial branches of the inflorescence. **K** Leaf, showing the reticulate venation. **L–M** Flower from one side and from above. **N** Tepal of outer whorl and the opposite stamen. **O** Capsule. **P** *Tricyrtis* sp., seed. (All orig. B. JOHNSEN)

and bifurcate (Fig. 108 M). The stigmatic surface is of the Wet (*Tricyrtis*) or the Dry (*Clintonia*) Type. The ovules are anatropous and weakly crassinucellate (nucellus of "*Scoliopus* Type"; BJÖRNSTAD 1970); no parietal cell is developed. Embryo sac formation is of the *Polygonum* (or rarely the *Clintonia*) Type (OGURA 1964). Endosperm formation is nuclear.

The fruit in *Tricyrtis, Kreysigia* and *Uvularia* is a globose to elongate cylindrical-triangular capsule which is septicidally or loculicidally dehiscent, in *Schelhammera* it is a somewhat fleshy capsule and in *Disporum* s.lat. and *Clintonia* it is a berry. The seeds are flat and disc-like (*Tricyrtis, Streptopus*) or generally globose (the other genera). The testal characters are probably variable; the endosperm consists of cells storing aleurone and fatty oils, and the embryo, at least in some cases, is rather small and little differentiated, for example only $^1/_5$–$^1/_{12}$ of the length of the endosperm in *Tricyrtis*. The basic chromosome numbers are, $x =$ 13 (*Tricyrtis*), 14 (*Uvularia, Schelhammera, Kreysigia*), and 16 (*Disporum* s.lat., *Streptopus*).

Distribution. The family as circumscribed here occurs mainly in the Northern Hemisphere, with *Tricyrtis* in eastern Asia, *Uvularia* in North America, and *Disporum* s.lat. (see below), *Clintonia* and *Streptopus* in both continents. Of the smaller genera, *Kreysigia* ranges from Malaysia to Eastern Australia, and *Schelhammera* from New Guinea to Australia.

It is very uncertain that Uvulariaceae with this circumscription is a homogeneous family but it should at least be more adequate than previous constellations. Further investigations into the correlation of morphological, embryological and chemical characters is needed. For instance, uncertainty as to the borderline between Uvulariaceae and Colchicaceae might possibly be cleared up by an investigation of alkaloids.

Tribus Tricyrtideae

Within the family, the genus *Tricyrtis* (11) stands out as quite distinct. It occurs in Eastern Asia, and is characterized by its purple spotted, variegated flowers, provided with globose nectariferous pouches on the outer tepals. The capsules are elongate and septicidal, and in each locule have numerous flat pale seeds, ovate to orbicular in outline, which are piled upon each other as in several genera of Liliaceae (e.g. *Lilium, Tulipa, Fritillaria*). The outer epidermis of the testa may contain lignin, whereas the inner is totally collapsed. – *T. stolonifera,* from Formosa, *T. hirta,* from Japan, and other species, some with a rather *Lilium*-like appearance, are frequently grown as ornamentals.

Tribus Uvularieae

The remaining genera generally have smaller and paler flowers, and the fruits, whether loculicidal capsules or berries, are more globose, and their seeds are globose rather than flat. The following three genera have baccate fruits.

Disporum (20) (Utech and Kawano 1976) occurs both in southern and eastern Asia and in North America. The American species are fairly similar to *Tricyrtis* in having leaves with reticulate venation and non-spurred tepals. The Asiatic species lack distinct reticulate venation, and the tepals often have distinct spurs, although they always have nectar grooves. The American species are probably quite distinct from the Asiatic and should be placed in a separate genus, *Prosartes* (Conover 1983), which has a greater similarity to *Tricyrtis* than has *Disporum* sensu stricto. – *Clintonia* (6) with a similar distribution, has the leaves more basally concentrated and the flowers are solitary or several together in umbel-like inflorescences. The leaves of *C. borealis* (Labrador to North Carolina) can be used as salad. There is some doubt as to whether this genus belongs here or in the Convallariaceae.

Streptopus (4) consists of *Polygonatum*-like herbs with the flowers situated solitarily or in pairs, on filiform pedicels, displaced by recaulescence. The seeds may contain starch.

Uvularia (5) has campanulate flowers with mutually free, mostly pale yellow perianth members and anthers with a prolonged connective. The genus is reminiscent of taxa of Stemonaceae-Trilliaceae, to which it may also be distantly related. *U. grandiflora* is grown as an ornamental, and the young shoots of *U. sessiliflora* are edible!

Schelhammera (3) in Eastern Australia and New Guinea and *Kreysigia* (1) in approximately the same regions, consist of small-sized plants.

Scoliopus and *Medeola,* often referred to Trilliaceae, have proved to be more or less out of place in that family (Berg 1962a, b), but they are also very different from each other. Either or both of these is perhaps best placed in Uvulariaceae.

Calochortaceae Dumortier (1829) 1:60 (Fig. 109)

Erect, often slender herbs with a tunicated bulb having two thick, nutrient-storing leaves and a membranous or fibrous-reticulate coat. The stem bears only a few leaves, or sometimes there is only one basal leaf apart from the inflorescence bracts. The leaves are flat, dorsiventral and usually linear; there is normally a single basal leaf which is much larger than the cauline leaves. Bulbils may be formed in the axils of the lower leaves. Crystal raphides are lacking, as in Liliaceae.

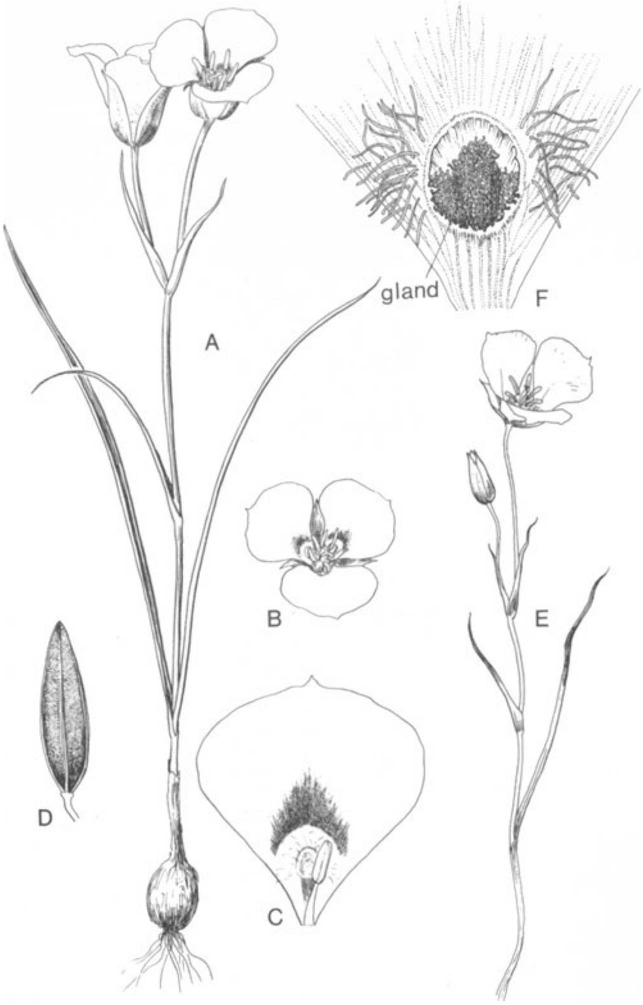


Fig. 109. Calochortaceae. **A–C** *Calochortus nuttallii.* **A** Plant. **B** Flower. **C** Tepal of inner whorl and opposite stamen. (Hitchcock et al. 1969). **D** *C. aureus,* fruit. **E–F** *C. excavatus.* **E** Plant. **F** Base of inner tepal. (**D–F** from Cronquist et al. 1977)

The inflorescence is a branched or unbranched raceme; the long-pedicelled flowers are situated in the axils of green, narrowly lanceolate or linear bracts, which are twisted into a position between the flower and the axis.

The flowers are hypogynous, trimerous, bisexual, and their tepals are free and conspicuously different in the two whorls. Those of the outer whorl are ovate or lanceolate, generally glabrous, and either green and sepaloid or of the same colour as the tepals of the inner whorl. The latter are generally broad, rounded or obtriangular to broadly obovate, petaloid, cuneate or clawed, frequently fringed or ciliate on the margins and sometimes pubescent or bearded on the inner face; their colour is usually yellow, rose or crimson, and they are frequently marked with conspicuous large or small spots, streaks or other patterns (nectar guides). Conspicuous nectary glands are present on the tepal bases, and are sometimes associated with a knee-like or spur-like pocket. The stamens, 3+3 in number, are free from each other and inserted at the bases of the tepals; their filaments are usually dilated, and their elongate anthers pseudo-basifixed, i.e. surrounding the tip of the filament with a tubular part of the connective (as in *Tulipa*). Anther dehiscence is by longitudinal slits. The pollen grains are sulcate and dispersed in the two-celled stage.

The ovary is tricarpellary and trilocular and the style very short or obsolete. The three stigmatic branches are situated directly on the apex of the ovary. Their surface is of the Dry Type. Each locule contains numerous anatropous ovules in two rows. As in the Liliaceae, the ovules lack a parietal cell, but embryo sac formation, unlike that of Liliaceae, follows the *Polygonum* Type. Endosperm formation is nuclear (Berg 1960). The capsules are linear to globose, three-angled or three-winged, and septicidal (as in *Tricyrtis*). Their seeds are lanceolate to circular and usually strongly flattened, although not as regularly horizontal as in most Liliaceae; in *C. macrocarpus* they are narrowly winged. In the seed coat, the outer integument consists of fairly intact cells and lacks pigments; its outer epidermis shows a hexagonally reticulate pattern (and is effectively water-absorbing). The inner integument is flattened but with the cells retained, and containing a lemon-yellow pigment. The endosperm cells contain fat and aleurone and the slender embryo is from about half to nearly as long as the endosperm. The chromosome number varies much, and $x = 7$–20.

Chemistry. Calochortus lacks oxalate raphides and chelidonic acid. The seeds of *C. macrocarpus,* at least, contain alkaloids.

Calochortus (60), "Mariposa Lily", is distributed over the temperate western parts of North America from British Columbia to Central America. The species grow in grassland, chaparral and semi-desert vegetation, less commonly in woodlands. Many species are highly decorative and are cultivated as ornamentals, e.g. *C. venustus.* The bulbs of many species were formerly eaten by the Indians because of their high starch content.

Calochortus seems to form a late evolutionary branch comparable to the Old World Liliaceae, which *Calochortus* resembles in important respects, e.g. the bulb, the leafy stem, the nectariferous tepals, the anther construction, the absence of a parietal tissue in the nucellus, the flat seeds, and the chemical contents. The septicidal capsules, *Polygonum* Type of embryo sac, and the basic chromosome number are different; *Calochortus* can easily be distinguished from Liliaceae in that the inner and outer tepals are strongly different from each other. There are also differences between the families in leaf anatomical characters. As remarked by Berg (1960) *Calochortus* is distinct in the combination of embryological details but in these comes closest to genera placed here in Colchicaceae and Uvulariaceae.

Liliaceae A. L. Jussieu (1789) 13:385 (Figs. 110–112)

Erect herbs, always with bulbs. The bulbs are of variable construction in the family, being tunicated or non-tunicated, and having from one (*Gagea*) to very numerous fleshy nutrient scales. The roots are contractile and contain vessels with scalariform perforations only.

The erect stem has from one to very many leaves, which may be basally concentrated (*Gagea, Tulipa*) or distributed all along the stem. The leaves are alternate or rarely verticillate (species of *Lilium* and *Fritillaria*). They are flat, dorsiventral, linear to ovate-lanceolate, bifacial, parallel-veined and often sheathing at the base. Further, the leaves may be dark-spotted, apically attenuate and sometimes petiolate. Bulbils are present in the leaf axils of several species of *Lilium*. Oxalate raphides are lacking.

The cauline stem ends in a determinate or rarely indeterminate inflorescence. It may form a raceme (*Lilium*) or be umbel-like (*Gagea*), or is sometimes restricted to a single terminal flower (*Tulipa* spp.).

The flowers are bisexual, hypogynous, trimerous and generally actinomorphic, but more rarely weakly zygomorphic. Their tepals are free from each other to the base and generally similar in the two whorls or, rarely, different, as in *Nomocharis,* where the inner three tepals, unlike the outer, are often fimbriate or pubescent. Nectaries are present on the tepal bases. The tepal colour is highly variable and patterns of striation, spotting or checkering are frequently present.

The stamens are 3+3 in number and in *Lilium, Notholirion,* and *Nomocharis* they have epipeltate anthers, and in the other genera pseudobasifixed anthers (the filament tip being surrounded by the tubular connective). The filaments are glabrous, free and narrow, sometimes dilated basally. Microsporogenesis is successive. The pollen grains are large, often coarsely reticulate and normally sulcate, only in *Tulipa* being occasionally operculate or with an irregular aperture. Further they are two-celled, the generative nucleus being enclosed in an easily stainable, rather wide cell almost as long as the diameter of the pollen grain lumen.

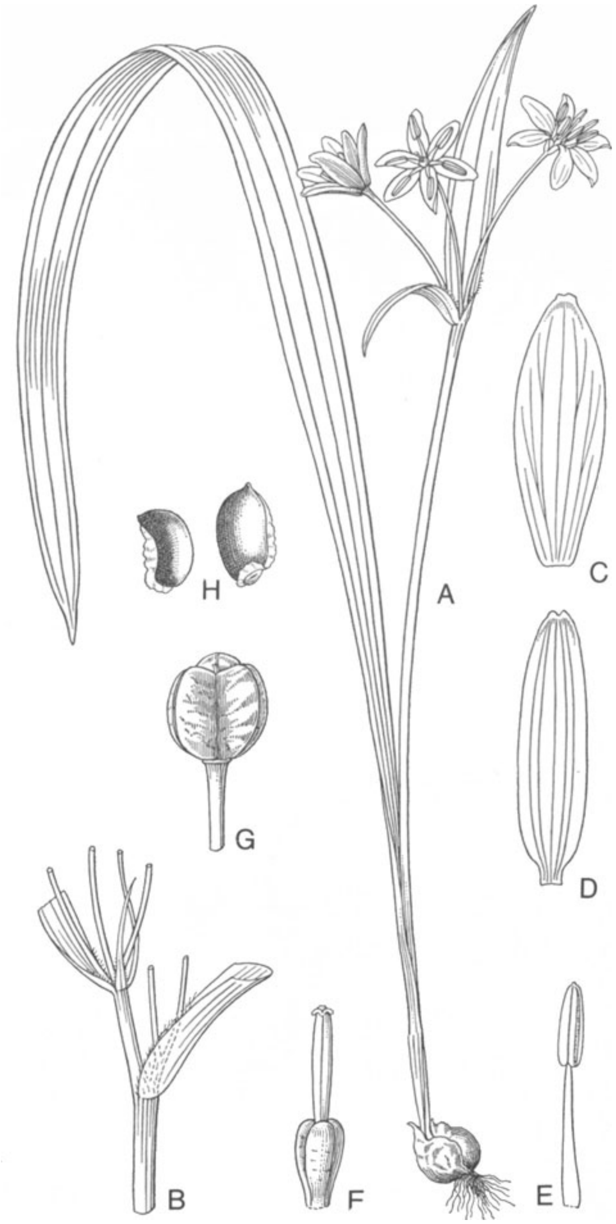


Fig. 110. Liliaceae. *Gagea lutea.* **A** Plant. **B** Part of branch system in the inflorescence region. **C** Tepal of outer whorl. **D** Tepal of inner whorl. **E** Stamen. **F** Pistil. **G** Capsule. **H** Seeds with appendage. (Ross-Craig 1972)

Fig. 111. Liliaceae. **A–F** *Tulipa borszczowii.* **A** Plant. **B** Lateral bulb. **C** Tepal of outer whorl. **D** Tepal of inner whorl. **E** Stamen. **F** Pistil. (SEALY 1938). **G–I** *Lilium columbianum.* **G** Part of inflorescence. **H** Leaves, in a pseudoverticel. **I** Bulb. (HITCHCOCK et al. 1969). **J–L** *Erythronium revolutum.* **J** Plant. **K** Flower. **L** Androecium and gynoecium. (HITCHCOCK et al. 1969). **M–O** *Lilium regale,* pollen and pollen tube development. **M** Two-celled pollen grain. **N** Part of pollen tube before division of generative cell. **O** Same after the division with two sperm cells. (COOPER 1936)

The pistil is tricarpellary, syncarpous and trilocular, and the style is short to long, apically trilobate or with three stigmatic crests. The stigmatic surfaces are papillate and Dry (species of *Erythronium* and *Tulipa*) or Wet (species of *Fritillaria* and *Lilium*). Each locule contains several to many anatropous ovules, which are rather tenuinucellate and in which a primary parietal cell is not cut off from the archesporial cell. Embryo sac formation normally conforms to the tetrasporic *Fritillaria* Type (see P. MAHESHWARI 1946; Fig. 112).

The fruits are loculicidal capsules, the seeds of which in typical cases are flat and disc-shaped, placed like piles of coins on top of each other, and often provided with a marginal rim. Sometimes, however, they are ellipsoidal rather than flattened or sharp-angled (species of *Gagea, Lloydia, Erythronium,* rarely *Tulipa*). They are not winged, but may have a lateral raphe-crest or a raphal elaiosome, the latter in *Gagea arvensis* and related species, while a chalazal elaiosome occurs in *Erythronium*. The outer integument of the seed coat is thin: sometimes only two-layered. Its cells are flat or even collapsed, and sometimes they have lignified walls, especially on the outer epidermis. The inner integument is strongly suppressed. In the endosperm of ripe seeds the cells mostly have rather thickened, pitted walls and contain aleurone and fatty oils but no starch. The embryo is generally little differentiated, ovoid or ellipsoidal, and only about $^{1}/_{5}$–$^{1}/_{12}$ the length of the endosperm. The seedling does not have a coleoptile-like cotyledon. The basic chromosome number is $x=12$.

Chemistry. Raphides and chelidonic acid are probably lacking in the family. Steroidal saponins occur at least in several genera, including *Lilium* (with the sapogenins lilagenin and yuccagenin), and steroidal alkaloids occur at least in *Fritillaria,* in which the family agrees with the tribe *Veratreae* of Melanthiaceae. The accumulation of x-methylene-glutamic acid derivatives is common. *Erythronium* produces x-lactone. Tuliposides were found by Slob et al. (1975) to be present in several genera.

Distribution. Liliaceae has a Northern Hemisphere distribution with a pronounced centre in South-Western and Himalayan Asia to China. The taxa are mostly spring-flowering plants growing in steppes and mountain meadows.

The present circumscription of Liliaceae is supported also by Huber (1969) and Schultze (1980); it is a rather homogeneous family, the closest relatives of which are undoubtedly the Calochortaceae, Uvulariaceae and Colchicaceae.

Gagea (90) (Fig. 110) is a widespread Eurasian genus of mostly small spring-flowered herbs with yellow (rarely white or purplish), externally green-banded flowers in (one- to) few-flowered, umbel-like inflorescences, which are usually subtended by two spathe-like upper leaves. The bulbs consist of two(–four) bulb scales, only one (rarely two or three) of which is a fleshy nutrient scale. *G. lutea, G. spathacea* and other species are common European species, growing in grassland and woods, *G. arvensis* in cultivated fields, and *G. pratensis* on dry, sandy ground. – *Lloydia* (18), widely distributed in the Northern Hemisphere, is a genus of small, white-flowered, *Gagea*-like herbs with bulbs having a single nutrient scale. *L. serotina* ranges from western Europe through the Alps and Himalaya to the western mountains of North America.

Tulipa (60–100) (Fig. 111 A–F), "Tulips", are distributed from western Europe (*T. sylvestris*) to Asia; the western and central parts of Asia being the centre of variation. The bulbs are few-leaved, and the erect stem has a limited number of basally concentrated leaves and mostly a single terminal flower. When there are two or more flowers, the lateral are ebracteate. Tepal colour is variable, often red or yellow, and often bicoloured (but white, violet and other colours also occur). Some species are polymorphic with yellow and red or orange phases. The anthers are pseudobasifixed (see above), and the stigmatic crests usually almost sessile on the top of the ovary. The floral parts are robust and it has been suggested that the flowers are adapted to beetle pollination. *T. sylvestris* is wild in central and southern Europe, a rather distinct subspecies, ssp. *australis* occurring in the western part of the Mediterranean. Many of the western Asiatic species have been brought into cultivation, often under the name *T. gesneriana.* Some of the commonly cultivated species are the mostly red *T. eichleri, T. fosteriana, T. greigii, T. kaufmanniana* (also yellow), *T. linifolia, T. praestans* and (violet) *T. violacea,* the yellow-flowered *T. kopalkowskiana, T. stellata, T. tarda* and *T. whittallii,* and the white-flowered *T. turkestanica.* Numerous crosses and aberrant forms have been produced, so that hundreds of cultivars are available on the market. In Holland, especially, but also in other countries, tulips have great economic importance. They are perhaps the commonest garden ornamentals in Europe.

Related to *Tulipa* is no doubt *Erythronium* (20) (Fig. 111 J–L) with the greatest concentration in North America and one species, *E. dens-canis,* occurring from southern Europe through Asia to Japan. In this genus the basal, green leaves are not more than two in number, often broad, subpetiolate and frequently spotted, and the nodding flowers are few or solitary. Their patent to reflexed tepals give them a *Cyclamen*-like habit. *E. dens-canis* and other species are grown as ornamentals.

