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The Biology and Systematics of Ebenaceae: a Review

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Abstract

In the course of a revision of Ebenaceae for "Flora Neotropica", "Flora of Ecuador", "Flora of the Guianas", and while preparing a corresponding treatment for Kubitzki's "Families and Genera of Vascular Plants", a study of the available literature was undertaken. Data pertaining to vegetative morphology and anatomy, indumentum, extrafloral nectaries, sexual polymorphism, inflorescence and flower structure, pollen morphology, pollination, embryology, fruits, seeds, seed dispersal, germination, seedlings, caryology, phytochemistry, ecology, geographical distribution, phylogenetic affinities, paleobotany, and use and economic importance are here compiled, together with relevant bibliography. In addition, a revised description of the family and its genera, and a key for the identification of *Diospyros* and *Euclea* are included.

Key words: Ebenaceae, *Diospyros*, *Euclea*, morphology, anatomy, extrafloral nectaries, sexual polymorphism, embryology, pollen, pollination, seed dispersal, germination, caryology, phytochemistry, phylogeny, paleobotany, literature review.

Zusammenfassung

Im Rahmen einer Revision der Ebenaceae für "Flora Neotropica", "Flora of Ecuador", "Flora of the Guianas", sowie der Vorbereitung eines entsprechenden Beitrages für Kubitzkis "Families and Genera of Vascular Plants", wurde die verfügbare Literatur ausgewertet. Eine Zusammenfassung der relevanten Daten betreffend vegetative Morphologie und Anatomie, Behaarung, extraflorale Nektarien, Sexualpolymorphismus, Infloreszenz- und Blütenstruktur, Pollen, Bestäubung, Embryologie, Früchte, Samen und deren Verbreitung, Keimung, Keimlinge, Karyologie, Phytochemie, Ökologie, geographische Verbreitung, Verwandtschaftsverhältnisse, Paläobotanik, Verwendung und ökonomische Bedeutung wird hier mit entsprechender Bibliographie vorgestellt. Aktualisierte Beschreibungen der Familie und der beiden akzeptierten Gattungen *Diospyros* und *Euclea*, sowie ein Bestimmungsschlüssel für die Gattungen sind gleichfalls inkludiert.

Introduction

The Ebenaceae (ebony family) are pantropical in distribution and encompass the genera *Diospyros* and *Euclea* with ca. 500 - 600 species. Only a few of them extend into temperate zones. Main centers of diversity are in SE-Asia, Madagascar, tropical Africa, and South America. The last comprehensive revision of the family dates back to the 19th century (HIERN 1873). In the course of a revision of Ebenaceae (WALLNÖFER 1999, 2000, 2001; WALLNÖFER & MORI 2002) for "Flora Neotropica", "Flora of Ecuador", "Flora of the Guianas", and the preparation of a corresponding treatment for Kubitzki's "Families and Genera of Vascular Plants", a study of the available literature was undertaken. A resulting compilation of relevant data concerning various aspects of the biology of this family is presented.

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Family description

Ebenaceae GÜRKE in ENGLER & PRANTL, Nat. Pflanzenfam. 4/1: 153 (1891), nom. cons. – Type: *Ebenus* KUNTZE, non L. (*Maba* J.R.FORST. & G.FORST.) [see GREUTER et al. 2000: 131].

Trees, shrubs, or rarely geoxylic subshrubs; most species evergreen, but some deciduous; bark of tropical species often black, charcoal-like and brittle; heartwood black in some species; latex absent; branchlets spine-tipped in certain species; growth architecture of many species according to Massart's model (HALLÉ et al. 1978); bark of roots black in most species; root suckers produced by several species. Unicellular trichomes generally present, simple or 2-armed (but one of the arms usually very short); club-shaped multicellular glandular hairs conspicuous in some species; peltate hairs present on some African species. Leaves simple, usually alternate, rarely opposite to subopposite, or in pseudo-whorls of three, spirally or distichously arranged, petiolate or rarely subsessile, induplicate or involute in bud; stipules absent; lamina of leaves ± coriaceous in many species, less frequently chartaceous, pinnately veined; leaf margins usually entire, very seldom finely crenulate, usually with strongly revolute margins at base, at least when dry; leaf apices spinose in one species; abaxial leaf surfaces of most species with scattered "Flachnektarien" (type of extrafloral nectaries) usually near base of lamina, but often also near midvein and leaf apex; epidermal papillae on abaxial leaf surfaces often present. Plants usually dioecious, less frequently monoecious, sometimes polygamous. Inflorescences determinate, axillary, rami- or sometimes cauliflorous, multi-bracteate, cymose, fasciculate, pseudo-racemose or paniculate, usually rich-flowered when bearing male flowers, or uniflorous, especially when having female flowers. Flowers usually unisexual, less often structurally (very rarely also functionally) hermaphroditic (especially in *Diospyros* sect. *Royena*); male and female flowers usually markedly dimorphic, articulated at base, actinomorphic, 3 - 5 (- 8)-merous. Calyx mostly gamosepalous, less frequently polysepalous (chorisepalous), persistent, often accrescent in fruit; lobes valvate or imbricate, often spreading or reflexed in fruit, sometimes absent in some gamosepalous species (calyx then truncate). Corolla gamopetalous, usually isomerous with calyx, shortly to deeply lobed, tubular, campanulate or urceolate, white, or cream-colored, yellow, pink or reddish; tube usually prominent, but sometimes extremely short in male flowers; throat wide open, or restricted to a small pore; lobes usually contorted sinistrorsely. Male flowers: stamens (3 -) 12 - 20 (- ca. 100), often unequal in size and setulose, commonly inserted at the base of the corolla tube, sometimes on the receptacle or higher up in the corolla tube, episepalous and, if more numerous, then also epipetalous, hidden within the corolla tube or somewhat exserted, often in two hardly distinguishable whorls. Filaments usually short and flattened, free or united in pairs, triads or fascicles, or sometimes even into a central cylinder. Anthers linear or lanceolate, rarely ovate, erect, basifixed, distally often apiculate, tetrasporangiate, dithecious, the outermost introrse, the innermost extrorse, and those in-between latrorse, dehiscing by lateral, longitudinal slits (initially sometimes resembling pores near apex). Pistillode usually represented by an irregular lump of tissue lacking style, stylodia and ovules, rarely absent or, to the contrary, well-formed in the terminal flower of a male cyme (the flower then being structurally, and sporadically also functionally hermaphroditic). Pollen prolate-spheroidal to prolate (globular to ellipsoid), tricolporate, smooth to very finely warty, with ora usually lalongate, 24 × 20 μ to 75 × 60 μ [p/e (0.9) 1.2 - 1.5].

Female flowers: staminodes episepalous and, if more numerous, then also epipetalous, arranged in a single whorl, inserted at base of corolla tube, rarely higher up in direction to the throat, often more or less rudimentary, fewer in number than stamens in male flowers of the same species, rarely absent; rudimentary anthers introrse. Disk absent or well-developed and fleshy, fimbriate, or sometimes undulate. Ovary superior, sessile, 2 - 8-carpellate, eu-syncarpous, glabrous or hairy; style usually quite short; stylodia (free style branches) as numerous as carpels, usually longer than the style, distally simple or slightly bifid; stigmas often variously lobed; carpels biovulate, in a few species unilocular (number of biovulate locules per ovary: 2, 3 or 4), but in most species bilocular (due to a longitudinal, false, secondary septum, originating from the carpellary wall opposite the placenta, which bisects the carpellary chamber, hence each locule uniovulate; number of uniovulate locules per ovary: 4, 6, 8, 10, 12, 14 or 16); placentation apical-axile. Ovules pendulous, oblong, anatropous, bitegmic, tenuinucellate, with the raphe descending on the outer side; totaling 4, 6, 8, 10, 12, 14 or 16 per ovary. Fruit usually an indehiscent berry with a 2 - 3-layered pericarp, and usually with a more or less well developed hypodermal stone-cell layer; exocarp thin or thick, and coriaceous or hard; mesocarp thick or exiguous in many species, fleshy, spongy or fibrous; endocarp absent in a few species, but in general pulpy, sometimes fibrous, tightly adhering to the seeds and superficially resembling a sarcotesta. Seeds 1 - 16 per fruit, pendulous, usually with a persistent, distinctly raised (rarely inconspicuous), straight, and sometimes branched (*Diospyros*) or curved (*Euclea*) vascular strand longitudinally encircling it; hilum small, apical, inconspicuous; testa of outer integumentary origin (exotesta), pigmented, thin, parenchymatous, soft to leathery, histologically simple; endosperm hard, abundant, smooth to ruminate, consisting of closely packed, thick-walled, oil-bearing cells; embryo enclosed within the endosperm, straight or slightly curved in its plane (*Diospyros*), or the cotyledons strongly flexed out from this plane (*Euclea*), with two oval, well-developed foliaceous cotyledons and a strongly developed radicle pointing towards the apex of the fruit (germination through the micropyle).

Vegetative morphology

Euclea species are subshrubs, shrubs or trees up to 10 (- 12) m tall. Many species of *Diospyros* are small to medium-sized trees in the forest understory, but some species attain the size of large canopy trees. Various species of *Diospyros* from Sri Lanka are reported to be slow-growing, and a few others have been observed to form clusters of 3 - 14 thin stems with a common, matted system of roots (WRIGHT 1904). At least two species occurring in the fire-prone savannas of South America and Africa are geoxylic subshrubs, developing a xylopodium (subterranean, woody rootstock; e.g., *Diospyros hassleriana* in Paraguay, and *D. galpinii* in SE-Africa [the latter according to WHITE 1962]). A few African species of *Diospyros* are known to be rheophytes (WHITE 1998). Some species may proliferate by root-suckers, turning into often large monoclonal stands or coppices: e.g., *Diospyros burmanica* (TROUP 1921), *D. melanoxylon* (TROUP 1921; RATHORE 1971; AWASTHI 1986, 1990), *D. texana* (TISSERAT 1995), *D. virginiana* (SKALLERUP 1953a; see also figure in NICHOLS 1913), *Euclea divinorum* and *E. racemosa* (WHITE 1983; POOLEY 1993). *D. virginiana* is self-pruning: some twigs are abscised after their first year, a majority after their second, and still others during successive years, with only relatively few being retained and becoming the robust secondary branches of the tree (SKALLERUP 1953b; WOOD & CHANNELL 1960). Some Asiatic species of *Diospyros* occasionally exhibit spine-tipped branchlets (SHU-GANG et al. 1996; KOSTERMANS 1981), whereas *D. grisebachii* from Cuba develops spinose leaf apices.

The growth architecture of many species of *Diospyros* conforms to Massart's model (HALLÉ et al. 1978) that is determined by an orthotropic, monopodial trunk with rhythmic growth, and which consequently produces regular tiers of plagiotropic branches at subsequent (distal) new levels established by the trunk meristem (HALLÉ et al. 1978). The leaves are distichous on branches, but spirally arranged on trunks. On the latter they are often much reduced in size, or even only scale-like. While HALLÉ et al. (1978) mention 13 species of *Diospyros* conforming to this model, FRANCESCHI (1993) even quotes 34 species. According to the latter author, there are only few exceptions to Massart's model: one species conforms to Roux's model (for model definitions see HALLÉ et al. 1978), in another the architecture seems to be intermediate between Massart's and Cook's models, and three others take an intermediate position between Massart's and Roux's models.

Vegetative anatomy

The anatomy of seedlings of Ebenaceae (development of phloem and xylem, lignification and differentiation of vascular elements) is discussed in detail by WRIGHT (1904), who also found out that, in species with long-lived cotyledons, each cotyledon usually possesses 2, and in species with short-lived cotyledons, 3 traces (at least in species native to Sri Lanka).

The bark of many tropical species is black, charcoal-like and brittle (see photos in RIBEIRO et al. 1999). In cross-sections of trunks, branches, twigs, and roots, the bark of many species shows a characteristic thin layer of black tissue (e.g., GENTRY 1996; RIBEIRO et al. 1999). Even the roots of probably all (?) species are conspicuously black, except for the root tips, which are whitish (NG 1976; TROUP 1921). In some species, a slash of the trunk reveals the junction of inner bark and sapwood to be yellow (WALLNÖFER & MORI 2002).

The leaves are usually dorsiventral, but tending to be isobilateral in some species of *Diospyros* and *Euclea*. Depending on species, the cells of the epidermis differ considerably in shape and size. Their anticlinal walls are either straight, curved, or often undulated. Epidermal papillae occur on abaxial leaf surfaces of several species of *Diospyros*. All epidermal cells (except those bearing a hair) yield a more or less centrally placed, coronulate papilla. The papillae are connected by cuticular folds (ELSLER 1907). In some groups of species, papillae tend to be restricted to the cells around the sunken stomata (NG 1971). Stomata are usually confined to the abaxial leaf surfaces, although in some species a few have also been found on adaxial sides (e.g., in *D. mespiliformis*, *D. virginiana*, *Euclea pseudebenus*). Guard cells differ little among species, usually being level with other epidermal cells, or slightly protruding or sunken, and deeply sunken in only a few species. In *D. austro-africana* stomata occur at the bottom of crypts. The number of cells around each stoma varies from (3 -) 4 - 6 (- 9) and these cells do usually not differ from other epidermal cells (anomocytic condition, or of the ranunculaceous type). In some species, however, these subsidiary cells differ somewhat in shape, size and orientation, and in having straight anticlinal walls. Their arrangement is somehow similar to the cyclocytic condition as described by STACE (1965). According to WILKINSON (1979), *Euclea pseudebenus* exhibits actinocytic stomata. In species studied by DITSCH & BARTHLOTT (1997) cuticular waxes were absent.

A hypoderm is usually absent in leaves, rarely present in a few species. Yellow, sclerified, pitted cells, either solitary or in clusters and sometimes branched, are present in the mesophyll and particularly in the palisade layers of numerous species of *Diospyros*. In both, *Diospyros* and *Euclea*, stone cells occur in the parenchymatous portions of the veins of petioles. Secretory cells, similar to those in the stem, are abundant in the cortical region and sometimes in the phloem of the petiole. Large, solitary crystals, as well as clustered crystals (said to consist of calcium oxalate), occur in idioblasts of the mesophyll of leaves, but also in various other parts of the plants.

According to WOOD & CHANNELL (1960), nodes posses 1 trace from 1 gap, whereas WATSON & DALLWITZ (2000) describe them as uni-lacunar or tri-lacunar. In transverse section through the distal end, petioles of *Diospyros* exhibit a solitary, crescent-shaped, vascular strand. Its form is species-specific and varies from open and slightly concave to deep with strong incurved ends.

In young stems of *Diospyros*, cork is usually formed immediately below the epidermis, but in *Euclea* and in some species of *Diospyros* (especially in those of sect. *Royena*, but also in *D. oppositifolia* of sect. *Melonia*) it is of pericyclic origin. In *Diospyros*, the pericycle usually contains a composite and continuous ring of sclerenchyma, but in some of its species and in *Euclea*, isolated strands of fibers sometimes occur in this region. The secondary phloem is usually devoid of fibers, but stone cells are present in certain species. Secretory cells are abundant in the cortex, phloem, rays, and pith of many species, but are missing in some of these tissues in some species. [For more details concerning the subjects of the previous paragraphs, see: MOELLER 1882; PARMENTIER 1892; SOLEREDER 1899; WRIGHT 1904; BUSCH 1913; REINDERS-GOUWENTAK & STAHEL 1948; METCALFE & CHALK 1950; RAO 1951].

Characters of the wood are remarkably constant throughout the family: vessels are solitary and in radial multiples of 2, 3, 4, or sporadically more, and with simple perforations; pits between vessels, as well as between vessels and ray cells or parenchyma, are small (up to 8 μ in diameter). Parenchyma is predominantly apotracheal, scattered, and in numerous uniseriate lines, sometimes forming vasicentric sheaths round the vessels. Rays are 1 - 2 cells, rarely to 3 or 4 cells wide, less than 1 mm high, heterogeneous. Fibers posses small pits, and walls thinner than lumina, rarely thicker. Major sources of variation are in number of vessels in each cluster, arrangement of parenchyma, width of rays and thickness of fiber walls (description taken from NG 1971; but see also the very detailed description in METCALFE & CHALK 1950). The xylem of *Diospyros* consists of a continuous cylinder only traversed by narrow rays. Growth rings are inconspicuous in tropical species. *D. cordifolia* and *D. melanoxylon* have helical thickenings on vessel element walls (NAIR 1987). Ray cells in wood of all species examined for *D.* sect. *Royena* and *Euclea* contain solitary globular silica grains (MORTON 1994; MORTON et al. 1997). For further publications on wood anatomy, see bibliography in GREGORY (1994).