Fritillaria (100) (Fig. 112) is restricted to the Northern Hemisphere with an Asiatic centre. It has few- or many-leaved stems with alternate or

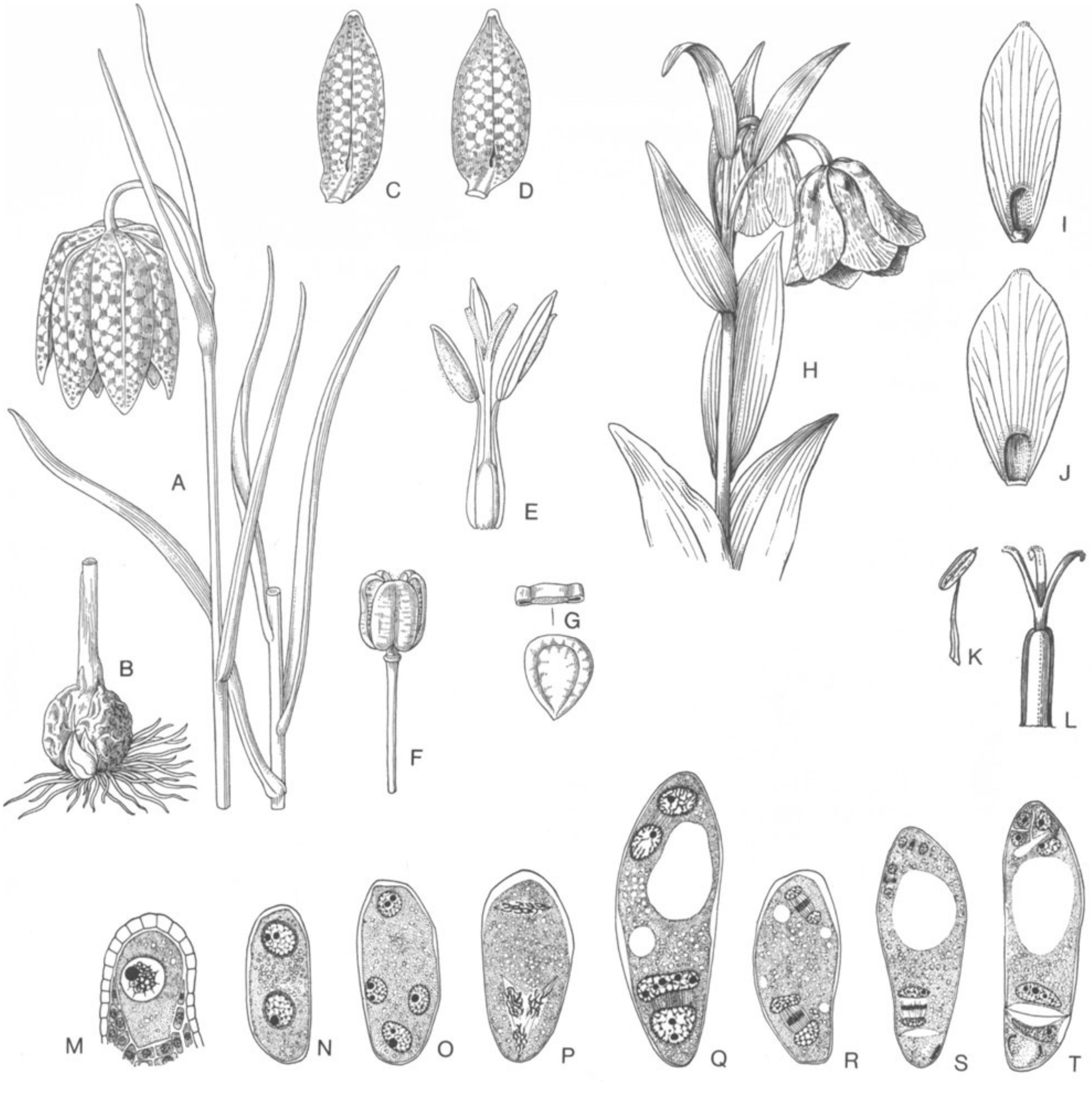


Fig. 112. Liliaceae. **A–G** *Fritillaria meleagris*. **A** Plant. **B** Bulb. **C** Tepal of outer whorl. **D** Tepal of inner whorl. **E** Androecium and gynoecium, two stamens removed. **F** Capsule. **G** Seed, sectioned above. (Ross-Craig 1972). **H–L** *Fritillaria davisii*. **H** Upper part of plant. **I** Tepal of outer whorl. **J** Tepal of inner whorl; note the basal nectar grooves. **K** Stamen. **L** Pistil. (Turrill 1943). **M–T** *Fritillaria persica,* embryo sac formation of the *Fritillaria* Type, see further in the text on p. 14. (Bambacioni 1929)

verticillate leaves, and the flowers are almost always nodding or pendulous, campanulate but with free perianth members. The tepals are yellow, orange or pale to dark brownish, rarely white and frequently variegated; they are supplied with a nectariferous pit above the base. Many species are grown as ornamentals. Best known is perhaps *F. imperialis,* a large herb from Iran and Afghanistan, with verticillate leaves and a whorl of nodding flowers below an apical crown of leaves. Also conspicuous are *F. meleagris* (purplish with checkering or white) and *F. aurea* (yellow with checkering). These belong to the largest section of the genus, which has unifloral stems. *F. meleagris* is Central

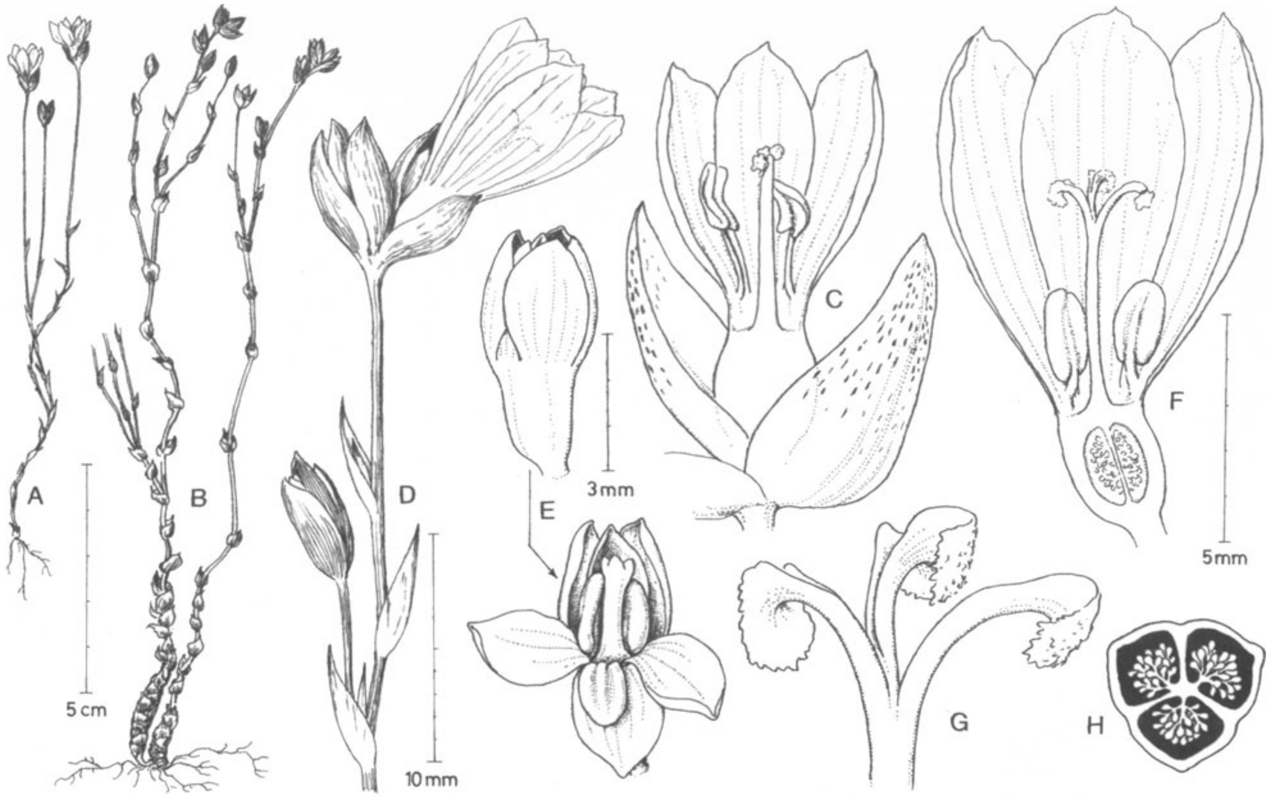


Fig. 113. Geosiridaceae. *Geosiris aphylla.* **A** and **B** Plants. **C** Flower with bract and bracteole; 3 tepals and 4 stamens removed. **D** Inflorescence; note the prophylls of the laterals. **E** Flower bud; *below* opened to show stamens and pistil. **F** Flower, longitudinal section; note the extrorse anthers. **G** Stylar branches. **H** Ovary, transverse section. (Orig. B. Johnsen)

and South European, and *F. aurea* Turkish. The multiflorous *F. pallidiflora* and *Lilium*-like *F. camtschatcensis* are also cultivated. A number of the West-Asiatic species with sombre campanulate flowers appear to be pollinated by queen wasps (*Hymenoptera, Vespinae*).

Lilium (75), "Lilies", is a variable genus, widely distributed over the Northern Hemisphere. The bulbs generally have numerous imbricate fleshy scales, and the stem is often multifoliate with alternate or verticillate leaves at several levels. Sometimes, as in *L. bulbiferum,* dark-coloured axillary bulbils are developed. The flowers are few or numerous and are borne in racemose or sometimes umbellate inflorescences, or they may be terminal and solitary. They are mostly large and magnificent, funnel-shaped, often with more or less recurved tepals, which vary in colour from white to yellow, orange, bright red or dark purple, the inner side being mostly spotted and sometimes supplied with hairs. The anthers are epipeltate and their coarsely reticulate pollen grains often bright red. – Many species are grown as ornamentals. Among the white-flowered are *L. candidum* from Greece to Syria, *L. regale* and *L. langkongenese* from China and *L. auratum* from Japan. *L. speciosum,* likewise from Japan, has white to pink tepals with red spots. Yellow-flowered ornamentals are, for example, *L. canadense,* from eastern North America, *L. pyrenaicum,* from the Pyrenees, and various hybrids. *L. henryi,* from China, *L. bulbiferum* and *L. croceum* from Central Europe and other species have orange-coloured, *L. japonicum* rose-coloured and *L. pardinarium* and *L. martagon* purple flowers. Among the ornamentals many are hybrids and cultivars.

Related to *Lilium* is the Asiatic genus *Notholirion* (4) in Central Asia, mostly Himalaya, which differs from *Lilium* in forming subterranean bulbils from the main bulb, in having a tunicated (not scaly) bulb, and in having long basal leaves. – *Nomocharis* (13), in highland meadows in Burma, Tibet and inner China, generally has open, pink, more or less nodding flowers and short stamens. *N. pardanthina* and *N. saluenensis* are sometimes grown as ornamentals. – *Cardiocrinum* (3) is another Himalayan lily-like genus and has petiolate cordate leaves. It is a large plant with trumpet-shaped flowers and a bulb which is replaced annually.

Whether also the genus *Medeola* (2) should best be treated in Uvulariaceae or Liliaceae is not yet fully clear (see Berg 1962a, b; Utech 1978a).

Geosiridaceae Jonker (1939) 1:1 (Fig. 113)

A small, sparingly branched, achlorophyllous mycorrhizal saprophyte with small, scale-like, lanceolate to ovate, hyaline leaves more densely situated on the lower than on the upper part of the erect stem. Rhizome and corm are both obviously lacking, the basal part of the stem being supplied with thin mycorrhizal roots. The inflorescence has not been thoroughly analyzed. It is few-flowered and each lateral branch is supplied with a basally inserted prophyll, as in many Iridaceae. Apically it often bears two or more densely set flowers in the axils of relatively large bracts more than half the length of the flowers, and supplied with a prophyll, in the axil of which a floral bud may develop. No information on vegetative anatomy is available.

The flowers are bisexual, actinomorphic and epigynous with 3+3 subequal, obovate, petaloid, pale tepals, which are fused basally and inserted at the top of the ovary, the outer lobes slightly overlapping the inner marginally. The three stamens are opposite the outer tepal lobes (i.e. they represent the outer staminal whorl, as in the Iridaceae) and are inserted on these at their base. Their filaments are relatively short and their anthers subbasifixed, extrorse, tetrasporangiate and longitudinally dehiscent. The pollen grains are uniaperturate (Cronquist 1981). The ovary is trilocular, with branched intrusive placentae and numerous minute ovules (Fig. 113H). There is a single style which is apically tribrachiate with flattened deflexed stigmatic ends. The fruit is a triangular-obconic pyxis or capsule (Jonker 1939), with an annulus at the truncate end. The seeds are numerous and minute.

The single species, *Geosiris aphylla* (Fig. 113), occurs on Madagascar and some islands of the Indian Ocean.

The strong similarity in appearance between *Geosiris* and the Burmanniaceae is probably due to convergence. In several features, such as the inflorescence, the floral construction (e.g. the three episepalous stamens) and the style it is in close agreement with Iridaceae. We assume that it is derived within some group of that family, possibly Iridaceae subfamily Iridoideae, and would logically be included in this, as it was originally by Baillon (1894), but we keep it distinct until the embryological details have been fully investigated.

Iridaceae A.L. Jussieu (1789) 70:1.400 (Figs. 114–118)

Mainly herbs, but a few genera woody at the base and sometimes shrubby at length. The underground parts consist of rhizomes or subterranean corms, which are usually tunicated (in *Ferraria* non-tunicated), rarely (in genera allied to *Iris*) bulbs. The tunic enclosing the corm in many genera is longitudinally or reticulately fibrous and characteristically sculptured. The roots usually have simple or, in particular in the Aristeoideae, scalariform perforation plates. Otherwise vessels are lacking in stems as well as in leaves (a notable exception is *Sisyrinchium,* where vessels with simple and scalariform perforation plates have been observed in the stem).

The stems are generally erect and leafy and often compressed. In a few genera (*Klattia, Nivenia, Witsenia*) the stem is basally woody and has secondary thickening growth, which is otherwise not known in Liliales. The densely leafy stem of, for example, *Witsenia* may be up to 2 m high. The leaves are generally distichous, narrow or broad, either flat and dorsiventral or terete or, most often, ensiform (unifacial), linear or rarely lanceolate or filiform, sheathing at the base and parallel-veined. They are glabrous or provided with simple hairs. Crystal raphides are invariably lacking, calcium oxalate being instead accumulated in the form of long, prismatic crystals contained in characteristic dead cells.

The inflorescences in subfamilies Iridoideae and Aristeoideae are panicles, thyrses or cymes composed of monochasial units (rhipidia), but in the large subfamily Ixioideae they are spikes. They frequently have a complicated construction and may be difficult to interpret, especially in the Aristeoideae; sometimes they are arranged in one plane because of the strictly distichous, unifacial leaves and the sometimes compressed stems.

The flowers are trimerous, epigynous (hypogynous in *Isophysis*), mostly bisexual, and actinomorphic or often weakly, but sometimes strongly, zygomorphic. The outer and inner whorls of tepals are both petaloid, but in a number of genera (e.g. in *Libertia* and *Iris*) they are conspicuously different in shape and colour, the inner sometimes much smaller than the outer. They are blue, violet, white, yellow, red, purple, and even blue-green (*Ixia viridiflora*), and variegation and striation are rather common, in particular in the Tigrideae and Mariceae. Nectaries are present on the tepal bases except in subfamily Ixioideae, where the pistils have septal nectaries.

Fig. 114. Iridaceae. **A–E** *Nivenia binata*. **A** Flowering branch. **B** Pair of flowers enclosed by brown bracts. **C** Flower, longitudinal section. **D** Ovary, transverse section. **E** Base of flower, part of the tube removed to show lobate top of ovary. **F** *Nivenia corymbosa*, fruit. **G** *Nivenia dispar*, woody stem. **H–I** *Nivenia* sp., cluster of fruits and seeds. (All orig. B. JOHNSEN)

The stamens are generally three in number (two in *Diplarrhena*), representing the outer whorl of hexastaminate Liliiflorae. The filaments are narrow and free from each other, or sometimes connate basally or entirely; they are often inserted in the tepal tube (e.g. *Tigridia, Sisyrinchium, Patersonia*). The anthers are basifixed, often basifixed-sagittate, or rarely hypopeltate; they are always extrorse, and dehisce by longitudinal slits. Microsporogenesis, interestingly enough, is simultaneous in all cases studies. The pollen grains are generally sulcate, rarely bisulculate (as in *Tigridia*), spiraperturate or inaperturate (in forms of *Crocus* and *Syringodea*). (See SCHULZE 1971).

The pistil is tricarpellary and trilocular (in *Hermodactylus* unilocular), the style either tribrachiate and often with the branches dichotomous or further branched or differentiated, sometimes strongly petaloid (e.g. in *Iris, Dietes, Moraea*). The stigmatic surfaces are papillate and of the Dry Type (HESLOP-HARRISON and SHIVANNA 1977). Each locule usually contains numerous ovules, rarely few or even a single ovule. The ovules are anatropous, and the archesporial cell cuts off a parietal cell, which forms one or more parietal layers. Embryo sac formation conforms to the *Polygonum* Type. Endosperm formation is nuclear.

The fruit is a loculicidal capsule with a thin to leathery, rarely hard, wall. The seeds are semi-globose or angular, rarely round and flat (*Diplarrhena*) or elongate-ellipsoidal (e.g. *Cypella* and *Nivenia*). The raphe often forms a ridge or wing, especially in subfamily Ixioideae, and a wart may also be present on the micropylar side. Arils occur in some sections of *Iris*, elaiosomes derived from chalaza and raphe are found in *Patersonia*, and others derived only from the chalaza occur in *Hermodactylus*. The outer integument of the testa usually consists of several cell layers which are retained for the most part in the seed. The outer epidermis is retained or is rarely collapsed, and usually has brownish contents, while the inner epidermis is mostly well-developed; the inner integument is often partly collapsed. Aleurone and fatty oils are accumulated in the endosperm cells, which have thick, pitted walls (thus being also rich in cellulose). Starch is mostly not found in ripe seeds (an exceptional case, *Radinosiphon*, is reported by HUBER 1969). The embryo is straight and cylindrical and from about one third to two thirds as long as the endosperm. As in Colchicaceae, the cotyledon of the seedling has a coleoptile-like appearance.

Chemistry. Characteristic of Iridaceae are prismatic oxalate crystals (see above) and mucilage ducts. Chelidonic acid is rarely present (as in *Lapeirousia, Romulea* and *Trimezia*). Alkaloids largely seem to be lacking, although certain alkaloids or alkaloid-like compounds, like homeridin, which has a digitalis-like effect on heart function, occur, for example, in *Homeria*. Steroidal saponins are known to occur in corms, flowers or fruits of a number of genera (e.g. *Crocus* and *Gladiolus*). Several genera accumulate phenolic compounds such as leucoanthocyanins, anthraquinones and tannins. The flavonoid spectrum is more varied than in other families of Liliiflorae. The corms and rhizomes accumulate carbohydrates, such as saccharose, fructan and starch in variable proportions. The contents of the styles in *Crocus sativus*, "Saffron", include lycopin, β- and γ-carotin, zeaxanthin, the water-soluble orange pigment crocin, and the strongly fragrant safranal.

Distribution. The Iridaceae are most richly represented in the Southern Hemisphere, where the subfamily Ixioideae forms a climax group in the winter rainfall area of South Africa. Another comparable centre is in tropical and subtropical America. The genus *Isophysis*, which is probably a relict, having hypogynous flowers, occurs only in Tasmania. A few genera show markedly disjunct distributions. Among these are *Libertia*, occurring in New Zealand, New Guinea, Australia and Chile, *Diplarrhena* in Australia and South America, and *Orthrosanthus* in Australia and both North and South America.

Subfamily Isophysoideae

This is clearly a member of Iridaceae as judging from the vegetative characters. It consists of a single species, *Isophysis* (1) *tasmanica*, endemic in Tasmania, a herb with a thick rhizome, distichous, ensiform leaves and a solitary, actinomorphic and stellate flower. This has subequal, lanceolate, free tepals and a pistil with *superior* ovary, a short style and simple, recurved stigmatic branches. If the superior ovary does not represent a derived state, i.e. in this case a reversal (epigyny is generally assumed to be an irreversibly derived state), and the ensiform leaves have not arisen two or more times, then there is evidence that the ancestral Iridaceae resembled *Isophysis*, and that the dorsiventral leaves in many Iridaceae are secondary.

Subfamily Aristeoideae

Subfamily Aristeoideae consists of evergreen rosette herbs or even shrublets, often with persistent leaf sheaths, as in the Velloziaceae. The roots have vessels with mostly scalariform perforations. Secondary thickening growth has been recorded in the stem and roots of a few genera. The leaves are distichously inserted and either unifacial-ensiform or terete (most species of *Bobartia*). The inflorescences are bracteate panicles or thyrses with lateral components of rhipidial monochasia. Sometimes they are strongly contracted. The flowers are actinomorphic, with frequently fugacious, violet, more rarely white or yellow tepals which are generally fused into a tube of variable length. Nectar secretion takes place at the tepal base. The stylar branches are short or obsolete and the filaments are free. The seeds lack wings and other appendages. Their seed coat, as in *Aristea*, may have a testal layer of only two unpigmented cell layers, one often carrying lipids, and a thick, several-layered tegminal layer. The testal layer may dissolve. In the endosperm cells the walls are thin and unpitted. The embryo is very small, only ca. $^1/_{10}$ to $^1/_5$ of the endosperm length. This subfamily is wholly African and concentrated mainly in the winter rainfall regions of South Africa. It consists of four to five genera.

Aristea (50) has its centre in the Cape but extends to Madagascar. It is naturalized in the New World tropics. The frequently branched inflorescences consist of rhipidia which are one- or few-flowered. The tepals are blue, violet or white and fugacious. – Related is *Nivenia* (8; Fig. 114A–I) in South-Western Cape. It is a shrub with branched woody stems bearing scars of old leaf sheaths. – *Witsenia* (1) in the same region is a slender shrub up to more than 2 m tall. It has bird-pollinated, tubular cylindrical flowers, that are green, black and (apically) yellow in colour, and hairy on the outer side. – *Bobartia* (15), likewise in the Cape, should possibly also be referred to this subfamily. It has yellow (rarely violet) flowers in dense and contracted clusters, rarely loose panicles. The stem is leafless and the leaves mostly terete and stiff, giving the plants a *Juncus*-like appearance. Alternatively, *Bobartia* may have its closest relatives in Iridoideae, near *Dietes,* with which it shares pollen shape and chromosome number ($x = 10$) (Goldblatt 1971).

Subfamily Sisyrinchioideae

This consists of herbs with a rhizome. They rarely (*Patersonia*) have secondary thickening growth. The roots have vessels with scalariform and/or simple perforation plates, and vessels have been reported in stems and leaves of *Sisyrinchium.* The leaves are distichous but bifacial and flat or triangular in transection. As in the Aristeoideae, the inflorescence is principally a panicle with rhipidial components. The flowers are actinomorphic; the tepals are free or basally fused into a short tube and the two whorls are generally similar in shape and size. Nectaries are present on the perigone. The stamens have free or basally connate filaments. The ovary lacks septal nectaries, and the three stigmatic branches, which alternate with the stamens, are undivided or slightly divided only. The seeds are normally globose or ellipsoidal and only in *Diplarrhena* are they flat and disc-shaped. A lipid-rich elaiosome is present in *Patersonia.* The outer integument of the seed coat contains several layers of cells (as also in the following subfamilies); its outer epidermis tends to be completely collapsed and is either red-brown or colourless (Huber 1969). The embryo varies in length, but is very short in *Patersonia.*

This somewhat dubiously homogeneous subfamily has great affinities to subfamily Aristeoideae.

All genera have rhizoms. *Patersonia* (20) in Australia, Borneo, the Philippines and New Guinea, stands out as remarkable. The leaves are basally concentrated, sometimes on a short, woody and linear stem, the aerial stem is leafless and ends, as a rule, in a double rhipidium with blue or yellow flowers. Of the six tepals the inner three are reduced to small teeth; the staminal filaments are connate into a tube around the style, and the three simple stigmatic lobes are deflexed, rather broad and ciliate. In addition, the seeds have terminal appendages.