In various species, the sapwood is less hard, significantly less heavy, and considerably less durable than the heartwood (HILLIS & SOENARDI 1994) which is usually hard, heavy, fine-textured, close grained, diffuse-porous and, species dependent, colored either dirty-white, greenish, yellowish, red, blackish or jet-black (ebonised). The so called ebony wood is the transformed heartwood of ca. 30 Asian and African species. If present, the ebonised wood is abruptly set off from the sapwood, and varies considerably in proportion, usually being asymmetric, and irregular in outline (in both, radial and longitudinal view), with increments not always conforming to the yearly growth (see figures in: HILLIS & SOENARDI 1994). It may be uniformly jet-black, or composed of a succession of darker and lighter colored, irregular streaks, giving it a variegated, banded, or marbled appearance. The extent to which ebony wood is formed, usually varies markedly within a species (also in neighboring trees), sometimes entirely being absent, even in large trees (WRIGHT 1904; HILLIS & SOENARDI 1994). Due to a dark substance filling the lumina (derivatives and oxidative decomposition products of, e.g., naphthoquinones), the wood of these species is very durable and resistant against fungi or insect-induced decomposition. This black material is said to have a high content of carbon and properties characteristic of humic acids (GRIFFIOEN 1934). Usually, these discoloring substances make their first appearance in cells of the medullary rays or wood parenchyma, later in tracheal elements, and lastly in fibers (WRIGHT 1904). According to this author, the only ebonised tracts in many young stems are directly associated with insect punctures and wounds. HILLIS & SOENARDI (1994), who studied the wood of 175 species, found that ebonised zones are often associated with knots, branch stubs, decay, insect holes or injury, and concluded that the black deposits are formed as a response to infection by fungi.

Indumentum

Four different kinds of gray, brownish, or often characteristically rusty-brown hairs can be found in Ebenaceae, usually on stem apices, young leaves, inflorescence axes, bracts, pedicels and calyces, but they are often shed on older organs:

1) Unicellular, simple trichomes are usually more or less appressed to the organ surface (less frequently patent in some species) and evenly distributed, rarely in tufts or clusters (e.g., *D. austro-africana*).

2) Unicellular, 2-armed, sessile, or rarely short-stalked trichomes occur in various species of *Diospyros*. The arm pointing toward the base of the organ bearing them is usually very short (often only a small protrusion near the hair-stalk), whereas the opposite arm is very long.

3) Small, multicellular, club-shaped, gray, glandular hairs are conspicuous only on abaxial leaf surfaces of some species of *Diospyros* and *Euclea* (in the latter according to MORTON et al. 1997), and consist of a stalk composed of an uniseriate row of cells, and a swollen, one- or few-cellular head. The latter may be divided by vertical, or by vertical and horizontal walls (SOLEREDER 1899). These glandular hairs are very dense in some species (e.g., *D. capreaefolia*, *D. martinii*), giving the abaxial leaf-surfaces a typically glaucous, gray appearance.

4) Peltate, multicellular hairs (BUSCH 1913; SOLEREDER 1914) are present in some African species of *Diospyros* and *Euclea* (e.g., *D. hildebrandtii*, *E. undulata*), and consist of horizontal plates of 6 - 10, or more, radiating, often warty cells centrally connected by an uniseriate, vertical stalk of 1 - 4 cells (NG 1971).

Extrafloral nectaries

A feature that is frequent in many species, is the presence of "Flachnektarien" (type of extrafloral nectaries) on most but not all abaxial leaf surfaces (ELSLER 1907; CONTRERAS & LERSTEN 1984; see photo in RIBEIRO et al. 1999: 71). Obviously, this feature is absent only in few (at least few American) species. From 1 - 15 such nectaries may be present on a single leaf. Usually, they are patelliform, and located near the base of the lamina, but regularly also occur scattered along, but somewhat away from the midvein (they are never seen in axils of the secondary veins), and sometimes even near the leaf apex (see figures in ELSLER 1907 and FRANCESCHI 1993). According to CONTRERAS & LERSTEN (1984), only "Flachnektarien" of the specialized *Benincasa*-type occur in Ebenaceae. This type is characterized by having several layers of small nectariferous cells, subtended by an irregular, 1 - 2-layered sheath of cells with extremely thick radial walls. Two subtypes can be distinguished in Ebenaceae: apovascular and paravascular "Flachnektarien", the former having two or more subglandular layers between vein and sheath, and the latter one separating subglandular layer. In *Diospyros*, both subtypes occur, whereas in *Euclea* only the second has been observed. "Flachnektarien" are secreting droplets of a transparent, sweet liquid attracting ants (ELSLER 1907; BUSCH 1913). Nectaries may sometimes induce ants to nest on *Diospyros*-trees (see WONG & PUFF 1995).

Sexual polymorphism

The large majority of species have unisexual, usually markedly dimorphic flowers and are mostly dioecious, or quite rarely monoecious (WRIGHT 1904; YASUI 1915; NG 1971; ATHAYA & MISHRA 1979; YONEMORI et al. 1993; OLIVEIRA 1996). In monoecious species, female flowers are usually borne in axils of younger leaves, commonly on leaders, whereas the male flowers are developed in leaf-axils of older, often already leafless parts of twigs, or on non-leaders (short lateral twigs) (WRIGHT 1904; YASUI 1915: fig. 1). The polygamous condition seems to be less common and can only be met with when hermaphroditic flowers are produced. The latter generally occur in species of *Diospyros* sect. *Royena* (formerly genus *Royena*), and are, according to SALTER (1953) and WHITE & BARNES (1958), only structurally but not functionally hermaphroditic. Among species of other sections, hermaphroditic flowers have been sporadically observed (8 species cited by WRIGHT 1904), and seem to be always associated with, and derived from male flowers, occupying the terminal positions in otherwise male inflorescences (YASUI 1915; NAMIKAWA et al. 1932; FRANCESCHI 1993). Most of these flowers are only structurally, but some are also functionally hermaphroditic, producing fruits with or without seeds. These fruits have been reported to be smaller and somewhat different in shape than those developed from female flowers (YASUI 1915; NAMIKAWA et al. 1932). Depending on the month in which the treatment is carried out, staminate flowers of *D. kaki* can be converted into either hermaphroditic, or pistillate flowers, by applying benzylaminopurine before or during flower initiation (YONEMORI et al. 2000). Individual trees of *D. kaki* are said to develop predominantly female flowers in one year and male flowers in another, thus yielding greatly varying numbers of fruits among years (YASUI 1915). In monoecious or polygamous cultivars of *D. kaki*, sex expression may be modified by the previous year's load of fruit and the nutritional status of the tree (YONEMORI et al. 1992).

Fortunately, leaves (and other vegetative parts) show no sexual dimorphism and are usually distinct enough between species to correctly identify male and female specimens as conspecific.

Inflorescence structure

The ebenaceous inflorescence is conventionally referred to as a cyme (NG 1991b; compare also FRANCESCHI 1993). It is always developed in the axils of leaves. In a few species they are borne on more or less warty thickenings along trunks and stems (cauliflory), and arise from adventitious axillary buds (compare fig. 11 in KOORDERS 1902). The peduncles always bear bracts, even when supporting only one flower. The pedicels are articulated and, if lateral, subtended by a bract. Solitary flowers are always terminal on the peduncle. Usually, male flowers of a given species by far outnumber the females. Quite often, the inflorescence is a 3-flowered dichasium, although numerous variations can be seen, ranging from 3-flowered dichasia to a multiflowered, multibranched, paniculate condition, but in nearly all cases, the terminal units resemble dichasia, i.e., the terminal flower develops earlier than those immediately behind (NG 1991b: fig. 3). Male inflorescences of *Diospyros* are usually many-flowered and arising in axils of older or fallen leaves, less frequently they are only 1-flowered, a condition especially seen in axils of younger leaves. Female inflorescences, on the other hand, are mostly 1-flowered and usually develop in axils of younger leaves, less frequently 3- and even more rarely up to 15-flowered. When flowers are sessile, as is the case in some species, there is often a great deal of abortion, the remaining flowers being surrounded by numerous bracts, all in all resembling a kind of involucre (WRIGHT 1904). In *D. toposioides*, vegetative shoots differ from reproductive ones in that the latter bear small dichasia (males), or solitary, bracteate flowers (females) in the axils of caducous bracts, and terminate in a vegetative bud, instead of a flower. From such terminal buds a leafy shoot may later develop (NG 1991b: fig. 2). The inflorescence of *Euclea* is usually unbranched, multiflorous and resembling a raceme, except at the apex which looks like a dichasium (NG 1991b: fig. 3b).

Flower structure

Flowers are actinomorphic and 3 - 5 (- 8)-merous. The persistent calyx is usually gamosepalous, sometimes polysepalous (chorisepalous), and has valvate or imbricate lobes. Due to the absence of lobes, in some species the calyx appears distally more or less truncate. In the Sri Lankan *D. toposia*, the calyx of the male flower is closed in the bud, and when opening, irregularly bursts into 2 or more segments (WRIGHT 1904). The corolla is gamopetalous, usually isomerous with the calyx. Its tube is usually prominent, but sometimes extremely short in male flowers. The throat may either be wide open, or restricted to a small pore. The corolla-lobes are usually contorted sinistrorsely. The number of floral parts is known to vary within species and cannot, therefore, be used effectively for their distinctions, as has been done in the past (e.g., CANDOLLE 1844; HIERN 1873).

Male and female flowers are usually dimorphic. In *Euclea*, male flowers are usually larger than female ones, but similar in shape. In *Diospyros*, male and female flowers differ, the former generally being smaller, and possessing a smaller calyx with narrower lobes, and a narrow, sometimes very short corolla tube. In both genera the stamens are usually numerous [(3 -) 12 - 20 (- ca. 100)] and arranged into two hardly distinguishable whorls. The innermost stamens are usually shorter and smaller than the outer ones. The filaments are free, or united in pairs, triads or fascicles, or sometimes into a central cylinder, and are commonly inserted at the base of the corolla tube, or sometimes higher up, or on the receptacle. The anthers of the outermost staminal whorl are introrse, those of the innermost whorl extrorse, and those placed in the center of the single fascicles latrorse (FRANCESCHI 1993). The pistillode is commonly reduced to irregular lumps of often hairy tissue, lacking style, stylodia and ovules, or may be completely suppressed. The staminodes of female flowers are arranged only in one whorl, and are often much reduced in shape. They are less numerous than the stamens in male flowers of the same species, or are rarely missing altogether. Usually, their number is equal to that of the corolla or calyx segments, but in some species they are more numerous, or their number an exact multiple of the segments (WRIGHT 1904). The rudimentary anthers are introrse. The ovary is superior, sessile, 2 - 8-carpellate, eu-syncarpous (see: CARR & CARR 1961), and develops into a fruit with basipetal growth (CORNER 1976). The style is usually quite short. The often quite long and distally simple, or slightly bifid stylodia (free style branches) are as numerous as the carpels (NG 1971, 1991b). Stigmas are of the dry type with non-papillate surface (HESLOP-HARRISON & SHIVANNA 1977; DAHLGREN 1991). Carpels are biovulate, rarely (depending on species) unilocular (each locule having 2 ovules), or mostly bilocular (each locule having only one ovule). In the first case, the number of biovulate locules per ovary is 2, 3 or 4. In the second case, a false (secondary) longitudinal septum (originating from the carpellary wall opposite the placenta) bisects the carpellary chamber. Hence, each locule is only uniovulate. The known number of uniovulate locules per ovary is 4, 6, 8, 10, 12, 14 or 16. The total number of ovules per ovary is 4, 6, 8, 10, 12, 14 or 16. The placentation is apical-axile. At or above the placentae, all the locules open into a common chamber ("compitum" sensu CARR & CARR 1961) which continues up the style as a single stylar passage, dividing into separate branches only to enter the separate style branches (NG 1991b). This stylar passage consists of a slit which, depending on the varying number of carpels, is multibranched and variously curved basally, and simple towards the style.

Hermaphroditic flowers (see chapter on sexual polymorphism) are derived from male flowers, differing from them in possessing a well developed, but often somewhat smaller ovuliferous ovary, and a larger calyx. Usually, these flowers are only structurally, or, very rarely, also functionally hermaphroditic.

Pollen morphology

The morphology of pollen is remarkably constant throughout the family. The main variations are in size, shape, and ora appearance (NG 1971). Pollen grains are tricolporate, prolate-spheroidal to prolate (globular to ellipsoid), binucleate or trinucleate at least in 4 species (SUGIURA et al. 1998), with a size range between 24 × 20 μ and 75 × 60 μ [p/e (0.9) 1.2 - 1.5] (NG 1971). The sexine is as thick as the nexine, or thicker, smooth (psilate), or very finely warty, with a ± obscure (subreticulate) pattern. The pollen grains of all the species examined of *D.* sect. *Royena* and *Euclea* exhibit granular sculpturing patterns (MORTON et al. 1997). Ora are mostly well defined, usually lalongate, sometimes with indistinct lateral edges, or rarely indistinguishable. [For more details see: SALGADO-LABOURIAU et al. 1969; ERDTMAN 1971; SHARMA & GUPTA 1979; AYALA-NIETO & LUDLOW-WIECHERS 1983; ROUBIK & MORENO 1991; FRANCESCHI 1993; JONES et al. 1995].

Pollination

The flowers of *D. virginiana* are visited by bees (HAGUE 1911). Some species of *Diospyros* from Mexico contribute in a major way to the production of honey (ORDTEX et al. in AYALA-NIETO & LUDLOW-WIECHERS 1983). According to POOLEY (1993), the flowers of *Euclea natalensis* and *E. undulata* attract bees, and those of *E. racemosa* "insects". The flowers of *Diospyros lycioides* are visited by bees, wasps, and butterflies, whereas those of *D. dichrophylla* attract sunbirds (POOLEY 1993). Beetles (considered to be the main pollinators), flies and wasps (all ca. 3 - 6 mm long) were observed visiting the male and female flowers of *D. pentamera* in Australia (HOUSE 1992; compare also IRVINE & ARMSTRONG 1990). In *D. hispida*, a species of the Brazilian cerrados, flowers have been seen to reach anthesis during the night, and to attract specialized, nocturnal, small lepidoptera (moths) (SILBERBAUER-GOTTSBERGER & GOTTSBERGER 1988: 657). As indicated by annotations on some herbarium labels, the anthesis of male flowers of various rainforest-species also seems to be nocturnal, the flowers then being shed the same night. Male flowers of *D. kaki*, on the other hand, open in the early morning, soon reaching anthesis, and are usually shed in the evening of the same day (NAMIKAWA et al. 1932).

Embryology

The anther wall comprises the epidermis, the endothecium, two middle layers, and multinucleate tapetal cells. The endothecium is non-fibrous in *D. kaki* (YASUI 1915). ANJANEYULU & LAKSHMINARAYANA (1989) report a fibrous endothecium for *D. virginiana* and *D. chloroxylon*, and a tapetum being dual in origin and dimorphic in nature. In the microspore mother cells, simultaneous cytokinesis follows meiosis. The microspore tetrads are tetrahedral, isobilateral, or decussate.

The ovule is pendulous, oblong, anatropous, bitegmic, tenuinucellar, with the raphe descending on the outer side. The testa only consists of the outer integument. After fertilization, the inner integument disintegrates, except for its inner epidermis, which persists and behaves as if it were the surface layer of the embryo-sack. The archesporial cell functions as megaspore mother cell, undergoes meiotic divisions, and produces a linear tetrad. The chalazal megaspore develops into a *Polygonum*-type of embryo sac. Fusion of polar nuclei does not always occur, and the three antipodal cells are small and ephemeral. The endothelium is well-developed. The development of the endosperm is of the cellular type. The embryogeny and organogenesis probably correspond to the polygonad type / chenopodiad variation or chenopodiad type. [compiled from: HAGUE 1911; YASUI 1915; DAVIS 1966; YAMAZAKI 1972; WHITE 1983; JOHRI et al. 1992].