The probably related *Libertia* (10) also has a Southern Hemisphere distribution. They are small or medium-sized rhizomatous herbs with narrow, flat leaves and flowers with white or blue inner tepals, the outer smaller than the inner and slightly "sepaloid" in nature. The stylar branches are simple and narrow-subulate. – *Orthrosanthus* (10), distributed in Australia and both North and South America, is doubtless related to *Libertia.* – *Diplarrhena* (2), in Australia, has totally zygomorphic, large flowers in a loose rhipidium. The stamens are unequal, the median one staminodial, and the

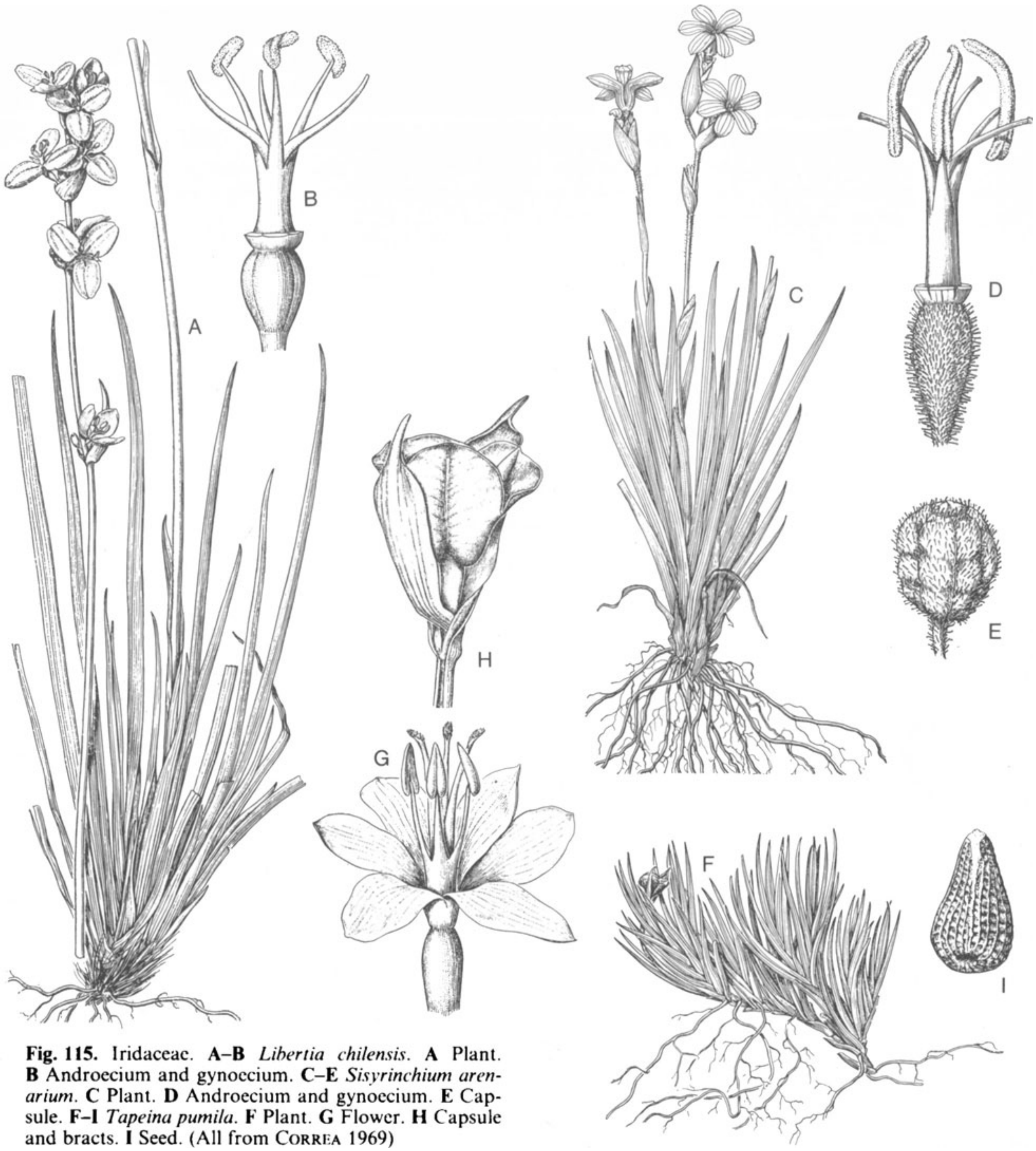


Fig. 115. Iridaceae. **A–B** *Libertia chilensis.* **A** Plant. **B** Androecium and gynoecium. **C–E** *Sisyrinchium arenarium.* **C** Plant. **D** Androecium and gynoecium. **E** Capsule. **F–I** *Tapeina pumila.* **F** Plant. **G** Flower. **H** Capsule and bracts. **I** Seed. (All from CORREA 1969)

stylodial branches, as is often the case in the following genera, are flattened.

More specialized than these genera is *Sisyrinchium* (80) in South America (principally in the Andes) and Central and North America, with an outlier in Ireland. It is a rhizomatous genus with ensiform leaves and paniculate or thyrsoid inflorescences with yellow, white or blue, actinomorphic flowers. Superficially the genus resembles *Aristea,* but there is no perigone tube and the stylar branches are longer, simple as in the previous genera, and not flat as in most of the Iridoideae. The seeds lack a lipid layer. – Several species are grown as ornamentals, e.g. the southern North American *S. bermudiana* with violet flowers and the South American *S. striatum* with pale yellow flowers.

Subfamily Iridoideae

Subfamily Iridoideae consists for the most part of herbs with leafy stems withering down each season. The subterranean parts consist of short or long, sometimes horizontal rhizomes or, quite often, of tunicated corms; rarely, in the tribe Irideae, are there true bulbs. The leaves vary from unifacial-ensiform to bifacial and flat or canaliculate; sometimes they are terete. The inflorescences are paniculate or simple and consist of one or more rhipidial cymes. The flowers are often large; they are epigynous and generally actinomorphic, and have free or connate tepals, which are frequently fugacious. There is often great difference in shape and size between the outer and the inner tepals, the former of which have basal nectar secretion, septal nectaries being absent. The stylar branches are generally apically bifurcate and in a number of genera flat and petaloid, more rarely narrow, showing rich differentiation in the subfamily. The seeds are half-ovoid, sometimes sharply angular, discoid or irregular-polyhedral, and always lack a wing. In the seed coat, the testal layer consists of several, sometimes many, persistent cell layers. If lipids are present they occur in one to several layers and contain amorphous masses of red-brown pigment. The testal cells are not radially elongated, as in the Ixioideae. The walls of the endosperm cells are pitted except in the periphery of the endosperm; the embryo in most genera is one third to two thirds as long as the endosperm.

Like the Ixioideae, this subfamily represents a climax group whose flowers have differentiated richly within a characteristic pattern of variation. One major complex of genera has radiated in the Old World, and makes up the tribe Irideae, while two smaller, probably more recent groups, the Tigrideae and Mariceae, have developed, respectively, almost entirely and wholly, in the New World.

Tribus Irideae

Tribus Irideae is the most variable of the three tribes and covers most of the above variation. Typical of most genera and possibly basic in the tribe are the often large, flat and petaloid stylar branches sheltering the three stamens and their extrorse anthers. Besides the genera traditionally referred here are included *Ferraria* and *Homeria,* sometimes referred to the Tigrideae.

Within the Irideae, the genus *Dietes* (6) in South Africa and on Lord Howe Island possesses a number of features, some of which may be basic and primitive in this tribe, being evergreen herbs and having unifacial leaves, a woody rhizome, flowers with free stamens and broad petaloid stylar branches (GOLDBLATT, personal communication). Superficially the genus is fairly *Iris*-like.

The remaining genera may be divided into two groups, which may be called the *Iris* and the *Homeria* Groups. The former has differentiated chiefly in the Northern Hemisphere (mainly the Old World), and the latter in Southern Africa.

The Iris Group, apart from the largest genus, *Iris,* includes three genera with bulbs, *Iridodictyum, Xiphium* and *Juno,* and two small genera with rhizomes, *Hermodactylus* and *Belamcanda.*

Iris (200) is the largest genus of the family. It has a wide, Northern Hemisphere distribution with a centre in Asia. When the above bulb-bearing genera have been excluded, as done by RODIONENKO (1960), which is debatable and not yet accepted by most taxonomists and horticulturalists, the remaining *Iris* s.str. is more easily defined than before. It then consists of rhizomatous species with equitant, ensiform or linear leaves, the shoots appearing as a rule quite flat. Further classification depends on whether the outer perianth members are crested or bearded or unornamented, on the seed shape and whether or not the roots are fleshy (see DYKES 1913; LAWRENCE 1953).

Subgenus *Nepalensis* consists of two deviating species, including *I. nepalensis,* with a short rhizome bearing a fascicle of fleshy roots. This subgenus is centred in Yunnan (China).

The other groups have a conspicuous rhizome. Among them certain species lack a crest or bearded zone on the outer tepals. One of the species, *I. dichotoma,* in eastern Asia, with stout stem and compressed seeds with parchment-like testa, constitutes subgenus *Xyridion.*

Most other species without crest or beard comprise subgenus *Limniris* (=sect. *Apogon*). They have other seed shapes and often comprise large plants. They represent a large group of Eurasian as well as North American species, including *I. sibirica, I. orientalis, I. macrosiphon, I. foetidissima, I. ruthenica, I. spuria* and *I. unguicularis.* Certain interesting features occur among some of these, *I. sibirica* and *I. orientalis* having a hollow aerial stem; *I. macrosiphon* and other species being North American; *I. foetidissima* having orange-red seeds; *I. ruthenica* being low and grass-like; and *I. unguicularis* having a floral tube 10–20 cm long. Subgenus *Limniris* (subsect. *Laevigatae*) includes species from Europe (*I. pseudacorus*), Eastern Asia (*I. laevigata*) and North America (*I. versicolor*), having a thin-walled capsule which breaks up irregularly at maturity.

Subgenus *Crossiris* (=sect. *Evansia*) comprises relatively few, mainly small-growing species having a crest (but not a hairy ridge) on the outer tepals. *I. cristata* in Atlantic North America almost lacks an aerial stem. The

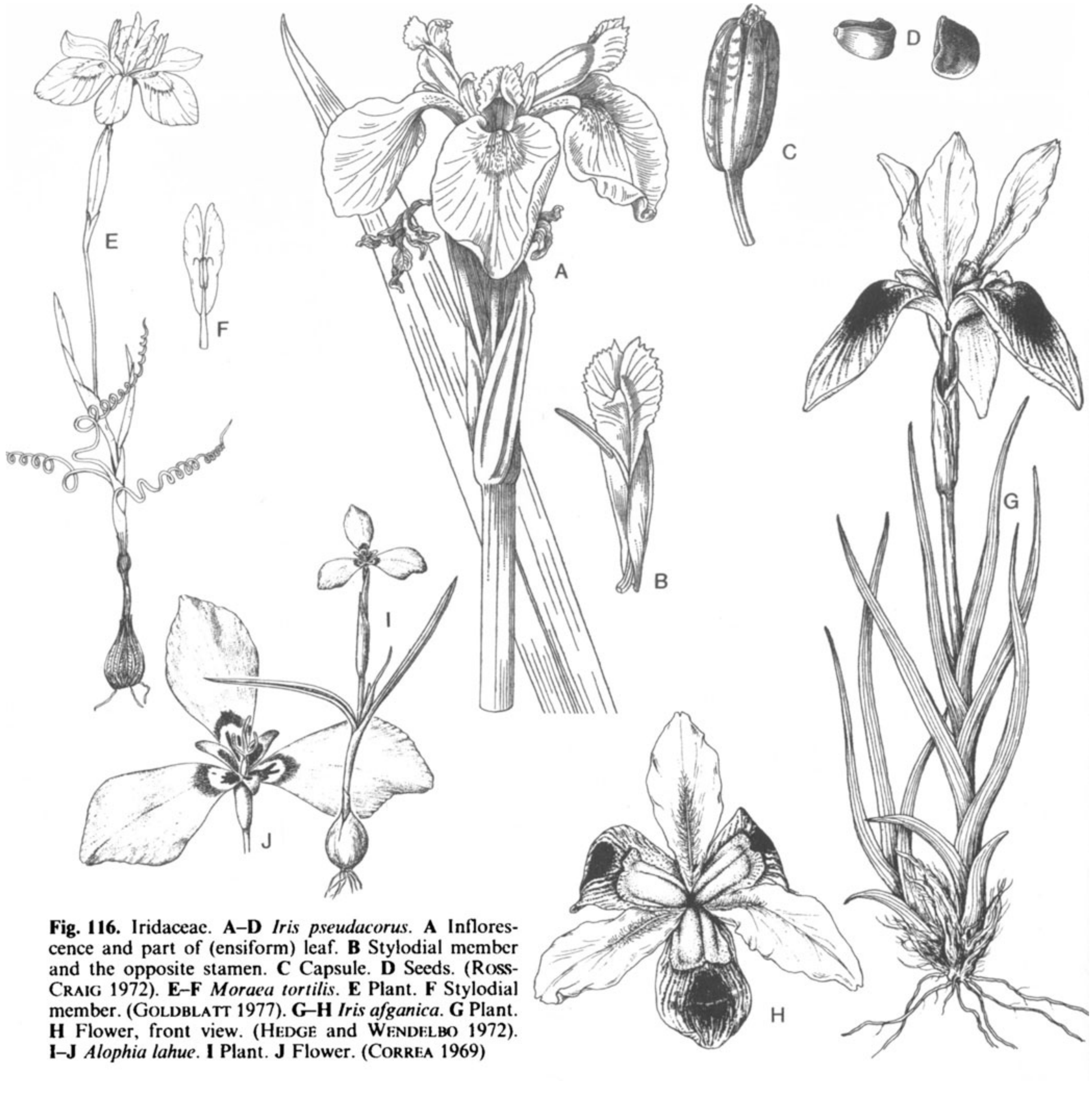


Fig. 116. Iridaceae. **A–D** *Iris pseudacorus*. **A** Inflorescence and part of (ensiform) leaf. **B** Stylodial member and the opposite stamen. **C** Capsule. **D** Seeds. (Ross-Craig 1972). **E–F** *Moraea tortilis*. **E** Plant. **F** Stylodial member. (Goldblatt 1977). **G–H** *Iris afganica*. **G** Plant. **H** Flower, front view. (Hedge and Wendelbo 1972). **I–J** *Alophia lahue*. **I** Plant. **J** Flower. (Correa 1969)

other species occur in Japan and China and other parts of eastern Asia, among them the violet and large-flowered *I. tectorum*.

Subgenus *Iris* (incl. the sections *Oncocylus, Regelia, Pseudoregelia,* all with arillate seeds, and sect. *Pogoniris,* without aril), is characterized by having a bearded ridge or crest in the centre of the outer tepals. This subgenus is large and variable and includes both large and small-sized species. The *Oncocyclus* species are often small-sized and have unifloral spathes and seeds with a yellowish white aril. They are concentrated in western Asia and include the small *I. paradoxa* and the larger *I. susiana*. The related *Regelia* species are also West-Asiatic, but usually have two to three flowers per stem. Among these may be mentioned *I. falcifolia*. An aril smaller than the seed characterizes sect. *Pseudoregelia*, with a few species with twisted rhizomes. They range from Himalaya to Western China, and include *I. hookeriana*. The species of sect. *Pogoniris* are fairly numerous, at least 40, and occur in Asia and southern Europe. Here belong a number of unbranched, blue, violet or yellow-flowered species, including *I. pumila, I. tigridia* and *I. flavissima,* and species with branched stem, such as *I. aphylla, I. variegata,* and the frequently cultivated *I. germanica.*

The genus *Xiphidium* (=*Iris* sect. *Xiphium*) (7), in the western Mediterranean, are often slender herbs with dorsiventral, flat or canaliculate leaves and a bulb with entire, smooth and membranous tunics. The nominate species of these "bulb irises" is *X. xiphium,* used in horticultural breeding and represented in cultivation by white-, yellow-, violet- or brownish-flowered forms. Others are *X. filifolia* and *X. juncea.*
Juno (=*Iris* subgen. *Scorpiris* or sect. *Juno*) (20) with a centre in Western Asia (Iran and neighbouring countries), are less slender, often stout plants with dorsiventral, broad and broadly sheathing, flat leaves. The bulb has entire smooth tunics, and fleshy roots both of which persist during the dormant period. The inner tepals are small or even minute. Here belong *J. persica, J. bucharica,* and *J. aucheri,* sometimes grown as ornamentals.
Iridodictyum (=*Iris* subgen. *Scorpiris* or sect. *Reticulata*) (10), with a centre in western Asia, consists of erect herbs with short stem, one flower, narrow tubular leaves with four or eight ridges, and a basal bulb with fibrous tunic; as in *Xiphidium* the roots do *not* persist in the dormant period. These small plants, often less than 20 cm high, are often grown as ornamentals and blossom quite early in the spring. They include *I. reticulatum, I. histrioides* and *I. danfordiae.* – *Hermodactylus* (1) is a Mediterranean genus with thick rhizome, linear, four-angled leaves, and a long spathe with one flower and parietal placentation. The flowers are blackish brown. The perianth members in the two whorls are dissimilar, the outer being erect, the inner smaller and erect-spreading.

The South African group of genera, centred around *Homeria,* is characterized by having a tunicated corm rather than a rhizome or bulb. The leaves vary from equitant to terete or dorsiventral and canaliculate to flat.
Homeria (31), in Southern Africa, has mostly short stems, which bear one or more long, linear leaves which exceeds the stem in length. Generally the tepals, which vary much in colour, are of about equal size and shape, while the filaments are fused into a tube, and the stylar branches are linear or somewhat broader. – The related *Galaxia* (12) has similar, very ephemeral flowers; it consists of small, acaulescent plants, often with rather broad leaves. – *Moraea* (110) occurs in sub-Saharan Africa and has a pronounced centre in the winter rainfall regions of South Africa, where ca. 60 species are concentrated. Like *Homeria* and *Galaxia* it has a fibrous corm tunic and thus approaches these genera rather than the superficially more similar *Iris* (Goldblatt 1977b). The filaments are also fused for half of their length and like the anthers are pressed against the flat stylar branches. In contrast to *Iris* the leaves in *Moraea* are flat and bifacial (? a secondarily reversed state). Some species of *Moraea* are cultivated for their decorative flowers, e.g. *M. neopavonia, M. villosa* and *M. aristata* (=*glaucopsis*). A considerable number of species are very local and close to extinction. – *Gynandriris* (9) is another mostly South African genus with tunicated corms; it is closely allied to *Moraea. Gynandriris* also includes the common Mediterranean species *G. sisyrinchium,* often referred to *Iris.*

Tribus Tigrideae

This is a wholly American group consisting of about six genera, of which *Tigridia, Cypella* and *Alophia* are mentioned here. These are characterized by "woody" bulbs and flat, ensiform, plicate leaves. The flowers are often conspicuous with their bright-coloured and variegated tepals, the inner of which are often much smaller than the outer. The stylar branches are variable, often being narrow and bifurcate.
Tigridia (15) ranges, mainly along the Cordilleras, from Mexico to Chile. *T. pavonia* and other species are frequently cultivated ornamentals. – *Cypella* (10) and *Alophia* (10) (Fig. 116I–J) are also Central and South American.
Other genera, sometimes treated in a separate tribe, Cipureae, have their proper place in Tigrideae, e.g. *Cipura* (1), with simple stylodial branches, and *Nemastylis* (21) and *Calydorea* (15), where the stylodial branches are divided.

Tribus Mariceae

Tribus Mariceae exhibits a parallel trend, possibly more primitive, in its possession of rhizomes or bulbs, than the Tigrideae, and is mainly concentrated in the Americas. The leaves are flat, equitant and ensiform, and are not plicate. The flowers are reminiscent of those in the Tigrideae, the inner perianth segments being for example smaller than the outer and mostly variegated.
Neomarica (15) is concentrated in neotropical regions with its centre in Brazil. Some species have ornamental value. – *Trimezia* (6) ranges from Mexico through Central America to Southern Brazil. It is naturalized in the Old World tropics.

Fig. 117. Iridaceae. **A–D** *Ixia flexuosa*. **A** Inflorescence. **B** Corm and leaves. **C** Stamen in different views. **D** Pistil. (LEWIS 1962). **E–H** *Crocus stridii*. **E** Plant. **F** Corm, tunics splitting at the base. **G** Stamen. **H** Style apex. (PAPANICOLAOU and ZACHAROF 1980). **I–K** *Romulea* sp., development of seed coat, three successive stages from above. The seed coat is here rather thin; it does not contain a black layer on the outer epidermis. (STEYN 1973)

Subfamily Ixioideae

Subfamily Ixioideae consists of herbs, always with a tunicated corm, the tunic structure of which often supplies good taxonomic characters. It may consist entirely of lignified layers or of soft reticulate fibres. The roots have vessels with mostly simple perforation plates. The leaves are sometimes bifacial, and flat or canaliculate, as in *Crocus* or *Syringodea,* but are more often unifacial (ensiform). The plants generally wither after each season. One of the most important characteristics is that the inflorescence is basically indeterminate: a simple or rarely compound (*Pillansia, Lapeirousia*) spike, which may become panicle-like. The tepals in all genera are connate into a tube, which may, however, be very short, as in most species of *Romulea.* Nectar glands are not present on the base of the tepals, but in glandular cavities opening at the style base, thus representing septal nectaries. The seeds are globose or subglobose and, in some genera, winged, e.g. *Gladiolus, Homoglos-*

sum, Oenostachys, Anomalesia and *Watsonia;* they have a multi-layered outer integument of persistent cells containing a lipid layer, one cell thick, of sometimes palisade-like cells. The cell walls in the endosperm in most cases are largely or totally unpitted (rarely pitted except in the periphery). This very large and well-defined subfamily has its centre in Southern Africa, especially in the winter rainfall area of the Cape Province. Only *Crocus* is distributed entirely outside southern Africa.

The subfamily has been revised by GOLDBLATT (1971). The infrasubfamilial division will not be presented in detail. The following genera are worthy of mention.

Watsonia (45) in Southern Africa consists of often large herbs with fibrous corm tunics and ensiform leaves. The spicately borne flowers are often large, and are long-tubular and brightly coloured; the seeds are winged. *W. aletroides, W. pillansii* and other species are grown as ornamentals; *W. meriana* is naturalized in Macaronesia and southern Australia. – *Lapeirousia* (25) are mostly smaller herbs, with ensiform leaves and a "flat" appearance. The woody tunics of the corms show variable sculpture. The flowers are short- to long-tubed and variable in colour. The genus ranges from the Cape through Namaqualand to Ethiopia and to Nigeria. – *Schizostylis* (1) *coccinea* in Central to South Africa is a slender streamside plant with attenuated corm and rose-coloured, actinomorphic flowers. It is often cultivated. – Related genera are *Hesperantha* (50) and *Geissorhiza* (80), the former more widely distributed, the latter restricted to the Cape. – *Melaspherula* (1) *graminea,* in South-Western Africa, has a much-branched, thin and slender inflorescence with rather small, slightly zygomorphic, whitish flowers.

Ixia (44), *Sparaxis* (6) and *Dierama* (20), centred mainly in South Africa, are slender herbs with their corm covered by reticulate fibres. The flowers are unspecialized and actinomorphic or almost so, and highly variable in tepal colour. Several species are grown as ornamentals, e.g. *D. pulcherrima* with wiry inflorescence axes and pendent flowers.

Gladiolus (150) is a large, variable African to Mediterranean and western Asiatic genus with ca. 105 species in South Africa. It consists of small to fairly tall herbs. The corms are ovate or globose to flattened and generally clothed with entire, papery tunics. The bracts of the inflorescence may be rather large, and the flowers are tubular or funnel-shaped with syntepalous, actinomorphic or, more usually, weakly or often very strongly zygomorphic perianth. Some or all tepals may be conspicuously striate. A wide diversity of pollination syndromes is exhibited. The wild species are often fairly small in total size and have smaller flowers than the cultivated. *G. cardinalis* and *G. dalenii* (=*G. psittacinus*), besides various hybrids, are among the numerous cultivated forms originating in South Africa. Conspicuous South African species are *G. alatus, G. carinatus* and *G. carneus.* Common species in the Mediterranean region are the rose- to crimson-flowered, rather slender species *G. illyricus* (Fig. 118A–G) and *G. italicus,* the latter of which is a weed. – *Homoglossum* (10) and *Anomalesia* (3) in Southern Africa are closely allied to *Gladiolus* (there are fertile hybrids between *Gladiolus* and *Homoglossum*); in some species the narrowly tubular flowers have long protruding upper lobes. – *Freesia* (20), *Tritonia* (40) and *Crocosmia* (7) are additional South African genera with globose to depressed corms which are covered by tunics with fairly fine fibres. The tubular, often zygomorphic flowers are white, yellow, orange, red or violet and in *Freesia* mostly strongly scented. – While the wild forms of *Freesia* are usually yellow or white, the cultivated forms may be yellow, orange-red or lilac. They are ornamentals with great economic value. – *Tritonia* differs from *Freesia* in the entire or only apically (not deeply) bifid styles. The plants sometimes have rather short stems and membranous to scarious inflorescence bracts. The flowers usually have calluses on the lower perianth lobes. – *Crocosmia* has broader capsules than *Freesia* and slightly to strongly zygomorphic, yellow to orange-coloured flowers without tepal calluses, usually showing the syndrome of ornithogamy. *C. masonorum, C. aurea* and, especially, the artificial hybrid *C.* × *crocosmiiflora* with its different cultivars, are commonly grown ornamentals, and the last is naturalised in Western Europe and Australia.

Anapalina (7) has tubular, strongly zygomorphic, bright red flowers with hooded upper lobes. – *Babiana* (63) and the related *Antholyza* (2) are more or less hairy, low herbs with ensiform, plicate leaves. The former genus varies in flower colour, mostly in the white-violet range, while *Antholyza* has large, bright red tubular-zygomorphic flowers which are bird-pollinated. All these genera are concentrated in the Cape Province. Occasionally representatives of them are brought into cultivation. – *Romulea* (90) also has its centre in South Africa but ranges as far as the Mediterranean and the Canary Islands. Its species have a bulb-like corm and in many species the stem is short, and wholly subterranean. The few flowers (? in a spike)

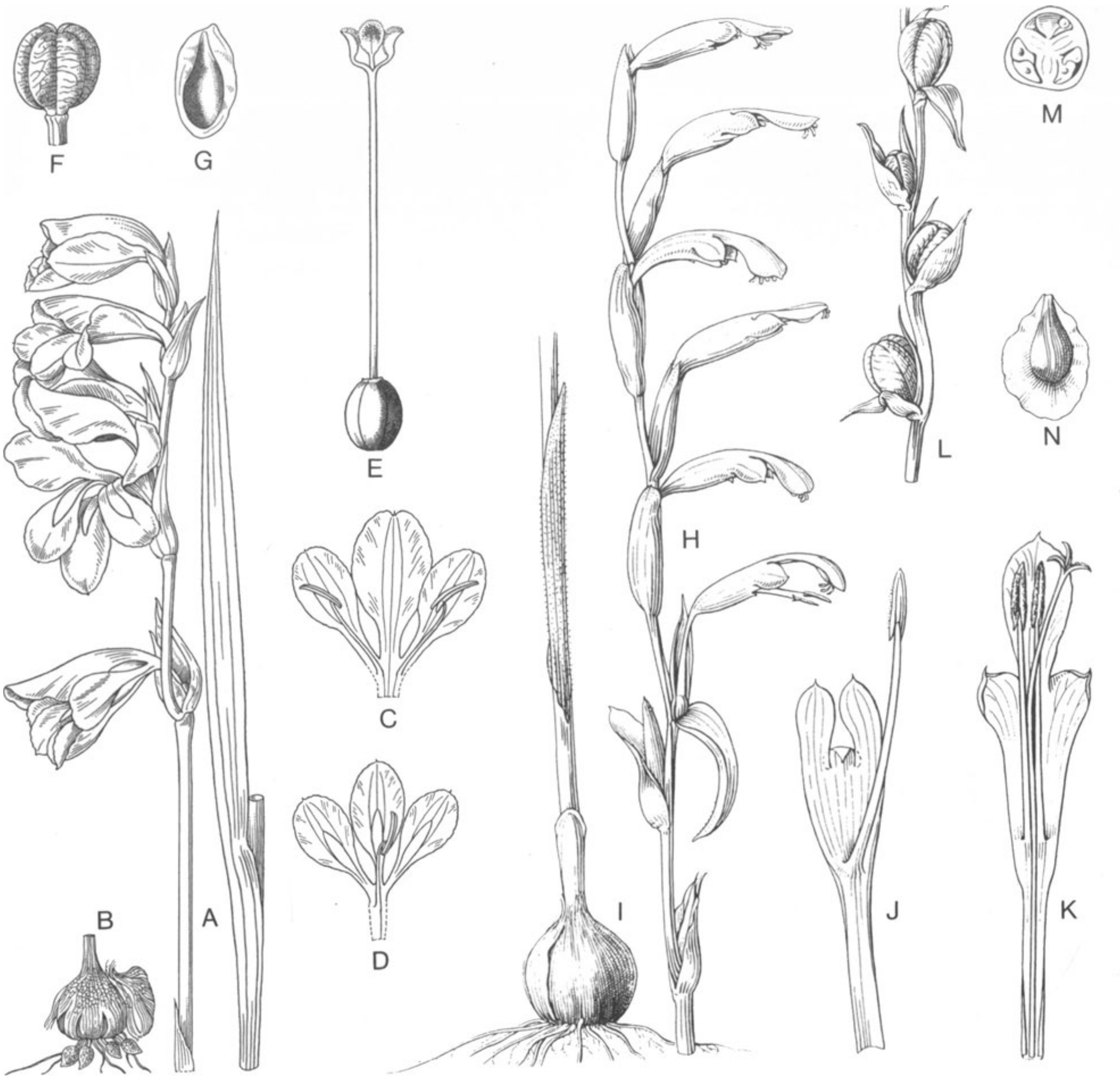


Fig. 118. Iridaceae. **A–G** *Gladiolus illyricus*. **A** Inflorescence and leaf. **B** Tunicated corm. **C** Upper perianth segments and two stamens. **D** Lower perianth segments and one stamen. **E** Pistil, the perianth and stamens removed from the top of the ovary. **F** Capsule. **G** Seed. (Ross-Craig 1972). **H–N** *Oenostachys vaginifer*. **H** Inflorescence. **I** Corm and basal leaves. **J** Lower perianth segments and one stamen. **K** Upper perianth segments, two stamens and style. **L** Capsules. **M** Ovary, transverse section. **N** Seed. (Milne-Redhead 1950)

appear one at a time. The leaves are principally ensiform, but often have adaxial longitudinal ridges. The flowers are actinomorphic and somewhat *Crocus*-like, usually with a short tube, and the stylar branches are bifid or rarely multifid. Several species are grown as ornamentals, e.g. *R. bulbocodium* from the Mediterranean region and *R. macowanii* from South Africa. – Related is *Syringodea* (8) in South Africa.

It is uncertain whether *Crocus* (80), which is distributed in the Mediterranean and western Asia to Iran, is closely related to *Romulea* and *Syringodea,* or whether the similarity could have developed by convergence. The leaves of *Crocus* are bifacial, flat or canaliculate. Most species flower in early spring, generally before the leaves are fully expanded. The flowers, as in *Romulea,* are sessile and the ovary does not appear above ground level. The perianth is actinomorphic and yellow, violet or white, and often bicoloured or tricoloured. Within the genus there is an interestingly great variation in the style, the three main branches of which may be repeatedly branched, palmate or fan-shaped; it is usually yellow to red in colour and may be rich in crocin and safranol (see the chemical characters of the family). *C. sativus* is cultivated in France, Spain and other mainly Mediterranean countries for its styles, which yield the yellow "Saffron", a spice used since antiquity to flavour and dye bread and other food. About a hundred flowers are needed to produce a gram of saffron. It is also used medicinally. Numerous species of *Crocus* are also grown as ornamentals, e.g. the early spring-flowering *C. vernus, C. chrysanthus, C. angustifolius, C. flavus, C. etruscus, C. laevigatus, C. minimus, C. sieberi* and *C. tomasinianus*. Some autumn-flowered species are also grown as ornamentals, e.g. *C. kotschyanus, C. nudiflorus, C. pulchellus, C. speciosus* and also the "Saffron Crocus", *C. sativus*.

Orchids

F.N. Rasmussen

The traditional order Orchidales is in this work included in Liliales sensu lato, expressing the view that the orchids have evolved within the Liliales. As the orchids are here treated as three distinct families (see the discussion below), and as no rank between order and family (suborder) is employed in this book, the orchids are left as a group without formal rank.

Another solution to the ranking problem, when the orchids are included in Liliales, would be to treat them as a single family, reduce the present families to subfamilies and create a new rank for the subfamilies of Orchidaceae, such as the contribes of Vermeulen (1966). However, the phylogenetic hierarchy of nature cannot be adequately expressed by the relatively few ranks employed in practical systematics. Thus, the ranking of the orchidaceous taxa in this treatment is only partly an expression of the supposed phylogenetic hierarchy (see Fig. 120).

Despite the lack of formal rank the orchids are here treated in the same way as the orders, with an introductory characterization of the group followed by the family treatments.

Three Families: Apostasiaceae, Cypripediaceae, Orchidaceae.

Perennial herbs, sometimes saprophytic. The Apostasiaceae and Cypripediaceae are usually terrestrial and the Orchidaceae prevailingly epiphytic but to a great extent also terrestrial. Orchid roots generally have a multi-layered velamen. In terrestrial species the roots are often swollen and tuberous; the epiphytic groups often have aerial roots.

The stems are sympodial or (in certain Orchidaceae) monopodial; they are often rhizomatous at the base and sometimes form corms. Internodes functioning as storage organs (*pseudobulbs*) are common in the Orchidaceae. The leaves are entire, linear to orbicular and have a tubular sheathing base; sometimes pseudopetiolate.

Hairs of different kinds are found on stems and leaves of most species, but few are distinctly hairy. Stomata are variable and include anomocytic and paracytic types. Silica bodies enclosed in special cells (stegmata) in stems and leaves are reported from both genera of Apostasiaceae, from *Cypripedium* in the Cypripediaceae and from numerous genera of the Orchidaceae (Solereder and Meyer

1930; Møller and Rasmussen, 1984). Calcium oxalate raphides are generally present.

The inflorescences are indeterminate and terminal or lateral (some Orchidaceae), rarely one-flowered.

The flowers are epigynous and zygomorphic with a trimerous perianth. The tepals of the outer whorl are usually referred to as sepals, although they are rarely truly sepaloid; the lateral tepals of the inner whorl are called petals, the median the *labellum.* The number of stamens is always reduced in relation to the two trimerous whorls of stamens of the complete monocotyledonous floral diagram. The median stamen of the outer whorl and the laterals of the inner are developed as either fertile stamens or as more or less distinct staminodes. Stamens and style are fused into a *gynostemium* which forms a "column" except in a few genera of Orchidaceae with almost sessile anther and stigma. The vascular strands of the adaxial stamens are always present in the gynostemium (Raunkiær 1895–1899; Swamy 1948). The anthers are basifixed to dorsifixed. The tapetum is glandular with uninucleate cells in all species investigated, except one species of *Paphiopedilum* (Cypripediaceae) and *Arundina* (Orchidaceae) with binucleate tapetal cells (Swamy 1949a; A.N. Rao 1967). Microsporogenesis is simultaneous. The pollen grains are single in Apostasiaceae and Cypripediaceae, but cohere in tetrads in the majority of Orchidaceae. The individual pollen grains are two-celled at dispersal.

The ovary is trilocular or generally unilocular. There are widely different interpretations of what is seen in a section of an orchid ovary. It appears to consist of six parts: three fertile elements bearing double placentae, alternating with three sterile elements (Fig. 123). The classic view (Brown 1833; Swamy 1948) holds that the ovary is tricarpellary with marginal placentae. However, Vermeulen (1966) and earlier workers cited by him have advanced the view that the ovary is indeed made up of six parts, the three sterile ones being either solid carpels or extensions of the receptacle. The orchidaceous ovary may be interpreted as tricarpellary with marginal placentation. The ridges seen on the outside of the ovary are the basal parts of the perianth-segments (Fig. 123, right), the sepal bases often splitting the carpels.

The style is more or less apically inflexed and terminated by a trilobate stigma with a Wet surface.

The numerous ovules are anatropous, tenuinucellate and usually bitegmic (unitegmic ovules are reported in *Paphiopedilum* of the Cypripediaceae and *Epipogium* and *Gastrodia* of the Orchidaceae). The development of the embryo sac is triggered by pollination. The actual fertilization sometimes takes place as late as 5–6 months after pollination (Wirth and Withner 1959). The information on embryology cited here is based on observations from the Cypripediaceae and Orchidaceae only. Embryogenesis of the few species investigated has proved very variable. The embryo is always immature in the ripe seed. Endosperm formation is arrested very early (not later than in the 16-nucleate stage) or wholly omitted. When it does take place it is nuclear.

The seeds are characteristically minute and numerous, but may nevertheless vary considerably in shape and size. Typically, only the outer layer of the outer integument persists as a membranaceous seed coat, which may have an adaptive significance with regard to aerodynamic properties and the wettability of the seed (Barthlott 1976b).

On germination the embryo forms a tubercle called a protocorm which is covered with rhizoids on most of its basal part. A radicle is not formed and usually no cotyledon; eventually several leaves develop from the apex (Veyret 1974). Most orchids under natural conditions will germinate only after establishment of symbiosis with a fungal mycelium (endotrophic mycorrhiza). The fungus in many cases is referable to the imperfect genus *Rhizoctonia,* but mycelia of several perfect genera, e.g. *Corticium, Clitocybe, Marasmius, Xerotus* and *Fomes* have been isolated from saprophytic Orchidaceae. The adult plants when green are usually able to grow without the mycorrhiza, but achlorophyllous, mycotrophic holosaprophytes are known from the Orchidaceae. The relationship orchid-fungus is usually imagined as one of parasitism by the orchid on the root fungus, but it is still being discussed whether the orchid mycorrhiza may be of mutual benefit for the organisms involved (Hijner and Arditti 1973; Hadley 1982).

Chemistry. Very little is known about orchid chemistry. So far as is known, the orchids have no distinct chemical characters.

Distribution. The orchids are distributed all over the world, but the vast majority of taxa on all levels are tropical. The smallest family, Apostasiaceae, is restricted to Indomalaysia and tropical Australia , and the Cypripediaceae are not found in Africa.

Relationships, Taxonomy. The orchids as circumscribed here correspond to one of the classic orders of flowering plants, comprising about 40%

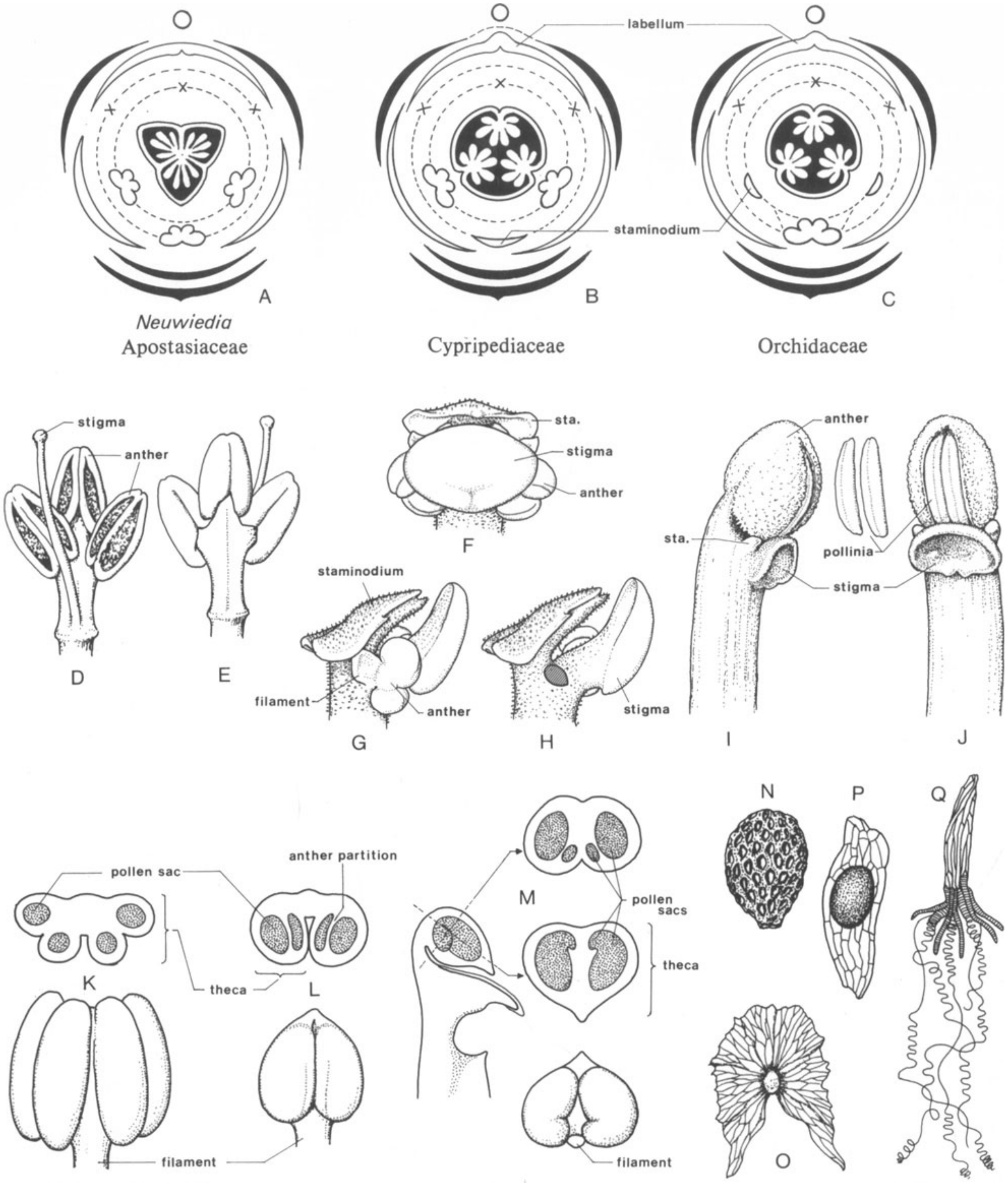


Fig. 119. Apostasiaceae, Cypripediaceae and Orchidaceae. **A–C** Floral diagrams of the three orchid families. **D–E** Apostasiaceae: *Neuwiedia inae,* androecium and style in different views. **F–H** Cypripediaceae: *Paphiopedilum appletonianum,* gynostemium in different views, one anther removed in **H. I–J** Orchidaceae: *Cephalanthera longifolia,* gynostemium in different views. **K–L** Anther in Liliaceae (**K**) compared with anther in Orchidaceae subfamily Neottioideae (**L**). **M** Details of gynostemium and anther in Orchidaceae subfamily Vandoideae. **N–Q** Seeds in Orchidaceae. **N** *Vanilla.* **O** *Galeola.* **P** *Orchis.* **Q** *Chiloschista.* (Orig. and redrawn after Barthlott, Johnsen and Rasmussen)

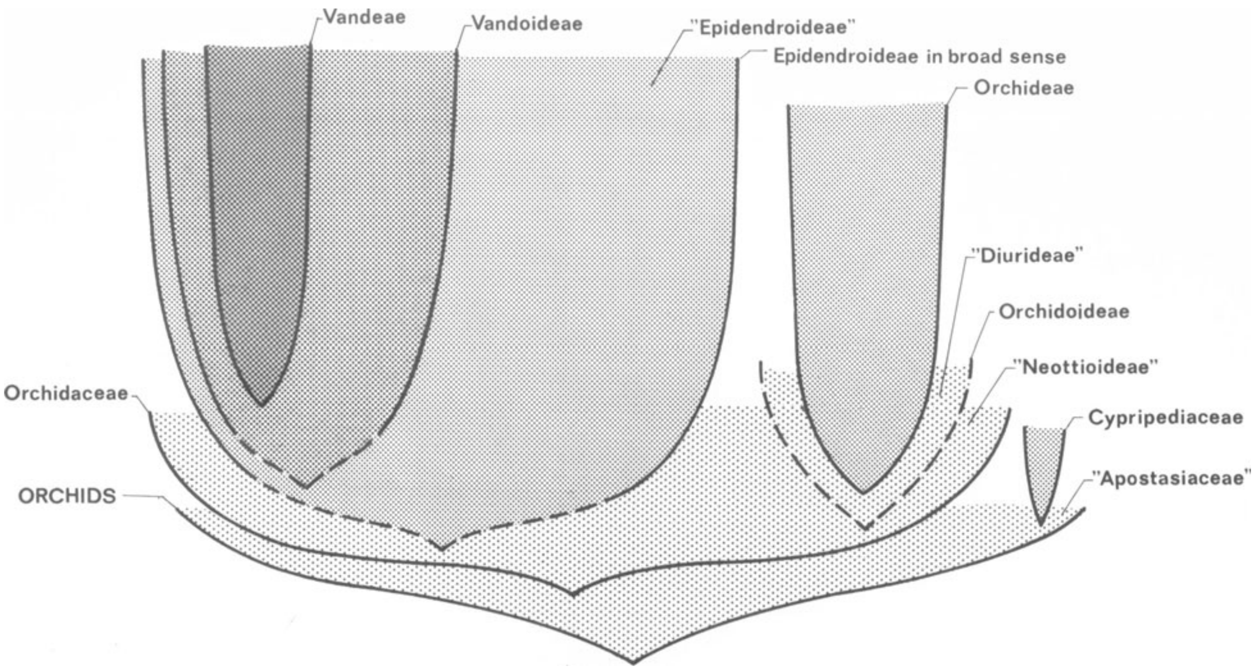


Fig. 120. Clades in the orchids. *Broken lines* indicate less certain clades. Names of clades are attached to the periphery of the respective groups, names of "remnant groups" are attached to the interior of the clades to which they belong and put in quotes in accordance with Wiley's conventions of phylogenetic classification (Wiley 1981). The clade Neottieae (in Orchidaceae) and many large lower-order clades, e.g. Angraecinae in Vandeae, are omitted for the sake of clarity in the scheme. The argumentation for each of the clades is found in the text. (Orig.)

of the monocotyledons. It is an almost certainly monophyletic group, distinct from all other orders in the reduction of the adaxial stamens plus the possession of numerous small, endospermless seeds (Fig. 119). The orchidalean gynostemium (Fig. 119) is a unique feature in the monocotyledons (analogous gynostemia are found in the Stylidiaceae and Asclepiadaceae among the dicotyledons).

The epigynous, zygomorphic flowers, the numerous small seeds and the mycotrophy are characteristics shared with the families here grouped as Burmanniales. This similarity has been stressed by several taxonomists when including both groups in one order, the "Microspermae". Hutchinson (1959, 1973) considered the Apostasiaceae "closely connected with the Hypoxidaceae, particularly with *Curculigo*", apparently mostly because of similarity in habit, and he excluded the family from the Orchidaceae. Vermeulen (1966) argued for a relationship between the Orchidaceae, the Commelinaceae and the Pontederiaceae, pointing out a reduction of the number of stamens as a common character. It is, however, not the same stamens that are reduced and the suggestion of relationship is contradicted by numerous differences.

The Orchids are most probably derived from epigynous Liliales-like ancestors with six stamens, simultaneous microsporogenesis and nuclear endosperm formation, through three-staminate forms comparable to the recent genus *Neuwiedia*. For a quite different interpretation see p. 95. A probable extant phylogenetic sister-group cannot be pointed out with our present knowledge.

While there seems to be a general agreement among different workers on the major groups of Orchids regarding their circumscription, their ranking and the supposed relationships between these groups differ widely. Many modern treatments follow Garay (1960, 1972) in considering the Orchids as consisting of one family, containing five or six subfamilies. The recognition of three families as suggested by Vermeulen (1966) is accepted here in accordance with the family concept applied throughout this textbook. Garay (1972) has argued that raising the Apostasiaceae and Cypripediaceae to family rank on morphological grounds would require similar recognition of the Orchidoideae s.str. as a distinct family. This statement was partly based on a later disproved interpretation of the rostellum in this group, and on incomplete information about the actual distribution of character states (see under Orchidaceae).