Fruit and seed

The fruit is a multiloculate, 1 - 16-seeded, usually indehiscent berry which is subtended by a persistent 3 - 8-lobed calyx. In many species of *Diospyros*, the calyx is accrescent and possesses appressed, spreading, or reflexed and often revolute lobes. It considerably enlarges during fructification, often developing large, intersegmental pouches, and as a whole, assuming a very sophisticated and species-specific, characteristic shape. However, in some species the calyx remains small and quite inconspicuous, or is rarely unlobed (truncate). In *Euclea* the calyx is not at all accrescent. The pericarp is 2- or 3-layered, and when mature either completely soft (e.g., in *D. kaki*), or with a thinner or thicker, leathery or hard outer layer (e.g., in *D. cayennensis* it is a hard shell several millimeters thick). A hypodermal layer of stone-cells, very rarely of radial fibers, or of a mixture of fibers and stone-cells is developed. The mesocarp is either thick and fleshy to pulpy, or often exiguous. A layer of pulpy (and usually edible), sometimes fibrous endocarp, closely adhering to the seeds and superficially resembling a sarcotesta, is developed in most (but not all) species (NG 1971, 1976, 1991a). According to WINTER (1963) and WHITE (1983), the fruits of some African species of *Diospyros* sect. *Royena* become dry, and occasionally tardily dehiscent. In no species of Ebenaceae, however, is the fruit completely and spontaneously dehiscent. Idioblasts containing tannins generally occur in the pericarp of the fruits (CORNER 1976; UTSUNOMIYA et al. 1998). The tannins are responsible for the characteristic astringent taste, which diminishes (but, except in some cultivars, only rarely disappears completely) when the fruits are ripe and become very soft (for more details concerning this very intensively investigated topic see YONEMORI et al. 2000). The fruits of some species are poisonous, presumably when raw, and are used in various parts of the world to catch fish. The diameter of mature fruits ranges from 5 - 100 mm (NG 1971, 1991a). The fruits of various cultivars of *D. kaki* are seedless, due to parthenocarpy (e.g., WETTSTEIN 1908; YONEMORI et al. 2000).

Seeds are pendulous. The 1 - 16 seeds of *Diospyros* are usually flattened laterally, but sometimes circular in cross-section, or often somewhat irregular in shape (very rarely subglobose), their size ranging from 8 × 4 × 2 mm to 40 × 25 × 7 mm or 40 × 20 × 20 mm (NG 1971). In *Euclea*, the seeds are usually solitary, subglobose, and 3 - 10 mm in diameter when ripe and, if more than one, then jointly forming a sphere.

In *Diospyros*, the seed is encircled longitudinally by a persistent, distinctly raised (rarely inconspicuous), straight, and sometimes branched, vascular strand (in a sort of loop). The situation is more complicated in *Euclea*, where only one seed normally develops. During growth, the other, abortive ovules, and the axis of the ovary, are pushed to one side of the fruit, and the axis leaves an impression on the seed in the form of a shallow, lateral groove down one side of the seed. The *Euclea* seed thus shows three lines radiating from its apex, one being the lateral groove already mentioned, and the other two consisting of distal parts of the curved vascular loop (curved like the sutures of a tennis ball) (NG 1971; WINTER 1963; WHITE 1983: tab. 54). In *Diospyros*, the plane of the cotyledons is usually oriented parallel to the median, radial plane of the fruit (and to the plane of the vascular loop), but in a few species it is more or less at right angles to the median radial plane, due to its displacement during growth. In *Euclea*, the latter situation has become the norm.

The hilum of the seeds is small, apical, and inconspicuous. The testa is pigmented, thin, parenchymatous, soft to leathery, histologically simple, but the shape, size and degree of cell-wall thickening of the outer epidermis is variable between species. The endosperm is hard (bony or flinty), abundant, smooth to ruminate (rumination of the *Annona*-type, according to PERIASAMY 1966), consisting of closely packed, thick-walled, oil-containing cells. In *Euclea*, the rumination takes the peculiar form of ingrowths from the testa, forming a cylinder around the whole radicle (NG 1971; WHITE 1983: tab. 54), or the rumination is said to be absent [?] in various species (WINTER 1963). In *Diospyros* sect. *Royena*, the rumination forms a shallow ingrowth only around the distal part of the radicle (see WHITE 1983: tab. 54). The embryo of Ebenaceae is turned upside-down, with the strong radicle pointing towards the apex of the fruits, and has two oval, well-developed, foliaceous cotyledons. It is straight or slightly curved in its plane (*Diospyros*), or the cotyledons are strongly flexed out from this plane in direction of the dislocated fruit-axis (*Euclea*).

Fruit and seed dispersal

Seeds are dispersed by various fruit-eating animals, such as civet cats, monkeys, bears, or by various birds (hornbills, pigeons, American blue-birds, mocking birds and American mallards) (RIDLEY 1930), by primates (TUTIN et al. 1996), such as baboons (LIEBERMAN et al. 1979), bats (TROUP 1921; PIJL 1957; GARDNER 1977), bush pigs, the blue duiker and other mammals (WHITE 1983), by bulbuls and various species of pigeons (PANNELL & WHITE 1988), by birds, rats, mongooses, antelope, monkeys, dogs, and dassies (POOLEY 1993), occasionally by elephants (LIEBERMAN et al. 1987), and in North America by coyotes, deer, foxes, opossums, quails, raccoons, ring-tailed cats, skunks and 7 species of other birds (SKALLERUP 1953a; WOOD & CHANNELL 1960; CHAVEZ-RAMIREZ & SLACK 1993; CYPHER & CYPHER 1999). For the African mainland PANNELL & WHITE (1988) have pointed out that the fruits of most species of *Diospyros* are dispersed by non-flying mammals. Fruits of coastal and riverine species, as well as those of species growing in periodically inundated areas, may perhaps also be dispersed by water, and in some cases probably also by fish (GOULDING et al. 1988).

Germination and seedlings

While nothing seems to be known concerning the germination of *Euclea*, that of *Diospyros*-seeds (WRIGHT 1904; TROUP 1921; NG 1971, 1976, 1991a; FRANCESCHI 1993) is usually epigeal, less frequently hypogeal, "semihypogeal", or of the "durian" type (= crypto-epigeal sensu DUKE & POLHILL 1981; compare also GARWOOD 1996). Dormancy of the seeds (at least as far as species from temperate zones are concerned) is due, in part, to the mechanical resistance of the seed coat, particularly the layer overlying the micropyle (WOOD & CHANNELL 1960). Germination periods range from 12 to 126 (250) days (NG 1991a), and up to 9 months in species with a particularly hard testa and a copious endosperm (WRIGHT 1904). The root of the seedling emerges from the apex of the seed, through the micropyle, and develops into a strong and usually black taproot. After having absorbed the endosperm, cotyledons may, by means of expansion and forceful bending, greatly facilitate splitting of the seed shells of various species.

In most species the hypocotyl is more or less prominent, initially arched and, by elongating, lifts up the body of the seed (epigeal germination). Whereas the cotyledons are long-lived in some species, they are short-lived in others (NG 1976, 1991a; FRANCESCHI 1993). In the first case, cotyledons emerge from the seed shell and become photosynthetic. In this group, the epicotyl (at least as far as Sri Lankan and Indian species are concerned) is always very short, and the tardily developing epicotyledonary leaves are alternate (spiral). In the second group of species the cotyledons are short-lived, being shed during or shortly after emergence, without ever becoming photosynthetic ("suicidal mode", sensu WRIGHT 1904). In these latter species (at least in Sri Lankan and Indian species) the epicotyl is long, and the first two, rapidly developing epicotyledonary leaves are usually opposite, very much resembling cotyledons (WRIGHT 1904). In both these groups of species the testa splits along the plane of the raphe (the latter being a particularly rupture-prone zone). However, in several species the plumule remains often trapped within the only partially split seed shell. This peculiar situation later very often causes the death of the seedlings. Apparently, successful germination in both these groups of species can only be achieved, either when the timing of cotyledonar pressure and subsequent dehiscence are well coordinated (NG 1971, 1976, 1991a), or when ingestion of the seeds by animals causes structural modifications of the seed shell. In the latter case, the rapid decline of populations of the involved animals, due to intensive hunting activities of man, could be responsible for the notorious rarity of several species of *Diospyros*.