Apostasiaceae Lindley (1833) 2:15 (Figs. 119, 121)

Erect, perennial, sometimes (*Apostasia*) rhizomatous herbs. Roots penetrate the bases of the lower leaves; branching takes place in the subterranean part, which is sometimes tubercled, swollen or woody. Vessels with prevailingly simple perforation plates are recorded (WAGNER 1977).

The stems are woody at the base and sometimes also branched. Pseudobulbs are never formed. The leaves are spirally arranged, entire, plicate and herbaceous to papyraceous. Paracytic stomata were reported by SIEBE (1903). The inflorescences are terminal, sometimes branched racemes.

The flowers may be resupinate by twisting of the pedicel in *Neuwiedia* but not in *Apostasia*. They are slightly zygomorphic, white or yellow, and have 3+3 free tepals. The median inner tepal ("labellum") may be broader than the others. The stamens are two or three in number, representing the median of the outer whorl (sometimes missing) and the lateral ones of the inner whorl. The stamens are only partly fused with the style in the gynostemium. The anthers are dorsifixed or subbasifixed, introrse and dehiscent by longitudinal slits. The pollen grains are free, monosulcate with an operculum, and reticulately sculptured (NEWTON and N.H. WILLIAMS 1978; SCHILL 1978). Pollinia are not formed. The style is terminated by a two- to three-lobed stigma.

The ovary is trilocular with central placentation (Fig. 121C). The fruit is a thin-walled or fleshy capsule, usually disintegrating (in *Neuwiedia veratrifolia* opening loculicidally by three valves). The seeds are ovoid to elliptic, 0.2–0.4 mm long, and usually alveolate to reticulate, rarely provided with long appendages.

Data concerning embryology and chemical contents are wanting.

Distribution. The Apostasiaceae are distributed in South-East Asia, from the Himalayas and Ceylon to New Guinea and Northern Queensland, Australia. The highest number of species is found on Borneo.

Relationships, Taxonomy. The Apostasiaceae, especially *Neuwiedia,* are very close to most botanists' concept of an ancestral orchid, and may be considered a phenetic link between the Liliales sensu stricto and the two other families of the orchids.

"Affinities" with Hypoxidaceae (HUTCHINSON 1973) seem to be based mainly on resemblance in habit to *Curculigo* (see p. 162). Most morphological evidence (DE VOGEL 1969) and also the anatomy of the flower (V.S. RAO 1974) support a close relationship with Orchidaceae.

It has been suggested by GARAY (1972) that the two genera of Apostasiaceae are not closely related. They do not share any unique, advanced characteristics which would suggest a close relationship, and they differ in some notable respects, such as the number of stamens and the occurrence of a rhizome.

Neuwiedia (7) (Fig. 121A–D), Thailand to New Guinea, are non-rhizomatous terrestrial plants with three fertile stamens (Fig. 119D–E). The flowers are resupinate by twisting of the pedicel. The inflorescences are more or less hairy. – *Apostasia* (incl. *Adactylus;* 11), Ceylon to Northern Queensland, Australia, are rhizomatous plants. The flowers have two fertile stamens; in *A.* sect. *Apostasia* the median stamen is present as a staminode. The inflorescence is glabrous and the flowers are not resupinate.

Cypripediaceae Lindley (1833) 4:100 (Figs. 119G–H, 121E–G)

Herbs, usually terrestrial, with fleshy or fibrous roots on short rhizomes. Vessels with simple perforation plates are reported in the roots of three of the four genera, but vessels are lacking in stems as well as leaves (ROSSO 1966).

The stems are sympodial with scattered or basally crowded, spirally arranged or distichous leaves. The leaves may be thin and plicate or fleshy and conduplicate; in the latter case they are usually strap-shaped. Stomata are anomocytic or paracytic, with agene or perigene ontogeny (H. RASMUSSEN 1982). The inflorescences are terminal racemes or sometimes one-flowered.

The flowers are resupinate, strongly zygomorphic and of various colours. The two lateral "sepals" are fused into a synsepalum. The lateral "petals" are often considerably longer and narrower than the other tepals, in some species of *Phragmipedium* reaching a length of 50 cm. The median petal (labellum) is characteristically slipper-shaped. The two lateral stamens of the inner whorl are always present, and the median stamen of the outer whorl is present as a characteristic, shield-like staminode. The filaments are fused with the style, forming a thick, inflexed gynostemium (Fig. 119F–H). The anthers are subglobose and latrorse, dehiscing by longitudinal slits. The pollen grains are free, sulcate, ulcerate or porate, and reticulate, verrucate or scabrate or may lack distinct sculpturing (NEW-

TON and N.H. WILLIAMS 1978; ZAVADA 1983). The pollen is more or less viscid, but true pollinia are reported only from *Phragmipedium longifolium* and *Selenipedium chica.*

The ovary is trilocular and with axile placentation or unilocular with parietal placentation. Embryology is of the Asterad Type as well as the Onagrad Type (VEYRET 1974), and the endosperm may reach the four-nucleate stage. The fruit is a capsule with numerous small, membranaceous seeds.

Chemistry. Very little is known about the chemical contents of Cypripediaceae. Alkaloid-positive reactions were found in some species of *Paphiopedilum* by LÜNING (1974).

Distribution. The Cypripediaceae are widely distributed in the northern boreal and north temperate zone (*Cypripedium*) and in the tropics of the Old as well as New World, but are lacking in Africa. The largest number of species is found in Indo-Malaysia.

Relationships. The Cypripediaceae form a very distinct and homogeneous taxonomic entity. They differ from Orchidaceae in having two fertile stamens, neither of which corresponds to the single fertile one in Orchidaceae. The flower is strongly adapted to insect pollination: once an insect has entered the "slipper" it will head for one of the two openings between the base of the labellum and the staminode, where it must pass the stigma and one of the anthers (NILSSON 1981).

Paphiopedilum (50) (Fig. 121 E–F) from India to the Solomon Islands, has conduplicate leaves and unilocular ovaries. Ornamental species and artificial hybrids of this genus are widely cultivated and commercially important, e.g. *P. insigne* (North India and Nepal). It has a characteristic white upper margin of the dorsal outer tepal and has been used extensively in breeding. *P. barbatum* and *P. callosum* (Thailand and Indo-China) have ciliate calli on the sepals. *P. villosum* (North India to Thailand) is an epiphytic species with large, brownish flowers. – *Phragmipedium* (10), in Central and South America, has conduplicate leaves and a trilocular ovary. – *Cypripedium* (35), in boreal, temperate and subtropical zones of America, Europe and Asia (the highest number of species in Asia), has plicate leaves and a unilocular ovary. *C. calceolus* ("Lady's Slipper") occurs in boreal Eurasia from France to Northeast Asia. The closely related *C. pubescens* occurs in temperate North America. – *Selenipedium* (4), in the Central and South American tropics, has plicate leaves and trilocular ovary. Some species become as tall as 5 m (Fig. 121 G).

Orchidaceae A.L. Jussieu (1789) ca. 730:20,000 (Figs. 119–126)

Perennial herbs with extremely variable morphology and size, terrestrial, litho- or epiphytic, sometimes climbers. Most of the "epiphytic" species are very well capable of growing on the ground when they are given the chance in forest clearings etc. Two completely subterranean species and several achlorophyllous saprophytic forms are known. The roots may be thin and wiry or sometimes form thickened, cord-like or tuberous storage organs. The roots of the epiphytic forms are usually thick and have a velamen; they emerge by breaking through the leaf sheaths. Chlorophyll-containing assimilating roots occur in some genera. Vessels have been observed in the roots of the few genera investigated for this character (WAGNER 1977).

The basal parts of the stems may be modified in various ways. Branching is usually sympodial and in terrestrial forms the branched part may be rhizomatous (Fig. 121 K), whereas in the epiphytes there may be branching leafy shoots which can be prostrate, erect or pendent. Many epiphytic orchids develop thickened storage organs called pseudobulbs from one or more internodes of the stem (Fig. 121 L–M).

In monopodial species the whole plant usually consists of a single continually growing shoot. As with sympodially branching orchids, roots may be borne on the leaf-bearing part (e.g. *Vanilla* and the tribe Vandeae, Fig. 121 N). Many species have a very short stem with crowded leaves. The texture of the stem varies from succulent to almost woody. Stems of very few species have been investigated anatomically; some have vessels with scalariform perforation plates (WAGNER 1977).

The leaves are alternate, rarely opposite or whorled, spirally or distichously arranged, sometimes closely imbricate. They are often jointed to their sheathing base, falling off when old. Their shape is generally linear to broadly ovate, more rarely circular, angular-cordate, hastate, etc., very rarely lobed. Their texture varies from membranaceous to coriaceous, in which case they may function as storage organs. The ptyxis of the mesomorphic leaves is often plicate or convolute, and the coriaceous often conduplicate. Terete and ensiform leaves occur in several groups. Some species have reduced, scale-like leaves only. Stomata with subsidiary cells have been found in most groups, but subsidiary cells are often lacking in subfamily Orchidoideae. The subsidiary cells, when present,

Fig. 121. Apostasiaceae (**A–D**), Cypripediaceae (**E–G**) and Orchidaceae (**H–N**). **A–B, D** *Neuwiedia inae.* **A** Habit. **B** Flower. **D** Fruit. **C** *N. veratrifolia,* ovary, transverse section. **E–F** *Paphiopedilum* sp. **F** A flower in lateral view. **G** *Selenipedium chica* habit. **H–N** Orchidaceae, roots, tubers and corms. **H–J** *Orchis,* tuberoid roots. **H** second year and first year tuberoid. **I–J** "Tuberoid", in longitudinal section and transverse sections, schematically. **K** *Epipactis,* rhizome with fibrous roots. **L–M** *Pholidota* (**L**) and *Bulbophyllum* (**M**), "pseudobulbs", which are swollen internodes. **N** *Vanda* sp., with monopodial growth, thick leaves and aerial roots. (Orig. and redrawn after Ames, Pfitzer and van Crevel)

generally have perigenous development, the perigene cells being formed by oblique divisions of surrounding cells; mesogene cells are reported from the genera of the tribes Cranichideae (N.H. WILLIAMS 1979) and Orchideae (H. RASMUSSEN 1981).

The inflorescences may be terminal or lateral; in some genera both terminal and lateral ones occur on the same shoot. Lateral inflorescences frequently break through the sheath of the subtending leaf or, if the leaves are closely set, those of several leaves. The inflorescence is always basically racemose, but many kinds of modification occur, from racemes or spikes to branched panicles, dense capitula, umbels, spadices, etc.

The flowers are usually resupinate by torsion of the pedicel and/or ovary. The flowers are generally bisexual, but unisexual flowers occur in some species. Their perianth may be almost actinomorphic, but is generally strongly zygomorphic. The shape of the tepals varies strongly. The median inner one, the labellum, is in the majority of species clearly different from the others. It is frequently spurred and often adorned with various keels or calli. Spurs and calli may occur also on the other tepals. Fusion of two or more tepals or of tepals and gynostemium is characteristic of many genera. The fused basal parts of the labellum and the lateral sepals (and, sometimes, also of the lateral petals) may appear as a ventral extension of the column carrying the labellum – "*column-foot*" as in, e.g., *Dendrobium* and *Bulbophyllum* (Fig. 125M). The sepals and the column-foot may form a chin-like projection called a *mentum.*

The androecium normally includes only one fertile stamen, the median one of the outer whorl, and two more or less distinct staminodes representing the lateral stamens of the inner whorl. However, a specimen with two fertile anthers, the median one of both whorls, has recently been described as a distinct genus, *Diplandrorchis,* apparently closely related to *Cephalanthera* (CHEN 1979). The anther in Orchidaceae varies from erect with four distinct pollen sacs to incumbent with indistinct partitions between the pollen sacs (Fig. 119L–M).

The connective is frequently dorsally and apically enlarged, enclosing the thecae as a tunic. The connective and the empty thecae are often then referred to as the "*anther cap*" or "operculum". The anther is introrse and dehisces by longitudinal slits. The pollen grains are generally united into tetrads, but are free in a few genera (*Cephalanthera; Vanilla* and allies). The pollen grains vary from prominently reticulate in most of the neottioid orchids to smooth and tectate, as in most epidendroid and vandoid orchids. The pollen grains generally appear as inaperturate, except for example, in some neottioid genera with ulcerate or porate pollen grains (SCHILL and PFEIFFER 1977; ACKERMANN and N.H. WILLIAMS 1980; ZAVADA 1983). The pollen grains of *Vanilla* and related genera have been reported to have three to four pores (ERDTMAN 1952). The pollen tetrads are agglutinated into *pollinia* by strands of sterile sporogenous material. The texture of the pollinia varies from very soft and easily disintegrating, to waxy or bony. The basic number of pollinia is four, one for each pollen sac. The interior strands of anther-tissue which are not differentiated into pollen will remain as septa between the pollinia and form the so-called anther partitions, which dry up together with the anther cap. By reduction of the partitions between the pollen sacs (microsporangia) (or, ontogenetic confluence of the sporogenous areas in the anther) the pollinia may be only two, and by formation of secondary partitions the number of pollinia may increase to up to twelve. In some orchids the pollinia are further divided into granular packets called *massulae,* in which case the pollinia are said to be *sectile* (Fig. 124F). Each massula corresponds to one pollen mother cell (HOFMEISTER 1861).

The style is apically inflexed and terminated by a three-lobed stigma. The three stigmatic lobes – i.e. the apices of the three carpels – are seen in the early developmental stages of all orchids, but they usually become obscured during the growth of the gynostemium eventually forming a "stigmatic cavity", the margins of which represent the apices of the carpels. The median stigma lobe, as well as participating in the formation of the stigmatic cavity, is always more or less modified apically. Its modified apical part is often referred to as the *rostellum.* However, the term rostellum is also frequently defined as "the median stigma lobe", i.e. including the receptive basal part *and* the modified apical part. The latter usage gives the term a more precise morphological connotation and is strongly recommended. It is often stated in textbooks that the median stigma lobe is sterile (non-receptive). This error originates from confusion in the use of the term "rostellum", and the discussions in orchid literature as to whether the rostellum is fertile (receptive) or not are in fact caused merely by contradictory definitions. In the majority of orchid species most of the receptive stigmatic surface does in fact belong

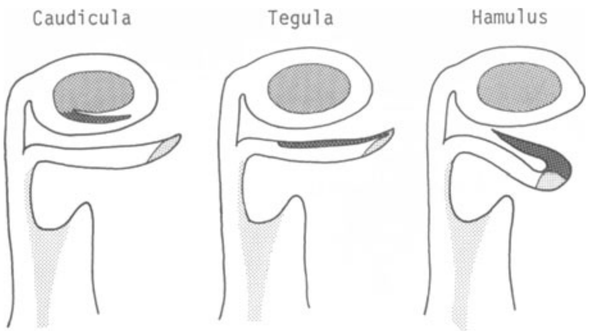


Fig. 122. Orchidaceae. Different kinds of pollinium stalks, schematically. A caudicula is formed inside the anther whereas a "stipes" is derived from the rostellum. A tegula is an epidermal strap, and a hamulus is the recurved apical part of the rostellum. (Orig.)

to the median stigma lobe, as seen in the column ontogeny of *Doritis* (Fig. 126F–K).

In its simplest form the rostellum is only slightly larger than the lateral stigma lobes (e.g., *Cephalanthera,* Fig. 124A), but usually it is more elaborate, e.g. elongated into a prominent beak-like structure, the rostellar projection (as in many vandoid orchids, Fig. 126K). It can also be lobed (Orchidoideae) or transversely folded (*Epipogium*). The rostellum plays an important role in the pollination of the species of Orchidaceae, as the pollinia are deposited on its abaxial side (the "*clinandrium*") after the beginning of anthesis, and are glued to the pollinator by viscid material orginating from its apex. This principle is often developed into very intricate relationships of structures: in many orchids the viscid apex is detached from the rest of the rostellum and removed in its entirety together with the pollinia. The portion of the rostellum that produces the viscid matter is termed the *viscidium* ("retinaculum", "glandula", "viscid disc"). Two viscidia may be present if the rostellum is lobed or bifid.

The pollinia in most species are connected with the viscidium by some kind of *pollinium stalk* (Fig. 122). This may simply be an elongation of the pollinia (*caudicula*), consisting of sporogenous tissue with scattered pollen tetrads embedded in it, as in many epidendroid orchids (Fig. 125L). The anther partitions may also take part in the formation of an elastic, hyaline pollinium stalk, e.g. in Orchidoideae (Fig. 125C) and *Epipogium.* Alternatively pollinium stalks in some orchids can be differentiated from the rostellum in various ways. In one type a ridge or strap-like plate of thick-walled cells (a *tegula,* litt.: "small roof", Fig. 122) becomes freed from the abaxial side of the rostellum by disintegration of the anticlinal cell walls; after anthesis this is glued to the pollinia by means of viscid sterile sporogenous material (most vandoid orchids, Fig. 126K; some Goodyerinae). Another kind of pollinium stalk is the hook-like *hamulus* (Fig. 122), formed by apical growth of the rostellum; it is found in some neottioid orchids, the subtribe Prasophyllinae of the Diurideae (Fig. 124K), a few species of *Bulbophyllum* and perhaps some related genera. The pollinium stalks provide diagnostic characters in orchid classification, and various intricate (and often confused) terms have been applied to them. The term *caudiculae* (sing. *caudicula*) is most frequently reserved for stalks derived from the anther itself, while stalks of rostellar origin are collectively termed *stipites* (sing. *stipes*). The pollinia are generally attached to their stalks by their apices ("acrotonic" orchids), but in forms with an erect anther and a relatively short rostellum the attachment may be lateral or basal ("basitonic" orchids, e.g. *Cephalanthera,* Fig. 119I–J, and all Orchideae). The unit that is removed as a whole by the pollinator is termed a *pollinarium* [one or more pollinia plus stalk(s), if present, and a viscidium].

The ovary is unilocular except in very few genera. Embryo sac formation is occasionaly bisporic (*Allium* Type), but the majority of species studied have the monosporic "*Polygonum* Type", although often with a reduction in the number of nuclei. Polyembryony and apomixis have been observed in many orchids (Veyret 1974). Embryogeny is either of the Asterad or the Onagrad Type, and also irregular types are reported. Proper endosperm is not formed, but formation of a few endosperm nuclei has been observed in ovules of some genera (up to 12 or 16 in species of *Vanilla* and *Galeola;* Veyret 1974). Double fertilization generally does not take place at all.

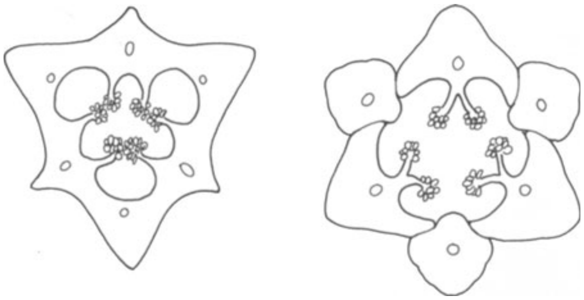


Fig. 123. Orchidaceae. Transverse sections of ovaries. *Left Cephalanthera rubra.* (Redrawn from Raunkiær 1895–1899). *Right Nervilia fordii.* (Orig.)

The fruit is a capsule, opening by three or six longitudinal slits, except in the baccate fruits of certain species of *Vanilla* and *Galeola* and *Palmorchis* (all Vanilleae) and in *Rhizanthella* of the Diurideae.

The seeds vary considerably in shape and size (Fig. 119N–Q), from almost filiform types where the membranaceous testa is exserted at each end, reaching a length of up to 5 mm, to very minute, oblong to subglobose and less than 0.1 mm long. It has been observed in a species of *Chiloschista* (Vandeae) that one end of the seed coat has specialized cells with strong spiral thickenings, sending out long threads (to 4 mm) when moistened (BARTHLOTT and ZIEGLER 1981). *Vanilla, Galeola* and related genera have a different kind of seed with opaque, sclerotic seed coats.

Chemistry. Biochemical data on Orchidaceae are very scattered. LÜNING (1974) and other investigators, who tested 2,000 species of 281 genera for presence of alkaloids, found that only few species are alkaloid-rich.

Distribution. Orchidaceae is a subcosmopolitan family, with representatives in all phytogeographical regions and climates, but the majority of taxa on all levels are tropical. Most genera are, however, restricted to only one continent; only 11 genera are pantropical, and only 21 more genera show a transoceanic distribution, 27 of these being terrestrial, which may indicate an early expansion of the family, before the epiphytic mode of life evolved (GARAY 1964).

Pollination Biology. The Orchidaceae are famous for their unique examples of complicated adaption to insect pollination. The components of the orchidaceous pollination-biology character syndrome may be summarised thus: (1) Zygomorphy of the flower imposes a unidirectional approach by the pollinator (as is usual in other groups). (2) Pollen is presented to pollinators in only a few packages per flower and it is glued to their bodies. (3) Floral attributes restrict the range of potential visitors to each species: this is achieved by special attractants on the one hand and structures with a selectively exclusive effect on the other. (4) The limited range of visitors makes possible precision in placing the pollen on their bodies; without this, the above-mentioned packaging of the pollen would not be effective. Special adaptations, by which insect visitors are positioned in the flower and the pollinia (pollinaria) are positioned upon the insect, are developed. (5) For the same reason, the shaping and positioning of the stigmatic cavity are adapted to the removal of the pollen from the correct part of the body of the right insect. A few orchids are bird-pollinated.

This syndrome has far-reaching effects on the biology and, hence, on the evolution of the family. It may lead to closer and closer specialization and more and more opportunities for speciation based on floral isolation [see, as general sources, VAN DER PIJL and DODSON (1966), PROCTOR and YEO (1973), NILSSON (1981), DRESSLER (1981)]. This floral isolation may become effective not only by using different insects but by depositing pollinia on different parts of an insect which is attracted to more than one species of orchid.

In the course of progressive floral specialisation, arrangements for the positioning of the insect have evolved beyond simply shaping the flower to fit the insect closely when it has attained the reward (in fact, there may be no reward). There may be loss of control by slipping, temporary imprisonment or intoxication. A further step is active "handling" of the insect by motility which is passive (pivoted epichile in various genera, e.g. *Drakaea* and, especially, *Bulbophyllum*) or active (irritability of the epichile or whole labellum, e.g. *Pterostylis*). An intermediate step is the enforcement of a one-way passage through the flower as in *Coryanthes* (see also Cypripediaceae). Handling and intoxication also appear to have a rôle in promoting outcrossing by stimulating the insect to move to another plant and/or causing a delay sufficient to allow the pollinia to adjust their position for reception by a stigma.

The orchids display amazing diversity of form and colour of the flowers and even of inflorescences, the axes of which may function visually or mechanically in the pollination process. Some orchids offer nectar to potential pollinators in a conventional way, but never pollen. However, a specially produced pollen-like foodstuff ("pseudo-pollen") is offered by some species of *Polystachya* and some other genera, and nutritive oil is probably offered by some genera (VOGEL 1978b). The food-gathering instincts of insects may also be exploited without the offer of any reward: deceit may be achieved by a normal-looking flower, perhaps with a spur, which is devoid of nectar (some Orchidoideae) or by visual imitation of anthers (*Arethusa, Calopogon* and *Calypso*) or pollen (*Cephalanthera*: DAFNI and IVRI 1981); alternatively the flower may mimic another flower in the habitat (some *Oncidium* spp., *Epidendrum ibaguense*). Also, the Orchidaceae exploit, to a degree shown by no other plant group, instincts other than those of food-gathering, namely mating (*Ophrys, Cryptostylis, Caladenia,* etc., attract male Hymenoptera; other genera attract male Diptera), egg-laying by imitation of substrates such as carrion (*Bulbophyllum* spp.), fungal fruit bodies (*Dracula,* and probably *Corybas* (VOGEL 1978a) or aphids (*Epipactis consimilis;* IVRI and DAFNI 1977); gathering of sexual pheromones (chemical signalling compounds) (occurring especially in members of subtribes Catasetinae and Stanhopeinae, pollinated by male bees of the family Apidae, tribe Euglossini); territory-holding (some *Oncidium* spp., pollinated by male bees); and roosting (*Serapias,* pollinated by male bees; DAFNI et al. 1981, and earlier references therein).

Plant groups which rely on a restricted range of specialized pollinators tend to have weak post-pollinatory (physiological or genetic) sterility barriers between species. Orchids, the most specialized large family in this respect, are notorious for their interfertility, which readily transgresses the established generic boundaries. Such hybridization, while not common in nature, is the basis of a large and widespread horticultural industry. In nature it keeps open the possibilities of speciation or enhancement of variability by hybridization.

Although highly specialized pollination relationships are common in Orchidaceae, many orchids have a broader range of potential pollinators. Autogamy is not rare in the Orchidaceae; in some cases it may be a consequence of the breakdown of the pollination relationships. It is doubtful, however, whether any orchid species is pollinated exclusively by one insect species.

Taxonomy. The features chiefly emphasized when dividing the Orchidaceae into major groups (subfamilies, tribes) are:

1. Pollinia: texture soft and friable to waxy or cartilaginous; sectile or not.
2. Pollinium stalks: absent or present; when present: caudicula, tegula or hamulus.
3. Viscidium: absent or present; structure and shape.
4. Position of attachment between pollinia and viscidium: basal ("basitonic") or apical ("acrotonic").
5. Position and shape of the anther: erect or incumbent to deflexed; long and tapering or short and broad; overtopping the rostellum or not.
6. Persistence of anther wall: drying up and falling off after anthesis ("operculate anther") or not.
7. Number of pollinia.
8. Shape and length of the rostellar projection: broad, shelf-like to slender and beak-like; projecting between the thecae of the anther (as in Orchideae) or not.
9. Position of inflorescences: terminal on the shoots or axillary.
10. Vegetative habit and mode of growth: terrestrial with or without subterranean storage organs; epiphytic with or without pseudobulbs; sympodial growth or monopodial one-shoot plants.
11. Foliage: thin, pleated, convolute leaves or leathery, conduplicate leaves.

None of the larger groups (subfamilies, tribes) in any orchid classification is uniquely designated by any one of these characters (except, perhaps, the tribus Orchideae – see below). Attributes once believed to be confined to certain groups are often found in modern investigations to be more widely distributed, suggesting many parallelisms. Furthermore, many previously supposed homologies have proved to represent cases of convergence.

Among the most important characters on subtribal level are the arrangement of roots (fascicled or scattered on the rhizome); shape and structure of pseudo-bulbs; arrangement of leaves, and whether articulated or not; morphology of perianth and gynostemium. Recent research has revealed that micro-characters such as seed structure and seed sculpture, pollinium surface, stomata and stomatal development etc. may also characterize groups.

Table 2. *Subdivision of Orchidaceae*

- Subfamily Neottioideae
  - Tribus Epipactieae (subtribus Limodorinae sensu DRESSLER, 1981, pro parte)
  - Tribus Neottieae (subfamily Spiranthoideae DRESSLER plus subtribus Listerinae sensu DRESSLER)
    - The *Listera* Group (subtribus Listerinae)
    - The *Goodyera* Group (subtribus Goodyerinae)
    - The *Spiranthes* Group (tribus Cranichideae)
- Subfamily Orchidoideae
  - Tribus Diurideae
    - including subtribus Chloraeinae
    - The *Diuris* Group { (subtribus Diuridinae)
(subtribus Prasophyllinae)
  - Tribus Orchideae
    - The *Orchis* Group
    - The *Habenaria* Group
    - The *Disa* Group
- Subfamily Epidendroideae
  - Tribus Arethuseae
  - Tribus Vanilleae
  - Tribus Gastrodieae
  - Tribus Epipogieae
  - Tribus Coelogyneae
  - Tribus Malaxideae
  - Tribus Calypsoeae
  - Tribus Epidendreae
    - The *Epidendrum* Group (subtribus Laeliinae)
    - The *Eria* Group (subtribus Eriinae)
    - The *Pleurothallis* Group (subtribus Pleurothallidinae)
    - The *Dendrobium* Group (subtribus Dendrobiinae)
    - The *Bulbophyllum* Group (subtribus Bulbophyllinae)
- Subfamily Vandoideae
  - Tribus Polystachyeae
  - Tribus Cymbidieae
    - The *Cymbidium* Group (subtribus Cyrtopodiinae)
    - The *Catasetum* Group (subtribus Catasetinae)
    - The *Stanhopea* Group (subtribus Stanhopeinae)
    - The *Oncidium* Group (subtribus Oncidiinae)
  - Tribus Maxillarieae
    - The *Corallorhiza* Group (subtribus Corallorhizinae)
    - The *Zygopetalum* Group (subtribus Zygopetalinae)
    - The *Maxillaria* Group (subtribus Maxillariinae)
  - Tribus Vandeae
    - The *Vanda* Group { (subtribus Aerangidinae, in a broad sense, including subtribus Sarcanthinae nom. illeg.)
    - The *Angraecum* Group (subtribus Angraecinae)

The attempts of various authors to divide the family into "natural" groups have resulted in several highly contrasting systems of classification. Until now, the most influential has certainly been that of SCHLECHTER (1926). GARAY (1960, 1972), Dressler and Dodson (1960), Vermeulen (1966), and Dressler (1981) have suggested very different hierarchical arrangements of the larger groups and very different positions of the odd genera. The following division is modified from that of Dressler (1981). Dressler (1981) acknowledges 4 subfamilies, 21 tribes and 70 subtribes of monandrous orchids; 16 of these tribes are mentioned here (Table 2). A few names are different from the ones used by Dressler due to different positions of nominal genera. The "groups" mentioned here under some of the tribes in most cases correspond to Dressler's subtribes (names in brackets).

None of the classifications cited above has been claimed to be phylogenetic in the sense that all taxa are presumed to be strictly monophyletic groups (clades) with ranks reflecting the branching hierarchy of a hypothetical phylogenetic tree. Some groups are clearly paraphyletic "remnant groups", defined by shared primitive (ancestral) characters, other groups are given rank according to their degree of difference from other groups although they are supposed to have evolved within groups given equal or lower rank. At present far too little is known about the homology and actual distribution of characters in the Orchidaceae to construct a reliable phylogenetic scheme with a resolution of the "remnant groups", but the presumed status of the taxa mentioned here is noted under each taxon (see also Fig. 120).

Subfamily Neottioideae

The subfamily Neottioideae in most classifications comprises a number of genera with mainly primitive characters. The neottioid orchids are usually terrestrial hygro- or mesophytes and very few are epiphytes. They never have pseudobulbs or any other of the vegetative specializations characterizing the epidendroid and vandoid orchids. The anther is erect or bent slightly forward. It contains four or two bipartite, soft, granular or sectile pollinia often without pollinium stalks (although all known kinds of pollinium stalk have now been found in the Neottieae; F.N. Rasmussen 1982). The attachment to the more or less well-differentiated viscidium is usually acrotonic.

Recent investigations have demonstrated that certain of the genera and generic groups of the traditional Neottioideae are actually better conceived of as the most primitive members of the subfamilies with which they share apparently homologous advanced characters. As here circumscribed, the Neottioideae consist of one small unresolved "remnant group", the tribe Epipactieae, and one larger tribe, Neottieae, which is supposed to be a monophyletic entity.

Tribus Epipactieae (Subtribus Limodorinae pro parte in Dressler 1981) 7:50

This contains a number of mainly northern temperate genera, the most primitive of the monandrous orchids. They are terrestrials, often saprophytic, with elongated rhizomes carrying more or less clustered, rather thin roots. The leaves are spirally dispersed on the erect stem, convolute or plicate and nonarticulate. The inflorescences are terminal and the flowers have free tepals. The labellum may be spurred or saccate and is often divided into hypo-, meso- and epichile. The anther is slightly inflexed (Fig. 124A). The pollinia are very soft, and in *Cephalanthera* composed of single grains. The viscidium is not detachable. – *Cephalanthera* (12) ranges from between Europe and North Africa to Korea and Japan and has a single species in the Western U.S.A. The anther projects high beyond the hardly modified rostellum. The stigma is cup-shaped with somewhat revolute margins. *Epipactis* (30) is distributed over the Northern Hemisphere; most species are Asiatic but a single species extends in the south to Mozambique. *E. helleborine* is a common forest floor herb in central and North-Western Europe, naturalized in North America. Several autogamous species have been segregated from this species. *E. veratrifolia* (Asia Minor to China), *E. gigantea,* North America and Asia Minor to Himalaya, and *E. africana* are all stout herbs up to 2 m tall. *Limodorum* (1) *abortivum,* in Southern Europe, is a robust saprophyte with bracteal leaves and long-spurred, violet or bluish flowers.

Tribus Neottieae (Subfamily Spiranthoideae Dressler plus subtribe Listerinae) 85:1,000

This tribe has a worldwide distribution, but is centred mainly in the tropics of Asia and America. It is possibly a monophyletic group, which is characterized by the dorsal, erect anther and the corresponding elongated, tapering rostellum (Fig. 124B). This basic arrangement is varied in a number of ways, distinguishing separate phylogenetic lines within the group. The majority of genera have two bipartite pollinia, tapering towards the apex, where they connect with a distinct, detachable viscidium. However, all above-mentioned kinds of pollinium stalks are found in this tribe,

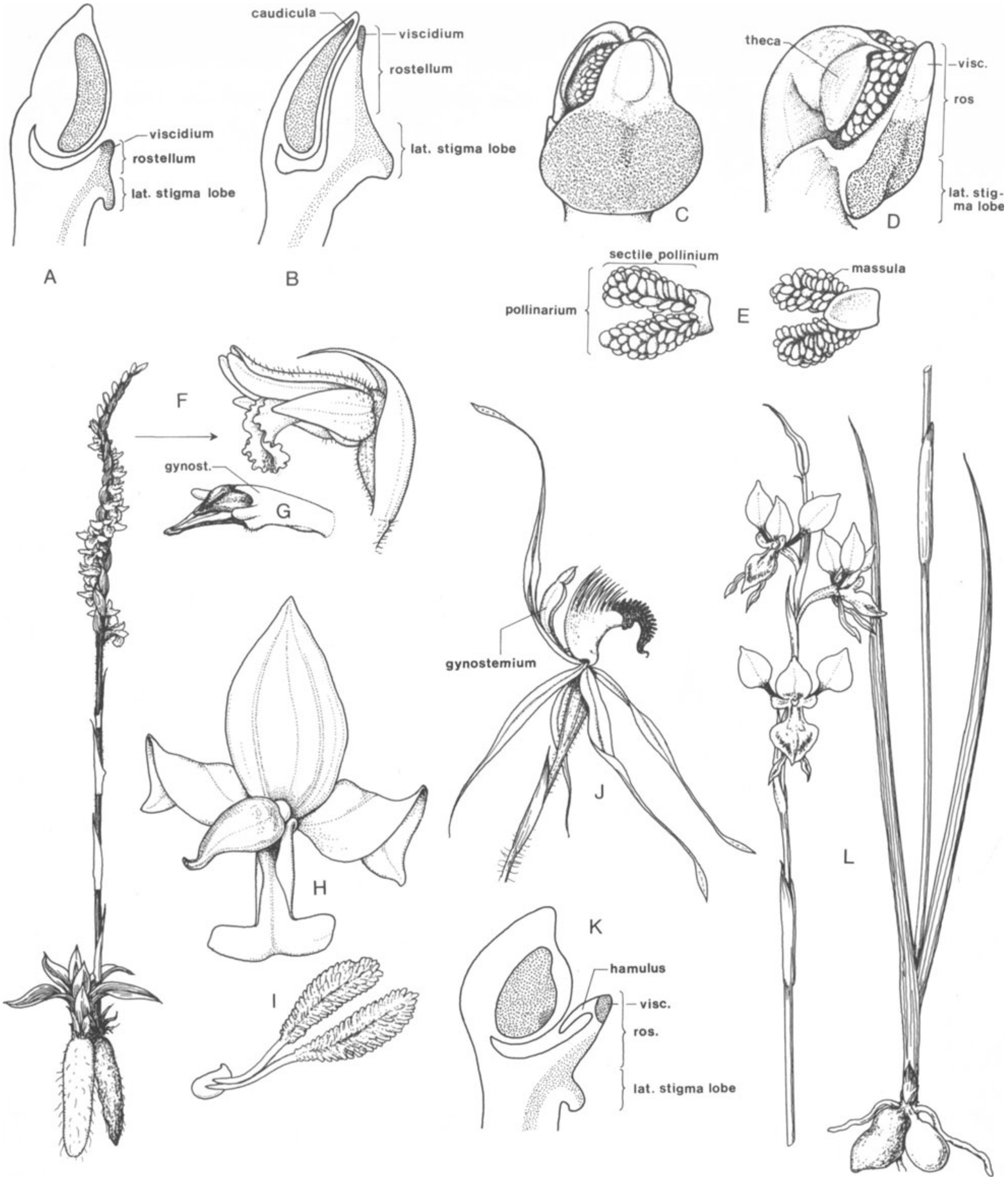


Fig. 124. Orchidaceae subfamily Neottioideae (**A–I**) and subfamily Orchidoideae tribus Diurideae (**J–L**). **A–B** Gynostemium in longitudinal section, *Cephalanthera* and *Spiranthes,* respectively. **C–E** Gynostemium in front (**C**) and side (**D**) views and pollinarium (**E**) in the genus *Goodyera.* **F–G** *Spiranthes spiralis* with flower and gynostemium (**G**). **H–I** *Ludisia discolor,* flower and pollinarium. **J** *Caladenia dilatata,* flower. **K** *Microtis,* gynostemium in longitudinal section. **L** *Diuris aurea.* (Orig. and redrawn after BRIEGER, NICHOLLS, RASMUSSEN and RUPP)

and two genera have a peculiar sensitive viscidium, which releases sticky matter when touched.

The Listera Group (Subtribus Listerinae) (3:40) in the Northern Hemisphere, is characterized by the sensitive rostellum. The green and assimilating leaves, when present, are only two in number. This group is often referred to the previous tribe, in which case the names of the tribes are different. DRESSLER (1981) refers the Listerinae and the Limodorinae to the subfamily Orchidoideae.

Listera (25) occurs in the temperate Northern Hemisphere. Characteristic are the two apparently opposite foliage leaves, hence "Twayblade". – *Neottia* (10), occurs in Northern and central Asia but with one species, *N. nidus-avis,* in Europe. It consists of brownish yellow saprophytes with bracteal leaves. The short subterranean rhizome carries a dense cluster of thick roots, hence the name "Bird's-nest Orchid".

The Goodyera Group (Subtribus Goodyerinae) (35:430). Pantropical and Northern Hemisphere. Forest floor plants with creeping, succulent rhizome and often more or less variegated leaves. The lateral petals are often fused with the dorsal sepal to form a hood over the gynostemium. The labellum is saccate or spurred, often with a two-lobed blade. Inside the spur there are sometimes conspicuous glands. The pollina are sectile.

Goodyera (50) occurs in temperate and tropical Eurasia. *G. repens,* which is circumboreal, is the only species in Europe. It is a small, creeping herb growing in the moss of coniferous forests. – *Erythrodes* (about 80) occurs in South-East Asia and tropical America. – *Ludisia* (1) *discolor* (Fig. 124) (syn.: *Haemaria d.*), in South-East Asia, has peculiar twisted flowers with a white perianth and a striking yellow anther. Its leaves are often vividly variegated. It is frequently cultivated. – *Anoectochilus* (40), in tropical Asia, is cultivated for the variegated leaves with a metallic lustre, "Jewel Orchids". – *Zeuxine* (50), in tropical Asia and Africa, has some species with tegula (see above). *Zeuxine* and *Anoectochilus* belong to a subgroup in which the stigma forms two dome-shaped areas, one on each side of the rostellum.

The Spiranthes Group (Tribus Cranichideae in DRESSLER 1981) (45:500). This is characterized by leaves in a basal rosette, and by clustered, often thick storage roots.

Spiranthes (40), is distributed in temperate zones of Eurasia and North America and has a few species in the tropics, including Eastern Australia; the small flowers are placed on a spirally twisted rachis. *S. spiralis* (Fig. 124F–G) ranges from North Africa to Denmark. *S. romanzoffiana,* in North America from California to Alaska, is also found in a few places in Ireland and western England. – *Stenorrhynchus* (40) occurs in temperate South America to South-East U.S.A.; it has a much elongated, bayonet-like rostellum and viscidium. Some species have fairly large, showy flowers. *S. speciosus,* Mexico, Northern South America and the West Indies, is cultivated for its bright red or purple flowers and inflorescence bracts. – *Cranichis* (50), in tropical America, especially the Andes, often has pseudopetiolate leaves and many small, non-resupinate flowers. – *Ponthieva* (25), related to *Cranichis,* includes some species with a pollinium stalk of the hamulus-type. The non-resupinate flowers with spreading sepals may be quite attractive. – *Cryptostylis* (10), Indo-Malaysia and Australasia, is probably also related to *Cranichis.* Pollination is by pseudo-copulation involving Ichneumonidae.

Subfamily Orchidoideae

The subfamily Orchidoideae contains about 115 genera with approximately 2,500 species. It is distributed all over the world, but mainly in the temperate zones. As here conceived, the Orchidoideae consist of one clearly monophyletic group, the tribe Orchideae sensu lato and an orchidoid "remnant group", the tribe Diurideae, within which the Orchideae may have evolved. This hypothesis is based on the shared occurrence in the tribes of so-called root-stem "tuberoids" (DRESSLER 1981), and on the scattered occurrence in the Diurideae of orchidoid characters, such as basitony. The tuberoid is a root structure around a core of stem tissue with an apical bud, which in the next season will grow into a new shoot, with one of the axillary buds forming a new tuberoid. The tuberoid is usually polystelic. It should be noted that its anatomy is known only from a few genera of Orchideae, and very little is known about root and tuber anatomy of other terrestrial orchids. As the genera of Diurideae do not share distinct and probably uniquely derived attributes with any other orchid group, the classification followed here is chosen as a tentative phylogenetic approach. However, the inclusion also of the Epipactieae and the Listerinae of the Neottieae (DRESSLER 1981) seems unjustified. As pointed out by DRESSLER (1981), the primarily South African Orchideae, the Australian Diurideae and the temperate South American *Chloraea* Group show an interesting vicariance pattern.

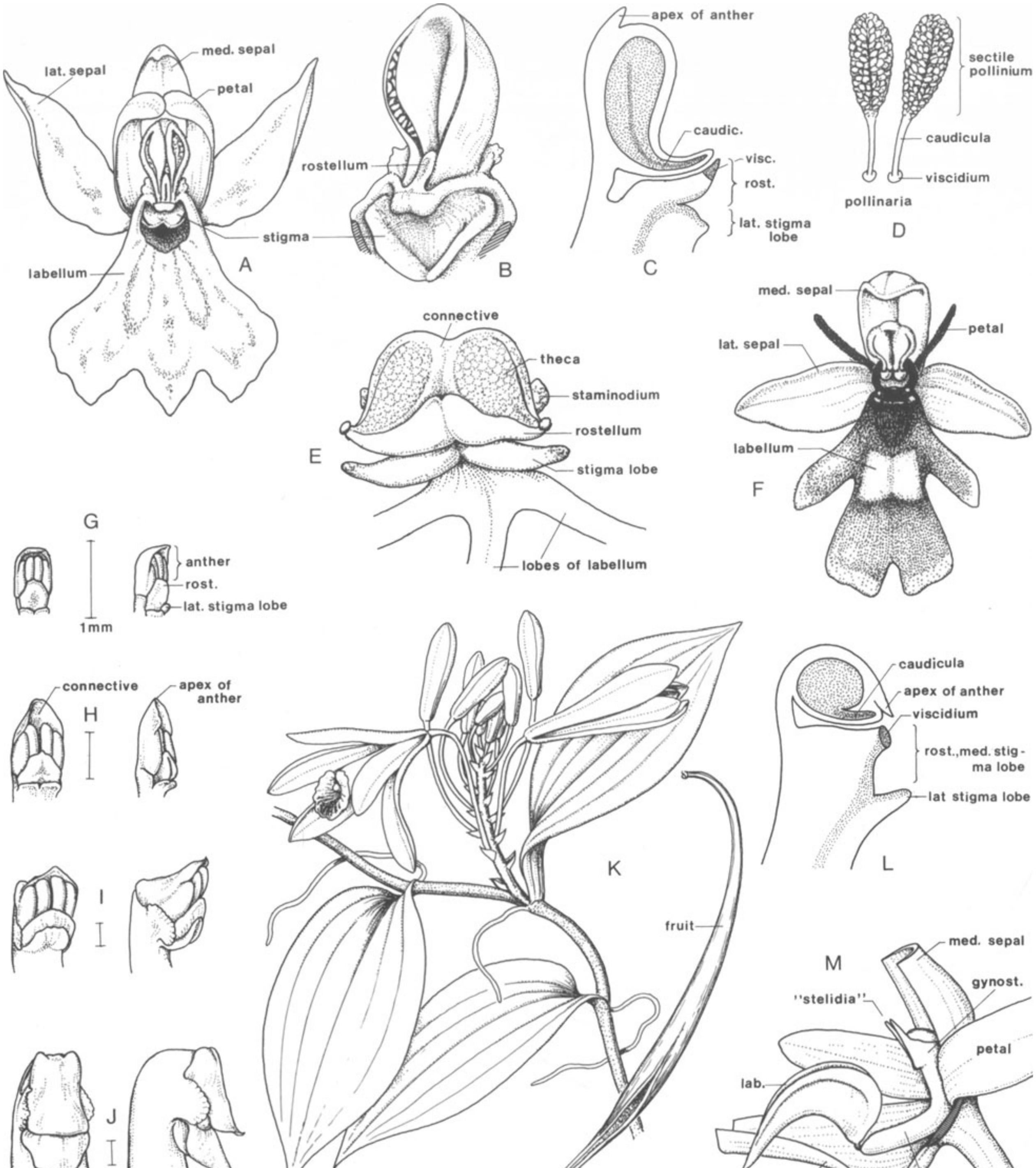


Fig. 125. Orchidaceae subfamily Orchidoideae (**A–F**) and subfamily Epidendroideae (**G–M**). **A–D** Flower and floral details in *Dactylorhiza maculata*. **A** Flower. **B** Gynostemium. **C** Gynostemium in longitudinal section. **D** Pollinaria (two for each flower). **E** *Habenaria reniformis*, gynostemium. **F** *Ophrys insectifera*, flower. **G–J** Ontogeny of the gynostemium in *Vanilla roscheri*. **K** *Vanilla planifolia*, flowering branch and fruit. **L** *Epidendrum*, gynostemium in longitudinal section. **M** *Bulbophyllum reptans*, details of flower. (Orig. and redrawn after BERG and SCHMIDT, BRIEGER, JOHNSEN, RASMUSSEN and SEIDENFADEN)

All Orchidoideae are small to medium-sized terrestrial plants, or very rarely epiphytes, usually with a rather primitive foliage of thin, spirally arranged, basally clustered, convolute, plicate or conduplicate, nonarticulate leaves. The inflorescences are always terminal and simple, with few to many spirally arranged flowers. The gynostemium may be from very short and hardly forming a column (as in certain Diurideae) to much elongated. The anther is usually upright or, in some Orchideae, strongly reflexed, but never becomes strongly inflexed during ontogeny as in the Epidendroideae and Vandoideae. The apex of the rostellum of all Orchideae and some Diurideae protrudes between the thecae of the anther and is laterally expanded between their bases, where viscidia may be formed (Fig. 125C). Pollinium stalks of the hamulus type occur in a few genera of Diurideae, whereas the Orchideae always have caudicles. Viscidia may be diffuse or detachable; the attachment is acro-, meso- or basitonic. The pollinia are always rather soft, often composed of single pollen grains in the Diurideae, but are otherwise sectile.