The testa of the Malesian *D. maingayi* does not split at all. The cotyledons do not emerge from the seed and are shed together with the body of the seed (crypto-epigeal germination, respectively of the "durian" type). The epicotyledonary leaves are either alternate or opposite (NG 1976; FRANCESCHI 1993).

In the African *D. lycioides*, the hypocotyl does not elongate, with the cotyledons subsequently remaining lying on the ground (NG 1971; "semihypogeal" germination sensu NG 1976, 1991a).

Hypogeal germination can be observed (NG 1976) in the Malesian *D. pendula*: during its first weeks of growth, the food reserves of the seed are transferred to the taproot which becomes much swollen. The cotyledons, which remain enclosed in the seed body, are later abscised, before the epicotyl starts developing. The latter bears scale-like leaves at first which are then succeeded by alternate leaves.

In seedlings and juvenile plants of several species (e.g., *D. blancoi*, *D. carbonaria*, *D. kaki*) grown in cultivation (own experiments), the black root system only consisted of a taproot and some major lateral roots, without any finer rootlets. This observation could be related to field surveys and experimental results showing *D. melanoxylon* (KUMAR et al. 2000) and *D. tsangii* (ZHUANG et al. 2000) to be independent of mycorrhiza. In *D. kaki*, to the contrary, mycorrhizal fungi had a significant effect on growth and performance (for details see MATSUBARA & HOSOKAWA 1999).

Caryology

The chromosome number is very stable. An euploid series of 2n = 30, 60, 90, and 135 allows inference of a basic number x = 15. Thirty-six species are reported to be diploid

(White & Vosa 1980; Bennett & White 1990; Franceschi 1993; Yonemori et al. 2000), with *D. lycioides* being diploid and tetraploid (White & Vosa 1980), *Diospyros ramulosa* and *D. rhombifolia* tetraploid (White & Vosa 1980; Yonemori et al. 2000), *D. virginiana* tetra- and hexaploid (Baldwin & Culp 1942), *D. ebenum* hexaploid (Franceschi 1993; Yonemori et al. 2000), and with *D. kaki* usually being hexa- and less frequently enneaploid and assumed to be an allopolyploid (Zhuang in Yonemori et al. 2000). In *Euclea*, 8 species have been investigated so far, all being diploid, with 2n = 30 (White & Vosa 1980).

Phytochemistry

Naphthoquinones, terpenoids (especially lupanes, ursanes, oleananes, taraxeranes), benzopyrones, polyphenols, and tannins are all widely distributed, and thus very characteristic for Ebenaceae. Other compounds are steroids, naphtalene-based aromatics, hydrocarbons, lipids, amino acids, carotenoids, and sugars (Mallavadhani et al. 1998; Hegnauer 1966, 1989). Naphthoquinones occur in several organs, especially in the bark, and are (e.g., plumbagine) active against fungi, bacteria, mollusks, insects, worms, termites etc. (Neuwinger 1998). Their derivatives and oxidative decomposition products are responsible for the dark brown to black colored tissues of the bark, heartwood, fruits, and leaves (Neuwinger 1998). Idioblasts containing tannins occur in various organs, including fruits (e.g., Utsunomiya et al. 1998; Yonemori et al. 2000). Serological comparisons have been carried out by Kolbe & John (1980).

Geographical distribution, habitat and ecology

Ebenaceae occur mainly in the lowlands of the tropical and, to a lesser extent, in subtropical regions of the Old and New Worlds. The small genus *Euclea* is restricted to Africa and southern Arabia, whereas the large genus *Diospyros* is pantropical. Many of its species are usually small to medium-sized trees in the forest understory, with an often remarkably low population density. Only few species penetrate the mountains and extratropical warm temperate regions. Several species grow along rivers, some of which evolved into rheophytes (White 1998). Others are characteristic inhabitants of periodically inundated, or permanently swampy areas. In Bolivia, *Diospyros yomomo* grows on small, floating islands, or mats, composed of organic material. Certain varieties of *D. ferrea* are reported to grow in the back of mangroves, or among beach communities (Tomlinson 1986). Some species prefer dryer vegetation types, or fire-prone tropical savannas, and still others (e.g., *D. lotus*, *D. virginiana*) temperate, deciduous forests.

Paleobotany

According to Raven & Axelrod (1974), the Ebenaceae are assumed to have evolved in the Cretaceous in western Gondwana, and to have reached Eurasia and North America, presumably by Paleocene time. Fossils are mainly known from the Tertiary, with only relatively few dating back to the Cretaceous (e.g., Berry 1923). Records of Ebenaceae in the older paleobotanical literature have already been compiled by Hiern (1873). More recent, although only partial accounts can be found in EDWARDS (1931), FRANCESCHI (1993), COLLINSON et al. (1993), and MAI (1995). Apart from *Diospyros* and *Euclea*, the following fossil (extinct) form-genera have been recorded: *Diospyrocarpum*, *Diospyropsis*, *Diospyroxylon*, *Ebenoxylon*, *Euebenoxylon*, and *Tricolporopollenites milonii*. BASINGER & CHRISTOPHEL (1985) carried out a very detailed study of *Austrodiospyros cryptostoma* from the Eocene of Australia.

The leaves of Ebenaceae are quite polymorphic, sharing features with those of many other families. Assignment of fossil leaves to this family, therefore, is problematic. Not much attention has been paid in the past to presence of e.g., extrafloral nectaries, or to coronulate papillae on abaxial leaf surfaces. Many fossils presently assigned to Ebenaceae may have to be re-evaluated.

Phylogenetic affinities

The Ebenaceae have traditionally been placed in its own order Ebenales, together with, at least in part, the following families: Sapotaceae, Styracaceae, Sarcospermataceae, Symplocaceae and Lissocarpaceae (see MORTON et al. 1997). *Lissocarpa*, the only genus of the monogeneric family Lissocarpaceae has been included in Ebenaceae by some authors, but is now recognized to deserve familial status. According to NG (1971) and FRANCESCHI (1993) it is the closest relative of Ebenaceae, an opinion which is also strongly endorsed by a recent molecular study (BERRY et al. 2001).

Recent molecular studies, based upon *rbc*L sequence data (MORTON et al. 1997), have demonstrated that Ebenaceae (with the genera *Diospyros* and *Euclea*; but *Lissocarpa* not having been analyzed due to lack of adequate material) are monophyletic. However, the order Ebenales appears polyphyletic. These studies indicate that Ebenaceae may be the sister-group of Primulales (including the families Myrsinaceae, Primulaceae and Theophrastaceae) within the large Ericalean clade, which, on the other hand, is part of the Asteridae clade among Eudicots. According to SOLTIS et al. (1997, 2000), who analyzed 18S ribosomal DNA, the position of Ebenaceae within the "Ericalean grade" is somewhat different. In the three cladograms presented by NANDI et al. (1998), based on *rbc*L and non-molecular data, Ebenaceae are located at three different positions within the clade "asterid III" which is part of the major clade "asterids". Further studies, based on more material, and in connection with anatomical and morphological comparisons, are clearly needed to resolve these contradictory, preliminary results.