Tribus Diurideae 35:550

One group (subtribus Chloraeinae, 6:100) occurs in temperate South America and New Caledonia, but the tribe is primarily Australian. A few genera are represented also in tropical Asia. The general characters are as described for the subfamily, but usually without the attributes distinguishing the Orchideae. There are many odd specializations in the foliage and, especially, in the flowers, notably in the Australian endemics, in this tribe. – *Chloraea* (50) from Chile to northern Peru, and *Gavilea* (13), in Argentina and Chile, perhaps lack the tuberoid but otherwise strongly resemble the Australian genus *Caladenia* (80) (Fig. 124J) and its allies. – *Drakaea* (4), *Spiculaea* (3) and *Caleana* (5) have bizarre flowers with a hinged and mobile labellum, functioning in pseudo-copulation with wasps: Scolioidea: Thynnidae (STOUTAMIRE 1974, 1975). – In *Pterostylis* (70), mainly in Australia, the sepals form a hood inside which the narrow, sensitive labellum is hinged, moving actively when touched, trapping small pollinating flies, so that these cannot escape without touching the anther. They are occasionally cultivated as "Greenhoods". – *Rhizanthella* (1), in South-West Australia is a subterranean saprophyte with a dense, capitate inflorescence, which is a few centimetres across and surrounded by large bracts. It barely reaches the soil surface. The unusually large seeds are perhaps dispersed by animals feeding on the succulent, indehiscent fruits (GEORGE 1980).

The Diuris Group (Subtribus Diuridinae and Prasophyllinae) (8:110) comprises genera with a short erect gynostemium and almost no column; the staminodes are erect, elongated and wing-like. – *Diuris* (35), mainly in Australia, has grass-like leaves and peculiar spreading petals. – *Prasophyllum* (70) and *Microtis* (10) in Australia and New Zealand, have a solitary terete and hollow leaf ("Leek Orchids") and sectile or granular pollinia, often attached to a distinct hamulus (Fig. 122). – *Thelymitra* (50), mainly in Australia but with a few species extending to Indonesia and the Philippines, has almost regular flowers; the staminodia and column form a kind of hood, "mitra", enclosing the anther and stigma; the apices of the mitra may be adorned with tufts of variously coloured cilia. The flowers are often brightly coloured, e.g. *T. ixioides* with blue flowers. Occasionally cultivated, "Sun Orchids".

Tribus Orchideae (Orchideae plus Diseae in DRESSLER 1981) 74:2,100

With world wide distribution, but mainly concentrated in temperate zones, especially Southern Africa. The Orchideae is one of the most distinct and indisputably monophyletic of all major tribes of Orchidaceae. It is characterized by the erect or (in part of the *Disa* group) reflexed anther, the base of which is completely united with the column, firmly fixing the anther in position relative to the much integrated rostellum. The anther contains two bipartite sectile pollinia, always on caudicles. The apex of the rostellum protrudes between the thecae, forming detachable viscidia at their base (basitonic attachment) (Fig. 125C). The interthecal part of the rostellum in some genera is conspicuously developed, in others rudimentary. The infratribal division followed here is rough and provisional.

The Orchis Group have parallel thecae, the bases of which are enclosed in two lateral pouches, "bursiculae", of the rostellum; there is however only one bursicula in genera with a reduced intrathecal rostellum part.

Orchis (35), is characterized by spheroidal tuberoids and *Dactylorhiza* (30) by palmate tuberoids; the two genera are distributed in subtropical, temperate and boreal Eurasia, the highest number of species being in Mediterranean Europe. Modern treatments of this intricate complex have segregated a number of smaller genera, e.g. *Galearis*

(7), in the Himalayas and East Siberia to North America, and *Amerorchis* (1), in northern U.S.A. to western Greenland. – Within *Ophrys* (25), a genus concentrated in Mediterranean Europe, North Africa and Asia Minor, all species are pollinated by bees or wasps through a process of pseudo-copulation, a pollination strategy first described for this genus. The flowers mimic female insects in odour, shape, colour and surface texture. The similarity is quite striking even to the human eye: thus for *O. insectifera* (Fig. 125F) the petals represent the antennae, the lateral labellum lobes the wings and the median lobe the body of the mock insect. However, the scent and surface texture appear to be more important than the form, suggesting that pseudo-copulation could be more widespread in orchids. In *O. speculum,* "Mirror Ophrys" the centre of the labellum is glossy blue, bordered by conspicuous brown hairs; the pollinator here is another Scolioid wasp, in this case belonging to the Scoliidae (cf. Diurideae). – *Serapias* (10) is another Mediterranean genus. In this the sepals form a helmet hiding the diminutive lateral inner tepals: the labellum is large and tongue-shaped. The connective of the anther is distinctly elongated. Other genera in this group are *Anacamptis* (1); *Himantoglossum* (4), *Barlia* (1) and *Aceras* (1). *Aceras anthropophorum,* "L'homme pendu", has greenish yellow flowers which resemble miniature human bodies.

The Habenaria Group is characterized by thecae which are more or less spreading and a rostellum which does not form bursicles.

Platanthera (85) has a world wide distribution, but is absent from Africa south of Sahara and South America. It has about 50 endemic species in East Asia, 7 in Europe and about 10 in North America. The delimitation of this genus is much disputed. – *Gymnadenia* (7) occurs in temperate Eurasia from Spain to Japan. – *Habenaria* (about 800) is distributed all over the world, but concentrated mainly in the tropics. It is one of the largest and most widely distributed genera of orchids. The stigma is divided into two convex stigmatic areas which are borne on stalks, "stigmatophores", which may be rather long and are parallel to the (sometimes widely) spreading thecae (Fig. 125E). The lateral petals and the spurred labellum are often deeply lobed, giving the flowers a spidery appearance. Some species have large showy flowers, e.g. *H. rhodocheila* in Malaysia and Indo-China, with scarlet or brick-red flowers.

The Disa Group generally has a reflexed anther, bending back from the column.

In *Disa* (150), which occurs in Africa, especially Southern Africa, the dorsal sepal has the shape of a hood or a spoon and is usually spurred. The flowers are often very conspicuous. *D. uniflora,* in the Cape Province of South Africa has large, brilliant scarlet to orange flowers, and is widely cultivated. – In *Satyrium* (115) in tropical and southern Asia, the Himalayas and western China, the anther is reflexed and positioned below the stigma. The hooded labellum of the non-resupinate flowers has two spurs, descending on each side of the ovary.

Subfamily Epidendroideae

The subfamily Epidendroideae, with the circumscription here adopted, is the largest of the subfamilies. It includes about 220 genera and perhaps more than 10,000 species, most of which are tropical epiphytes.

The attributes distinguishing this group in classical orchid systematics are the incumbent anther with broad tunica-like connective and caducous anther cap (the anther is "operculate"), the usually rather hard pollinia which either have caudicles or no pollinium stalks at all, and generally the possession of one or more vegetative adaptations for epiphytic life, such as thick aerial roots with multiseriate velamen, aerial corms made up of one or more internodes, articulate, coriaceous conduplicate leaves, etc. The next subfamily in the present treatment, Vandoideae (often included as a subgroup of the Epidendroideae) is segregated by having, in addition, stipites of the tegula type and even harder pollinia. However, these characters have now been demonstrated to have a wider distribution than was earlier believed. Thus pollinium stalks of all kinds are reported from the Epidendroideae in the present sense, although true tegulae seem to be very rare (tribus Calypsoeae?). Therefore, the incumbent anther and the horizontal or deflexed rostellar projection produced by a strong inflexion of the anther during ontogeny (Fig. 125G–J) appear to be the only features generally characterizing the Epidendroideae. In the Vandoideae, this inflexion begins much earlier in the ontogeny of the gynostemium and may continue to deflexion of both anther and rostellar projection through 180°, suggesting that this group represents a further development within the epidendroid orchids. It remains, however, an open question whether the anther inflexion may be regarded as a uniquely derived character, designating a monophyletic group. Some epidendroid orchids have erect anthers which, on the basis of this hypothesis, must be considered cases where this ontogenetic incumbence has been retarded. Recent investigations indicate that most probably the subfamily Vandoideae comprises several groups of relatively advanced orchids and forms an "evolutionary level" (DRESSLER 1974) rather than a single branch of evolution.

Despite the difficulties in reconstructing the phylogeny of the epidendroid orchids, it is a fairly easily recognized group according the present definition: incumbent anther and/or presence of one or more of the advanced characters mentioned above. When, in addition, very early ontogenetic inflexion of the anther occurs and a tegula is present, the orchid is referred to the Vandoideae.

The traditional orchid taxonomy encountered difficulties in delimiting the epidendroid orchids from the neottioid. This was because the subfamily Neottioideae was treated as a monophyletic taxonomic entity defined solely on primitive characters which were considered more important than the advanced ones. *Vanilla, Nervilia* and related genera have thus often been classified as being neottioid due to their soft pollinia.

Tribus Arethuseae 35:540

This tribe, with a worldwide distribution, consists mainly of cormous terrestrial plants, which often have slender reed-like stems and distinct pseudobulbs. The leaves are plicate or less often conduplicate, and may or may not be articulate. The inflorescences are most often lateral. The apical part of the column may be broad and petaloid, the pollinia, which may be soft or relatively hard, are very often two in each pollen sac due to incomplete development of the sporogenous tissue. The two pairs of pollinia are connected by ventral caudicles. The stigma is often somewhat emergent.

This tribe consists primarily of "primitive" epidendroid genera, having no conspicuous attributes justifying their grouping in separate taxa. They share no particular, advanced characters with any of the "advanced" larger tribes. Any one of the other epidendroid or vandoid groups could have evolved within the Arethuseae as here defined.

Arethusa (1) *bulbosa* is a small North American bog plant with an inflorescence bearing one or two attractive pink flowers. – *Calopogon* (4), in North America, consists of small herbs growing in wet habitats, "Grass Pink". – *Sobralia* (95), in the Central and South American tropics, consists of tall terrestrials with thin reed-like stems and broad, plicate leaves. The flowers are large and showy, but fugacious. – *Elleanthus* (70), in the American tropics and West Indies, has flowers in an inflorescence which is sometimes subcapitate and has hard conspicuous bracts, an adaptation to hummingbird pollination. – *Thunia* (5–6), in tropical Asia, and *Phaius* (30), in tropical Asia, Madagascar and Australia and one species in tropical Africa, are stout terrestrials with reed-like stems and large plicate leaves. *P. tancarvilleae*, in tropical Asia and Australia, may become up to 2 m tall; the many-flowered inflorescences carry very showy, white-and-brown flowers 10–12 cm across with a gullet-shaped lip. – *Calanthe* (ca. 200), in subtropical and tropical Asia, Australia and Africa, comprises stout terrestrial herbs with more or less pseudobulbous stems. Some species have leafy shoots alternating seasonally with inflorescences. The spurred flowers have a characteristic three-lobed, deeply bifid labellum, partly fused with the column. All parts of the plant become blue when injured. *C. triplicata,* which is widely distributed in tropical Asia and Australia, is a large species with showy white flowers with a red or yellow callus on the labellum; it is frequently cultivated. – Of the genus *Bletilla* (9), in East Asia, *B. striata,* from South China and Japan, is a popular, fairly hardy garden plant. It has several-flowered inflorescences with violet flowers 4 cm long.

Tribus Vanilleae 13:240

In this tribe will be mentioned the *Vanilla* Group only.

The Vanilla Group (Subtribus Vanillinae) consists of 5–7 genera with ca. 180 species. *Vanilla* is pantropical, the other genera being palaeotropical or neotropical, two small ones endemic to New Caledonia. They are terrestrial or monopodial lianas. Some genera are saprophytic. The leaves are rigidly coriaceous or fleshy, convolute or conduplicate and non-articulate. The flower is gullet-shaped and often provided with a tuft of retrorse hairs or crests, forcing visiting insects, when retreating, to raise their body and thereby touch the versatile anther. The four pollinia are very soft and mealy and are composed of free pollen grains. The three-lobed stigma is somewhat emergent; the broad rostellum, which forms a diffuse viscidium at its apex, is inflexed, hiding the lateral stigma lobes. The fruit of *Vanilla* and *Galeola* is unusual for the family in being dehiscent or indehiscent (a capsule or berry), somewhat resembling a banana. It contains numerous small seeds with a thick, opaque, sometimes black seed coat, which may be winged. The seeds of *Vanilla* were earlier regarded as primitive as they are superficially similar to seeds in Apostasiaceae. It is more likely, however, that they are derived, adapted to a new mode of seed dispersal in connection with the secondarily fleshy, fragrant fruits. SEIDENFADEN (1978) supposes that the fruits are eaten and dispersed by animals. – *Vanilla* (100), a pantropical genus, has thick, fleshy leaves or no leaves at all, and consists of vines with assimilating stems, climbing by the twining aerial roots which are produced opposite the leaves or bracts. *V. planifolia* (Mexico) (Fig. 125) is grown commercially throughout the tropics, especially Madagascar, for producing "Vanilla Beans", which are the dried and fermented fruits. The characteristic flavour of the product comes from a mixture of oleoresins and an aromatic compound, vanillin, formed during the fermentation (or, less efficiently, by natural ripening of the fruit) through hydrolysis of glucovanillin. "Vanilla" was used by the Aztec Indians of Mexico for flavouring chocolate. A few other species of the genus are grown locally for vanilla production, and quite a few are grown as ornamentals, e.g. the impressive *V. imperialis* (tropical Africa). – *Galeola* (25), in tropical Asia and Australia, consists of saprophytes, terrestrial humus plants or vines. The terrestrial species have striking red *Vanilla*-like fruits and wingless seeds; the vines have dehiscent capsules with winged seeds. *G. altissima* is said to reach 40 m, and is perhaps the largest of all saprophytic plants.

Tribus Gastrodieae 7:130

This occurs all over the tropics, but mainly in tropical Asia. The tribe consists of small terrestrial saprophytes (except the autotrophic genus *Nervilia*), frequently with subterranean corms. The tepals are often more or less fused and the pollinia are often sectile. – *Nervilia* (80), in tropical Asia, Australia and Africa has only one leaf which is almost circular or cordate, plicate and non-articulate. The leaf and inflorescence are produced at different seasons. – In *Gastrodia* (30), in tropical Asia and Australia ("Potato Orchid") the stigma is positioned at the base of the slender, erect gynostemium.

Tribus Epipogieae 2:3

This tribe consists of small peculiar-looking, succulent, leafless terrestrial saprophytes of the Old World. They are rhizomatous or bear a corm. – *Epipogium* (2) has spurred, non-resupinate flowers. The lumpy, incumbent anther holds two bipartite sectile pollinia, each on a long recurved caudicle. The stigma is basal on the gynostemium as in *Gastrodia,* but the systematic position and possible phylogenetic history of this odd genus have been much disputed. *E. aphyllum,* in the temperate and boreal zones of Eurasia, has a well-developed transversely folded rostellar projection with a detachable viscidium. The autogamous *E. roseum* is found in the Old World tropics.

Tribus Coelogyneae 42:440

These, which occur in tropical Asia and southern China, are epiphytes or lithophytes with pseudobulbs made up of a single internode. The flowers have four superposed pollinia with distinct caudicles. The column is often apically more or less petaloid. – *Coelogyne,* in tropical Asia, consists of over 100 species of epiphytes with distinct ovoid or conical pseudobulbs carrying one or two apical, plicate leaves; some have showy flowers and are cultivated. – *Pleione* (10) occurs in the Himalayas and the mountainous areas of Thailand, Laos, China and Taiwan; it consists of small but large-flowered epiphytic or lithophytic plants. They are frequently cultivated.

Tribus Malaxideae 6:900

These genera have a worldwide distribution but are mainly found in the tropics. They are small terrestrial or epiphytic plants, usually with pseudobulbs of a few internodes. The leaves are plicate or (in *Oberonia*) laterally flattened. The terminal inflorescence usually carries very small to small greenish, non-spurred flowers. The anther contains four rather hard pollinia, which are "naked", i.e. lacking pollinium stalks of any kind. The Malaxideae in this respect resemble the Dendrobiinae and the Bulbophyllinae. – *Liparis* (250), is cosmopolitan, but occurs mainly in the tropical zone. It usually has resupinate flowers with an erect, slender column. *L. loeselii* occurs in temperate Europe and North America. – *Malaxis* (synonym: *Microstylis*) (300), is a subcosmopolitan genus. The ovary is often twisted through 360°, so that the flowers appear non-resupinate. The column is shorter than in *Liparis*. *M. (Hammarbya) paludosa,* from Europe through Siberia to Japan, has leaves which often produce bulbils at their tips. – *Oberonia* (300), mainly in Asia, is a genus of small epiphytes with fleshy, laterally much compressed leaves, giving the plant a peculiar, fan-like appearance. The flowers are very minute, often less than 1 mm across, situated in whorls on a dense raceme.

Tribus Calypsoeae 2:3

Includes *Calypso* (1) *bulbosa,* a delicate, circumboreal, terrestrial herb with a single plicate leaf and a solitary, fairly large, pink flower. Its systematic position is uncertain.

Tribus Epidendreae 115:8,000

This tribe, as here circumscribed, is by far the largest of the orchidaceous tribes. It is very diverse and difficult to define on the basis of shared characteristics. Most probably it represents a group of various, relatively advanced lines of epidendroid orchids. Most of them are epiphytes with slender stems or pseudobulbs of one or more internodes. The leaves are often conduplicate, rarely plicate, and distichous. In many of the subgroups the flowers have a well-developed column foot and a mentum formed from the lateral sepals. Only a few genera have spurred flowers. The pollinia vary in number from two to eight, and are usually of a rather hard texture. Most genera have distinct caudicles of the same kind as those in Coelogyneae, situated as "runners" underneath the pollinia (see *Epidendrum,* Fig. 125L). The large subtribes Dendrobiinae and Bulbophyllinae have no pollinium stalks except for a hamulus found in a few species of *Bulbophyllum.* The small subtribe Sunipiinae, which is closely related to the Bulbophyllinae, has species with peculiar, tegula-like pollinium stalks.

The Epidendrum Group (Subtribus Laeliinae) consists of ca. 45 genera and 850 species, all neotropical. – *Epidendrum* (ca. 500) ranges from North Carolina to Argentina. Terrestrial and epiphytic species. They have slender, often branching stems and one to many leaves, which may be terete or flattened. The inflorescences are terminal (rarely lateral), racemose, sometimes almost umbellate, or paniculate. The flowers vary from minute to quite large and showy and have more or less spreading tepals. The column is adnate for its full length to the labellum and functions as a spur. The anther contains four waxy pollinia with runner-like caudicles. This genus comprises several popular greenhouse plants: *E. ibaguense* (incl. *E. radicans* and *E. schomburgkii*), which is common throughout tropical America, a variable terrestrial (or epiphytic) orchid up to 1.5 m tall, having subumbellate inflorescences with medium-sized, white to scarlet, flowers. The flowers of *E. medusae* (Ecuador) have a striking maroon-coloured labellum up to 5 cm broad with deeply fimbriate margins. – *Encyclia* (150), mainly in Mexico, has been segregated from *Epidendrum,* having pseudobulbs and only partial adnation between labellum and column or none. *E. cochleata* and *E. fragrans,* from Florida to Venezuela, have non-resupinate flowers. They are widely cultivated. – *Laelia* (ca. 50), from Mexico to Brazil, is closely related to *Epidendrum* and *Cattleya.* It has distinct pseudobulbs, few leaves, and mostly large and showy flowers with eight pollinia in the anther. – *Cattleya* (30), in the tropics of Central and South America, consists of epiphytic or lithophytic plants with more or less thickened pseudobulbous stems and one or two thickly coriaceous apical leaves. The one- or few-flowered inflorescence is subtended by a large spathaceous bract. The flowers are often very large and spectacular and have an anther with four pollinia. This is one of the most important genera of cultivated orchids. Intergeneric hybrids between *Cattleya* and other genera of Laeliinae play an important role in commercial orchid breeding. *C. labiata,* in eastern Brazil, has flowers 12–15 cm across.

The Eria Group (Subtribus Eriinae), 8:500, occurs in tropical Asia (one genus in Africa). It consists of small to medium-sized epiphytes with slender stems or with pseudobulbs of several internodes. The anther has eight pollinia with caudicles and usually with a well-defined viscidium. – *Eria* (300–400), in tropical Asia, is a vegetatively rather variable genus, which includes very minute plants with densely crowded button-shaped pseudo-bulbs as well as larger forms without distinct pseudobulbs but with fleshy, sometimes terete leaves. The flowers often have a distinct column foot, resembling that in small *Dendrobium* flowers. Several species are covered with a tomentose or woolly indumentum.

The Pleurothallis Group (Subtribus Pleurothallidinae) contains about 26 genera with about 3,800 species (according to Dressler 1981), all in tropical America. They have characteristic, unifoliate, non-pseudobulbous stems. The leaf is conduplicate and very fleshy, functionally substituting a pseudobulb. The flowers have a joint between the pedicel and ovary and usually exhibit characteristic adaptations to fly pollination like the mainly Asiatic group Bulbophyllinae. There are usually two pollinia; the caudicles are often very short, if existent.

– *Pleurothallis* (at least 1000 species, perhaps many more), consists of small to medium-sized epiphytes or lithophytes. The lateral sepals of this genus are more or less united, and often the column foot is distinct. The pollinia are waxy. – *Stelis* (ca. 500) is another small-flowered genus. – In *Masdevallia* (ca. 250), in tropical America, the sepals are united into a tube. The free apices of the outer tepals are spreading, giving the flowers a characteristic trilobate appearance when seen in front view. Many species are cultivated. – *Restrepia* (30), differs in having four pollinia. – *Dracula* (ca. 60), which has recently been segregated from *Masdevallia,* has strange-looking flowers said to imitate fungi, with their odour and labellum structure, attracting fungus gnats (Diptera: Mycetophilidae) which serve as pollen-vectors (Vogel 1978). *D. vampira* and related species are cultivated as curiosities (northern Ecuador).

The Dendrobium Group (Subtribus Dendrobiinae), which occurs mainly in tropical and subtropical Asia, contains about 1,700 species in one very large genus, *Dendrobium,* and six to seven small segregate genera. They include epiphytes and a few terrestrials. The vegetative morphology is highly variable. The inflorescences are only rarely truly terminal on the shoots. The flowers are characterized by having a pronounced column foot and four (sometimes two) ellipsoid pollinia, without pollinium stalks, in the versatile anther. The viscidium is diffuse and usually not detachable. This group seems to be further characterized by cells containing globular, muricate silica bodies. This type of silica body is restricted to *Dendrobium,* certain Eriinae and the Vandeae (Møller and H. Rasmussen, 1984).