Use and economic importance

Ebenaceae are the source of several economically important products, the most valuable being their fruits and timber (ebony). *Diospyros kaki* is the most important fruit-yielding species and is cultivated on a large scale and in many varieties, especially in temperate East Asia (e.g., China, Japan, and Korea), but on a smaller scale also elsewhere in the world (YONEMORI et al. 2000). The fruits are eaten fresh or dried, and are a source of sugar. Other frequently cultivated fruit trees are *D. digyna* (zapote prieto, black sapote), *D. blancoi* (the former "*D. discolor*"; velvet apple, mabolo), and *D. lotus*. The fruits of many other species are of regional or local importance. In India, for example, fruits of 18 species of *Diospyros* are eaten (Jayaraman & Singh 1988; Jayaraman 1996); in Africa, 15 species of *Diospyros* and 7 species of *Euclea* serve as food (Peters et al. 1992). In tropical West Africa, 33 species of *Diospyros* are used as food, timber, medicine, fish-poison, ingredient for arrow-poison, for dying, and for many other purposes (Burkill 1994). Also in Asia and America the fruits of several species of *Diospyros* are used to poison fish. The leaves of *D. melanoxylon* ("Tendu") are utilized on a wide scale in India as wrappers for cigarettes, called "bidi" (Rathore 1972; Hunter 1981). In North America, fruits of *D. virginiana* have been used to brew persimmon beer and those of *D. digyna* to make brandy (Standley 1920 - 1926; Carr 1947; Jayaraman 1996).

Ebony timber is among those exotic materials that have been highly valued since classical times. It was, and still is, used mainly for manufacturing musical instruments, for carved work, in cabinetmaking, as decorative veneer for furniture, and for interior decoration. True ebony timber is obtained from various species having a dark-streaked or jet-black heartwood. Economically most important in this respect are *Diospyros ebenum* and *D. melanoxylon* from India and Sri Lanka. Other important species are *D. celebica* (Macassar ebony from Indonesia), *D. crassiflora* (Africa), *D. insularis* (Papua New Guinea), *D. marmorata* and *D. oocarpa* (Andaman marblewood or zebrawood, both from the Andaman islands), *D. perrieri* (Madagascar), *D. quaesita* (Calamander or Coromandel wood from Sri Lanka), *D. virginiana* (persimmon from southeastern USA with a pale wood, used e.g., for heads of golf clubs), *Euclea pseudebenus* (black ebony from Africa), but many others are also highly estimated and mainly used regionally (Sadebeck 1887; Gürke 1891; Gottwald 1984; Dahms 1990; Wagenführ 2000). Some species are now heavily threatened due to their over-exploitation, and may soon become extinct in the wild.

Key to genera

1 Calyx usually accrescent on fruits; inflorescence cymose or fasciculate (but female flowers mostly solitary); fruits usually with more than one seed, rarely 1-seeded; seeds elongated and usually flattened laterally, less commonly circular in cross-section, or somewhat irregular in shape, usually with a persistent, distinctly raised (rarely inconspicuous), straight, and sometimes branched vascular strand longitudinally encircling it in a loop; embryo straight or slightly curved in its own plane; leaves with entire margins, usually alternate, very rarely opposite to subopposite; pantropical .... 1. *Diospyros*

1* Calyx not accrescent on fruits; inflorescence a simple or branched pseudo-raceme, sometimes uniflorous; fruits usually 1-seeded, rarely few-seeded; seeds subglobose (if more than one, then jointly forming a sphere), with three lines radiating from apex, one consisting of a shallow, vertical groove (impression of the dislocated fruit-axis), and the other two of the distal parts of the curved vascular loop; cotyledons strongly flexed out from the embryo-plane in direction to the dislocated fruit-axis; leaves alternate, opposite to subopposite, or in pseudo-whorls of three, with entire or rarely finely crenulate margins; restricted to Africa, Arabia, Socotra and the Comoro Islands .... 2. *Euclea*

1. *Diospyros* L.

Diospyros L., Sp. Pl., ed. 1: 1057 (1753) – Type: *D. lotus* L. [see: FARR et al. 1979]; – world monographs: CANDOLLE (1844) and HIERN (1873).

Trees, shrubs or subshrubs, dioecious, rarely monoecious or polygamous, evergreen or less frequently deciduous, rami- or less frequently cauliflorous; few species with spine-tipped branchlets. Leaves in the large majority of species alternate, in very few species opposite to subopposite; margins entire; leaf apices spinose in *D. grisebachii*. Inflorescences axillary, usually cymose or fasciculate, or flowers solitary, especially females. Flowers usually dimorphic in size and shape, males usually smaller than females. Calyx persistent and usually accrescent on fruits, very variable, usually 3 - 8-lobed, less frequently cup-shaped and unlobed or polysepalous (chorisepalous). Corolla 3 - 8-lobed, very variable. Stamens 2 to ca. 100; anthers dehiscing by longitudinal slits. Pistillode variable, from well-developed to absent. Staminodes present or absent, often well-developed. Disk well-developed or not, sometimes fimbriate. Ovary globose, ovoid or conoidal, glabrous or hairy, 2 - 8-carpellate; carpels biovulate, and in a few species unilocular (number of biovulate locules per ovary: 2, 3 or 4), or as in most species bilocular (due to a longitudinal, false septum, originating from the carpellary wall opposite the placenta, which bisects the carpellary chamber, hence making each locule uniovulate; number of uniovulate locules per ovary: 4, 6, 8, 10, 12, 14 or 16); stylodia (style branches) 2 - 8. Fruit a 1 - 16-seeded berry. Seeds usually flattened laterally, but sometimes circular in cross-section, or often somewhat irregular in shape (very rarely subglobose in some species), longitudinally encircled by a persistent, distinctly raised (rarely inconspicuous), straight, and sometimes branched, vascular strand (in a sort of loop); size of seeds ranging from 8 × 4 × 2 mm to 40 × 25 × 7 mm, or 40 × 20 × 20 mm. Endosperm smooth or ruminated; rumination in a few species forming a shallow ingrowth around the distal part of the radicle. Embryo straight or slightly curved in its own plane; surfaces of the cotyledons usually oriented parallel to the median radial plane of the fruit, rarely at right angles to it. $2n = 30, 60, 90, (135)$. Pantropical in distribution, with only few species growing at higher altitudes, or extending into warm temperate regions. Ca. 500 - 600 species, of which 200 - 300 species occur in Asia and the Pacific area, 98 species in Madagascar and the Comoro Islands, 94 species on the African mainland, ca. 100 species in the Americas, and 15 species in Australia.

A comprehensive, worldwide monograph is very much needed, the most recent dating back to 1873 (HIERN 1873). Besides *Diospyros* (with 15 sections), this monographer also recognized the genera *Maba* (with 6 sections), *Royena* and *Tetraclis*, all of which are now included in the former genus (WHITE 1980, 1983). While BAKHUIZEN VAN DEN BRINK (1936 - 1955) grouped the SE Asiatic and Pacific species into 5 subgenera with 36 sections, WHITE (1980) arranged the African species into 18 sections (compare table 1). But this infrageneric grouping of species continues to be unsatisfactory and controversial. *Diospyros*, as currently circumscribed, seems not to be monophyletic (FRANCESCHI 1993; MORTON et al. 1997). According to the latter molecular study, *Euclea* cannot be separated from *Diospyros*: together with *D. whyteana* (earlier included in the genus *Royena*), it appears to form its own group within the Ebenaceae-clade (MORTON et al. 1997). Molecular studies [for methods see also KIM et al. 1997] on a larger, world-wide scale are needed to finally achieve a more consistent new grouping of this large genus. First attempts in this direction are those of NAKAMURA & KOBAYASHI (1994) and YONEMORI et al. (1996, 1998), who studied the phylogenetic relationship of *D. kaki*.

Table 1: Comparison of infra-familiar and infra-generic classifications of Ebenaceae, as proposed by four of the most important monographers of this family. The number of species accepted by each author is given in parentheses.