Dendrobium (at least 1,400 species), exhibits an incredible variation of the vegetative parts. Yet the flowers, although quite variable as to size and form, conform to the characteristics described above. Some species have showy flowers and are of great horticultural importance. *D. nobile* (Himalaya to East Asia) has reed-like, slightly pseudobulbous stems, spreading whitish pink sepals and lateral petals, and a gullet-shaped labellum with maroon-coloured throat. It is one of the most commonly cultivated of all orchids. *D. bigibbum,* especially its variety *phalaenopsis,* (South-East Indonesia and tropical Australia) has durable white, purple or lilac flowers and is very common as a commercial cut flower. Commonly cultivated also are *D. chrysotoxum, D. lindleyanum* (syn. *D. aggregatum*) and *D. fimbriatum,* all with golden or yellow flowers. *D. senile* (Thailand and Indochina) has bright yellow, lemon-scented flowers and is conspicuously hairy on the pseudobulbs and leaves. Smaller waxy pinkish purple flowers in a dense one-sided inflorescence characterize *D. secundum,* "The Tooth Brush", which is a common dry forest epiphyte in tropical Asia. *D. leonis* (Thailand to Indonesia), with fragrant, dirty yellow-brown flowers to 1.5 cm across, belongs to a section with fleshy, laterally compressed densely distichous leaves, a vegetative appearance found also in other groups of orchids, e.g. in *Oberonia* and in several genera of the subfamily Vandoideae. *D. unicum* (Thailand and Indo-China; frequently misidentified as "*D. arachnites*") has bizarre, spidery, purple-striped flowers to 6 cm across, and is widely grown as an ornamental. – The genus *Flickingeria* (60), in tropical Asia and Australia, consists of much branched bushy epiphytes with flowers lasting for only a few hours.

The Bulbophyllum Group (Subtribus Bulbophyllinae) consists of one large genus, *Bulbophyllum,* and five to seven small genera. They are all small to medium-sized epiphytes with more or less conical or ellipsoid, sometimes angular or winged pseudobulbs, which are made up of one internode and carry apically one or two fleshy, conduplicate leaves. The inflorescence is lateral and arises at the base of the pseudobulbs. Its flowers have a column foot and usually naked pollinia. This group may be imagined to have evolved within the preceding group as a further development of one of the lines with single-internode pseudobulbs, leading to the reduced number of leaves and standardized architecture observed in *Bulbophyllum* (Fig. 121 M). However, it appears that the Bulbophyllinae have no silica cells; these may have been lost in the course of evolution. – *Bulbophyllum* (ca. 1,000), is pantropical but concentrated mostly in the Old World tropics, especially in tropical Asia (Figs. 10–11). The usually rather small flowers often show adaptations to fly pollination with various mobile appendages, with dark (often deep purple or violet) flower colours and sometimes with a disagreeable smell. The column is short and stout, with two often distinctly elongated teeth ("stelidia") on each side of the anther (Fig. 125 M). The characteristic, fleshy, curved labellum is hinged to the apex of a prominent column foot, on which the lateral petals are inserted. The pollinia are usually without appendages and only few species have a detachable viscidium. Two species with a distinct hamulus are known.

The distinct vegetative mode and basic construction of the flower make this an easily identified genus. There is nevertheless a substantial variation in the overall appearance of the species, especially concerning the inflorescence and arrangement of flowers. A number of more or less distinct subdivisions are recognized, e.g. sect. *Megaclinium* (Africa and tropical America), with a flattened, leaf-like inflorescence rachis, and sect. *Cirrhopetalum* with often subumbellate inflorescence and apically connivent lateral sepals much longer than the other tepals. Only a few species of *Bulbophyllum* are regularly cultivated, e.g. *B. lobbii* (Thailand, Indonesia), which has solitary brownish yellow flowers 6–10 cm across. *B. wendlandianum* (= *Cirrhopetalum collettii*), *B. fascinator* and related species have extraordinary flowers with caudate lateral sepals 20–30 cm long.

Subfamily Vandoideae

The Subfamily Vandoideae (tribus Vandeae in many older classifications) contains about 300 genera and 5,000 species, most being tropical epiphytes. In traditional orchid systematics, and as here accepted, it is an assemblage of the most advanced orchids, possessing one or more of several advanced attributes: lateral inflorescences, strongly inflexed anther and rostellum, indistinct anther partitions, superposed and hard, waxy to bony pollinia, a detachable viscidium, and a pollinium stalk of the tegula type. However, none of these characteristics is unique to the Vandoideae, nor is any of them shared by all members traditionally included, although only very few (some Cymbidieae and some Corallorhizinae) lack the tegula. The inflexion of the anther and rostellum apex begins very early in the ontogeny of the gynostemium of all vandoid genera of which the development has been investigated (Fig. 126F–K). Inflexion at an early stage may be a unique character of the Vandoideae as here defined, but in view of the otherwise conflicting character distribution it appears rather unlikely that the Vandoideae form a monophyletic group – most probably they consist of several advanced evolutionary lines from "epidendroid" ancestors (see Dressler 1981). Dressler (1981) interprets the vandoid anther as erect and opening basally, literally "basitonic". This is, however, generally not the case – it remains to be shown whether it is true for some genera.

The subdivision of Vandoideae into tribes and subtribes varies greatly in different classifications. However, at least the tribe Vandeae appears to be a distinct, monophyletic group.

Tribus Polystachyeae 4:220

This pantropical tribe contains the large pantropical genus *Polystachya* and three small Afro-Madagascan genera. They are epiphytic or more rarely terrestrial herbs, usually with slender reed-like stems or multinodal pseudobulbs. Most species have rather small flowers in racemose or paniculate, usually terminal inflorescences. A prominent column foot makes the flowers resemble those of the epidendroid genera *Eria* and *Dendrobium*, but the short but distinct stipes places the tribe Polystachyeae among the vandoids.

Polystachya (210), occurs predominantly in tropical Africa. The flowers are not resupinate. *P. concreta* (syn. *P. flavescens, P. tesselata, P. luteola*) is a variable pantropical species, perhaps the most widespread of all orchids.

Tribus Cymbidieae 130:1800

As circumscribed by Dressler (1981) this is a very heterogeneous group. It includes all vandoid orchids with two pollinia except the Vandeae. It is only in this very broad sense that it comprises as many species as indicated here.

The Cymbidium Group (Subtribus Cyrtopodiinae) contains about 25 genera and 430 species. It is pantropical, but is mainly concentrated in the Old World tropics, and consists of terrestrial or epiphytic plants; a few species are saprophytes. This group is very diverse, including principally the vandoid orchids having only one or a few of the advanced characters mentioned for the subfamily. Quite often the members have plicate leaves and multinodal pseudobulbs. The flowers often have a broad and somewhat winged column and a prominent column foot. The pollinia in most genera are attached to a broad tegula (Fig. 126D).

Eulophia (200), is a pantropical genus, but most species occur in Africa. They are mostly terrestrial herbs, often found in grasslands, but a few are saprophytes. Many species have large, showy flowers, for example *E. cucullata,* widespread in tropical Africa, which has purplish pink flowers. *E. petersii,* in dry habitats of East Africa, has thick, coriaceous, finely serrate leaves, resembling a small-sized *Aloë*. The branched flowering shoots may exceed 2 m. – *Ansellia* (1–2), widespread in tropical Africa, is epiphytic: it has showy yellow flowers with brown spots. *A. gigantea,* "Leopard Orchid", is frequently cultivated. – *Cymbidium* (ca. 50; Fig. 126A), mainly in tropical Asia, con-

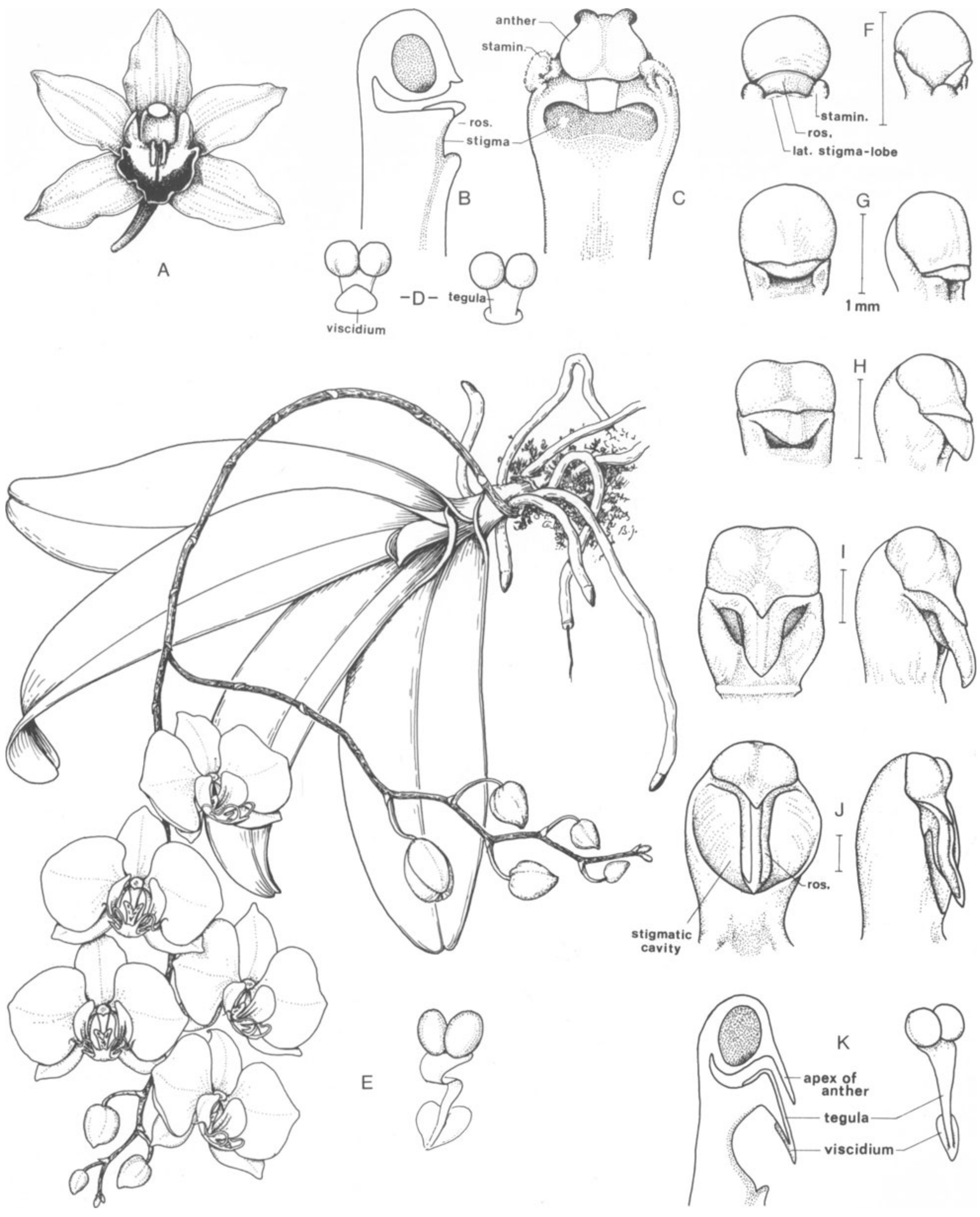


Fig. 126. Orchidaceae subfam. Vandoideae. **A** *Cymbidium lowianum,* flower. **B–D** *Eulophia andamanensis.* **B–C** Gynostemium, lateral and front views. **D** Pollinarium in different views. **E** *Phalaenopsis amabilis,* of the tribe Vandeae, with pollinarium. **F–K** *Doritis pulcherrima.* **F–J** Ontogeny of the gynostemium. **K** Gynostemium and pollinarium. (Orig.)

sists of epiphytic or rarely terrestrial herbs, usually with a short stem and long, narrow and tough distichous leaves. The often very showy flowers have a three-lobed labellum, borne on a short column foot. The labellum is usually conspicuously bicarinate at the base, and the midlobe is recurved. *Cymbidium* hybrids are among the most important commercially grown orchids. *C. viridioides* (syn.: *C. giganteum*), *C. lowianum* (tropical Himalaya) and a few closely related species (or varieties) and their hybrids are widely sold as cut flowers. In the flowers, up to 10 cm across, the labellum often contrasts in colour with the other, yellowish green tepals. *C. finlaysonianum,* in the lowlands of tropical Asia, is a robust epiphyte with dull yellow or brownish flowers up to 6 cm across. – *Grammatophyllum* (ca. 10), in tropical Asia, is apparently closely allied to *Cymbidium,* but has stalked pollinia. *G. speciosum* is a large epiphyte, with pseudobulbs up to 3 m long and 6 cm in diameter. The basal, erect inflorescence may be up to 2 m, carrying numerous, greenish yellow spotted flowers up to 10 cm across.

The Catasetum Group (subtribus Catasetinae), with 145 species in 5 genera, occurs in tropical America. It consists of epiphytes with multinodal pseudobulbs and scattered, distichous, plicate leaves. The inflorescences are lateral and racemose and the flowers often unisexual. The column usually bears two basal antennae, which function as levers releasing the large, elastic stipes when touched. The fairly large pollinarium is thus thrown off and the sticky viscidium may hit the scutellum of a visiting bee with considerable force. – *Catasetum* (50), found in tropical America, consists of epiphytes with unisexual flowers. Male and female flowers of the same species may look very different. Both monoecious and dioecious species are found. Some species also have facultatively hermaphroditic flowers, which may be different from either of the unisexual ones. The fleshy labellum is often helmet-shaped, and often with a fimbriate margin – especially in male flowers. Some species are widely grown.

The Stanhopea Group (subtribus Stanhopeinae), with 17 genera and ca. 190 species, occurs in tropical America. These are all epiphytes with uninodal pseudobulbs, terminally with plicate, usually petiolate leaves. Like many Catasetinae they are pollinated by male euglossine bees attracted by specific fragrances. The flowers do not provide any food but exude perfumes when scratched. In most genera the flowers are organized so as to take advantage of the retarded reflexes of the drugged insects which are manipulated to fall through a chute, down a slide, or (in *Coryanthes*) into the water-filled, bucket-shaped epichile of the labellum. When crawling out of this they have to pass the apex of the gynostemium. The flowers of Stanhopeinae are bisexual, self-pollination being prevented by dichogamy. – *Coryanthes* (c. 20), from Guatemala to Peru and Brazil, is the genus of the famous "Bucket Orchids", occasionally cultivated for their large, bizarre flowers. – *Stanhopea* (c. 25), widespread in tropical America, is epiphytic (occasionally terrestrial) consisting of medium-sized to large plants with one-leaved pseudobulbs and large fleshy flowers. The genus is frequently cultivated. – *Gongora* (25) is also frequently cultivated.

The Oncidium Group (subtribus Oncidiinae) comprises 60 genera and 950 species, predominantly epiphytes, in tropical America. Most taxa have uninodal pseudobulbs, but forms with slender stems, and even monopodial forms, occur in this group. The two pollinia are only slightly notched and attached to a rather long and slender stipes. The column top and pollinarium strongly resemble those in the Old World Vandeae, and it has sometimes been speculated that the Oncidiineae and the Vandeae represent respectively a neotropical and a palaeotropical evolutionary line from a common ancestral stock.

Oncidium (more than 400), in subtropical and tropical America, for the most part consists of pseudobulbous epiphytes. The labellum has a characteristic basal, warty callus, and the column top is mostly auriculate or winged. Infrageneric classification is difficult and the delimitation from several other genera of the subtribe is unclear. The flowers vary from minute to very large. Yellow and brownish flower colours are common. The flowers frequently have a characteristically three-lobed labellum with a bipartite spreading midlobe: "Dancing Girls". Many species are cultivated. *O. bicallosum* (Mexico and central America) has brownish yellow flowers up to 5 cm across. *O. kramerianum* and *O. papilio* also have large flowers with narrowly spathulate, upwardly directed sepals, 5–7 mm long and resembling the tentacles of an octopus, and with broad, wing-like, deflexed petals. *O. altissimum,* with flattened pseudobulbs, has scrambling inflorescences up to 3 m long with yellowish flowers. – *Odontoglossum* (ca. 100) occurs in subtropical and tropical central and South America, often at fairly high altitudes. The base of the labellum is parallel to and often partly adnate to the column. The genus contains many popular species. *O. grande,* a robust epiphyte, has showy flowers with purple-brown spots and yellow stripes; it is sometimes placed in a segregate genus, *Rossioglossum,* on account of the free labellum. *O. crispum,* in Columbia, has showy white or rose flowers, spotted with red or purple, but a yellow labellum. – *Miltonia* (20), in the Andean highlands (these often separated as *Miltoniopsis*) and South East Brazil, has a shorter column than that in the preceding genera. – *Brassia* (20), in tropical America, has linear-lanceolate sepals, and a short, wingless column.

Tribus Maxillarieae 80:760

As circumscribed by DRESSLER (1981) this tribe comprises all Vandoideae with four pollinia except the tribes Vandeae and Polystachyeae. Apart from certain members of the Corallorhizinae this is an entirely American tribe. The Maxillarieae are vegetatively very diverse. They generally produce a corm and have plicate leaves, but the more "advanced" members may have uninodal pseudobulbs and conduplicate leaves. A few genera are monopodial. The flowers are typically vandoid. Spurs are usually lacking, and the gynostemium usually has a long slender rostellar projection and a correspondingly slender tegula.

The Corallorhiza Group (subtribus Corallorhizinae) in the classification followed here consists of 9 genera with about 60 species distributed mainly in North Temperate and Tropical America (*Corallorhiza* being found also in the Old World). This is a group of terrestrial, often saprophytic cormous herbs with plicate (or reduced) leaves and terminal inflorescences. The details of the gynostemium are surprisingly poorly known, but it is reported to have a distinct, detachable viscidium and a small stipe. The *Corallorhiza* group is differently circumscribed by most authors and not associated with the Maxillarieae with which it has only the four superposed pollinia in common.

Corrallorhiza (ca. 10), distributed over the Northern Hemisphere, are saprophytic bog or forest plants characterized by the much branched, coral-like rhizome, "Coral Root". *C. trifida,* circumboreal (including Greenland), is the only species also found in Europe.

The Zygopetalum Group (subtribe Zygopetalinae) (including Lycastinae) (20:160) is tropical American. It consists mainly of epiphytes of varying habit, all genera except one being reported as sympodial. There is often a well-developed column foot. The rostellar projection is prominent and the tegula is often long and slender. – *Zygopetalum* (30–40), comprises tropical South American epiphytes which are usually recognized by the fleshy callus at the base of the labellum. The flowers are often showy. A popular, cultivated plant is, for example, *Z. intermedium.* – *Lycaste* (25), from Mexico to Peru, has uninodal, often somewhat flattened pseudobulbs. The attractive, often yellow flowers have large sepals. *L. virginalis* is a well-known greenhouse plant.

The Maxillaria Group (subtribus Maxillariinae) (9:400) likewise occurs in tropical America. It resembles the Zygopetalinae but has one-flowered inflorescences. Some species of *Maxillaria* are said to have no pollinium stalk.

Maxillaria (300), widely distributed in the American tropics, has coriaceous, non-plicate leaves and a prominent mentum formed by the bases of the lateral sepals and the column foot (*Maxillaria* = little jaw). The pollinarium has a rounded or crescent-shaped viscidium. There are two major groups in the genus, one with untufted plants with pseudobulbs borne on an elongated rhizome, the other with densely tufted plants. Cultivated are, e.g., *M. picta,* from Eastern Brazil, with clustered pseudobulbs and yellowish, purple-spotted flowers up to 6 cm across.

Tribus Vandeae 135:1,700

This occurs essentially in the Old World tropics; it includes only a few New World genera. They range from dwarf plants to very large epiphytes with showy flowers. The tribe is characterized by the monopodial habit and the vandoid gynostemium with a distinct tegula. Some genera have four pollinia, but others have two, which may be more or less notched or entire (see also Fig. 119M). The stem apex grows continuously and the base gradually dies away; pseudobulbs are not developed. The distichous leaves have generally taken over the water-storing function and may be very succulent, in some genera even terete. The lateral inflorescences and the thick aerial roots penetrate the imbricate leaf sheaths. However, a few genera lack foliage leaves altogether and have green assimilating roots. The leaves may be spaced on an elongated erect or pendent shoot, or may be condensed on a short shoot so that the long leaves become arranged as a fan. The flowers vary from a few millimetres to very large and showy. Their labellum may be pointed and is often saccate or spurred. The column may have a prominent foot, and the rostellum has frequently a long and beak-like projection, pointing downwards across the stigmatic cavity.

The Vandeae appear to form a monophyletic group distingishable by its habit. A few other orchids are monopodial (e.g. *Vanilla*) but all of these show other relationships demonstrating that the monopodial habit has in these cases evolved independently.

The Vanda Group (subtribus Aërangidinae in broad sense, syn.: Sarcanthinae nom. illeg.) contains ca. 120 genera and 1,300 species, ca. 1,000 of which are found in tropical Asia. There are almost no genera in common between Africa-Madagascar and Asia so the genera in these regions are often treated in different subtribes. The taxonomy of genera and generic complexes in this group is highly controversial.

Phalaenopsis (50), in tropical Asia, has a characteristic callus on the labellum. This genus contains several very important ornamentals, e.g. the large, white-flowered *P. amabile* or *P. aphrodite* and their hybrids (Fig. 126E), often seen in wedding bouquets. *P. cornucervi* has smaller yellowish brown flowers with a complicated callus. – *Kingidium* (2–3) and *Doritis* (2) are genera segregated from *Phalaenopsis; D. pulcherrima,* from South East Asia, is a common greenhouse ornamental. – *Aerides* (ca. 20), in South Asia, are robust epiphytes, with dense racemes of flowers, having a distinct column foot continuous with the three-lobed labellum. The spur is often forwardly projecting. *A. odoratum* is a commonly cultivated species. – *Vanda* (30–40), widespread in tropical Asia, comprises small to very large epiphytic or terrestrial orchids, often with very showy flowers. The spreading perianth segments are tapered towards their bases. There is no column foot. The tegula is broad, almost square. *V. tricolor,* (Java), is a coarse, erect epiphytic or terrestrial plant with large, variably coloured flowers; *V. coerulea,* from North India to Thailand, is famous for its pale blue or lilac flowers; and *V. teres* (sometimes referred to *Papilionanthe*), from Burma to Indochina, is a scrambling epiphyte with terete leaves. Several important commercial cultivars are intergeneric hybrids between *Vanda* and the related genera *Arachnis* and *Renanthera.* – *Cleisostoma* (syn.: *Sarcanthus*; ca. 100), widespread in tropical Asia, has small, fleshy flowers. – *Aërangis* (ca. 15), widespread in tropical Africa and Madagascar, has very short stems and long-spurred, often whitish flowers, borne in lax racemes. The attractive *A. luteoalba* var. *rhodosticta,* in Cameroun to East Africa, has a bright scarlet column. – *Taeniophyllum* (ca. 90), widespread in tropical Asia, extending to Eastern Australia (one species in Africa), and *Microcoelia* (26), in tropical Africa and Madagascar, are small leafless epiphytes with very short stems and more or less dense clusters of branching, assimilating roots.

The Angraecum Group (subtribus Angraecinae), with ca. 16 genera and 1,600 species, is mainly an Afro-Madagascan group, but includes four American genera. It is characterized by a notched rostellum and a correspondingly very short tegula. There are only two pollinia. This group has probably evolved within the Aerangidinae.

Angraecum (25) has its centre on Madagascar. It is a vegetatively variable genus, ranging from tiny plants, sometimes with flattened, densely imbricate leaves (e.g. *A. distichum*) to large *Vanda*-like species (e.g. *A. eburneum*). The genus is recognized by the spurred, concave labellum, which more or less envelops the column. The flowers are most often white or greenish. *A. sesquipedale,* on Madagascar, has spurs 30–35 cm long. The existence of a hawk moth with a correspondingly long proboscis was predicted by Charles Darwin 40 years before this moth became known to zoologists. – Closely related to *Angraecum* is probably *Polyradicion* (2–4) in Florida and the West Indies: leafless root-assimilating epiphytes having surprisingly large, long-spurred flowers (up to 12 cm across).