Candolle (1844) (worldwide)	Hiern (1873) (worldwide)	Bakhuizen (1936-1955) (SE-Asia + Pacific Area)	White (1980, 1983) (Africa)
Cargillia (2)	(incl. in *Diospyros*)	(incl. in *Diospyros*)	(incl. in *Diospyros*)
Diospyros (ca. 73) sect. *Amuxis* (1) sect. *Eudiospyros* (66) sect. *Otogyne* (5) sect. *Tetradiospyros* (1)	***Diospyros*** (ca. 170) sect. *Amuxis* (1) sect. *Cargillia* (2) sect. *Cavanillea* (8) sect. *Cunalonia* (2) sect. *Danzleria* (15) sect. *Ebenus* (16) sect. *Ermellinus* (18) sect. *Guaiacana* (6) sect. *Gunisanthus* (8) sect. *Leucoxylum* (3) sect. *Melonia* (20) sect. *Noltia* (9) sect. *Paralea* (19) sect. *Patonia* (11) sect. *Rospidios* (15)	***Diospyros*** (ca. 181) subgen. *Cargillia* (2) subgen. *Eudiospyros* (161) sect. *Acanthebenus* (1) sect. *Asterocalix* (1) sect. *Basithrix* (13) sect. *Brachycylix* (32) sect. *Campanulata* (8) sect. *Cavanilleastrum* (3) sect. *Caudifera* (2) sect. *Cladantha* (2) sect. *Confertiflora* (3) sect. *Didymanthera* (5) sect. *Ebenaster* (8) sect. *Ebenopsis* (6) sect. *Ebenus* (5) sect. *Eriantha* (5) sect. *Eucarpon* (7) sect. *Glutinosa* (6) sect. *Kurzella* (5) sect. *Liophylla* (4) sect. *Lotus* (1) sect. *Nesindica* (11) sect. *Pachycylix* (1) sect. *Phyllosepala* (2) sect. *Podophora* (3) sect. *Ptychocylix* (7) sect. *Reflexocalix* (2) sect. *Rigidophylla* (4) sect. *Saccocalix* (4) sect. *Sapotanigra* (1) sect. *Stelechantha* (1) sect. *Trisantha* (2) sect. *Truncicalix* (4) sect. *Verruculosa* (2) subgen. *Hierniodendron* (3) subgen. *Maba* (14) sect. *Cupulifera* (3) sect. *Ferreola* (2) sect. *Rhipidostigma* (4) sect. *Miquelia* (5) subgen. *Mabacea* (1)	***Diospyros*** (ca. 91) sect. *Asteropetala* (1) sect. *Brevistyla* (8) sect. *Brevituba* (13) sect. *Calvitiella* (10) sect. *Dodonium* (2) sect. *Entia* (1) sect. *Erikesi* (2) sect. *Forbesia* (ca. 8) sect. *Forsteria* (2) sect. *Katula* (1) sect. *Lagenaria* (1) sect. *Latibulum* (4) sect. *Marsupium* (1) sect. *Myrmecophila* (1) sect. *Noltia* (7) sect. *Rhaphidanthe* (1) sect. *Royena* (18) sect. *Tabonaca* (10)
Euclea (15) sect. *Rymia* (7) sect. *Ortheuclea* (8)	***Euclea*** (19)	***Euclea*** (-)	***Euclea*** (ca. 12)
Gunisanthus (1)	(incl. in *Diospyros*)	(incl. in *Diospyros*)	(incl. in *Diospyros*)

CANDOLLE (1844)	HIERN (1873)	BAKHUIZEN (1936-1955)	WHITE (1980, 1983)
Maba (17)	*Maba* (59) sect. *Barberia* (4) sect. *Ferreola* (24) sect. *Holochilus* (6) sect. *Macreightia* (9) sect. *Rhipidostigma* (9) sect. *Trichanthera* (7)	(incl. in *Diospyros*)	(incl. in *Diospyros*)
Macreightia (7)	(incl. in *Maba*)	(incl. in *Diospyros*)	(incl. in *Diospyros*)
Rospidios (1)	(incl. in *Diospyros*)	(incl. in *Diospyros*)	(incl. in *Diospyros*)
Royena (18)	*Royena* (13)	*Royena* (-)	(incl. in *Diospyros*)
-	*Tetraclis* (1)	*Tetraclis* (-)	(incl. in *Diospyros*)

Selected flora treatments: **Africa**: Central Africa (WHITE 1987); tropical East Africa (WHITE 1988; WHITE & VERDCOURT 1996); tropical West Africa (WHITE 1978a); Southern Africa (WINTER 1963; WHITE 1983); Cameroon (LETOUZEY & WHITE 1970a); Gabon (LETOUZEY & WHITE 1970b); Madagascar and Comoros (PERRIER DE LA BÂTHIE 1952a, 1952b); Mascarene Islands (RICHARDSON 1981); Rwanda (TROUPIN 1985); Senegal (BERHAUT 1975); Swaziland (COMPTON 1976); – **America**: Argentina (BURKART 1979); Brazil (MIQUEL 1856; CAVALCANTE 1963a, 1963b; LOPES 1998; RIBEIRO et al. 1999); Cuba (SAUGET & LIOGIER 1957 - 1963); French Guiana (WALLNÖFER & MORI 2002); Guatemala (STANDLEY & WILLIAMS 1966); Mexico (STANDLEY 1920 - 1926; PACHECO 1981); Nicaragua (POOL 2001); Panama (WHITE 1978b); Peru (MACBRIDE 1959); Venezuela (WHITE 1981; SOTHERS & BERRY 1998); – **Asia**: SE-Asia (LECOMTE 1930; BAKHUIZEN VAN DEN BRINK 1936 - 1955); China (SHU-GANG et al. 1996); India (CLARKE 1882); Malaysia (NG 1978); Sri Lanka (WRIGHT 1904; KOSTERMANS 1981); Thailand (PHENGKLAI 1981); – **Australia**: New South Wales (HARDEN 1990); – **Pacific area**: in general (BAKHUIZEN VAN DEN BRINK 1936 - 1955); Fiji, Samoa, and Tonga (SMITH 1971); Hawaii (ST. JOHN 1986); New Caledonia (WHITE 1993).

2. *Euclea* MURRAY

Euclea MURRAY, Syst. Veg., ed. 13: 747 (1774) – Type: *E. racemosa* L. [see: FARR et al. 1979]; – world monographs: CANDOLLE (1844) and HIERN (1873).

Trees, shrubs or subshrubs, dioecious and usually evergreen. Leaves alternate, opposite to subopposite, or in pseudo-whorls of three, with usually entire or finely crenulate margins (e.g., in *E. ovata*). Inflorescences axillary, simple, or less frequently in branched pseudo-racemes, or flowers occasionally solitary. Flowers dimorphic in size, males usually larger than females. Calyx 4 - 5-lobed, usually polysepalous (chorisepalous), shallowly cyathiform or patelliform, persistent but not accrescent on fruits. Corolla urceolate to subglobose and shallowly 5 - 8-lobed on the rim, or campanulate and deeply 4 - 5-lobed. Stamens 10 - 30; anthers at first often dehiscing by large ellipsoidal apical pores which later become longitudinal slits. Pistillode usually much reduced, with or without style and stylodia. Staminodes present or absent. Disk fleshy, fimbriate, sometimes undulate. Ovary globose, hairy, or covered with peltate scales, 2 or 3-carpellate;

carpels biovulate; carpellary chamber usually bisected by a longitudinal false septum, and hence with 4 or 6 uniovulate locules, or occasionally incompletely septate and hence with 2 or 3 biovulate locules; stylodia 2 - 3. Fruit usually a globose, 1 (3)-seeded berry. Seeds subglobose (if more than one, then jointly forming a sphere), 3 - 10 mm in diameter when ripe, with three lines radiating from apex, one consisting of a shallow, vertical groove (impression of the dislocated fruit-axis), and the other two of distal parts of the curved vascular loop encircling the seed (like the sutures of a tennis ball). Endosperm with rumination forming a cylinder around the whole radicle, or rumination altogether absent [?] in some species. Cotyledons strongly flexed out from the embryo-plane in direction of the dislocated axis, and oriented more or less at right angles to the median radial plane of the fruit. 2n = 30. Ca. 12 - 20 species restricted to Africa, Arabia, Socotra and the Comoro Islands; many of the species limited to the Cape flora.

Two subgenera are recognized. The species pertaining to subgen. *Rymia* (ENDL.) VERDC. only occur in South Africa, Namibia and SW Angola and can be distinguished by their urceolate to subglobose, shallowly 5 - 8-lobed corolla. Subgen. *Euclea*, on the other hand, is widespread and characterized by a campanulate, deeply 4 - 5-lobed corolla. *Euclea* shares some morphological features with *Diospyros* sect. *Royena* (the former genus *Royena*) (WHITE 1983; FRANCESCHI 1993), a relationship that is also supported by recent molecular studies (MORTON et al. 1997). These studies moreover indicate that *Diospyros*, as circumscribed today, may not be monophyletic. The formal inclusion of *Euclea* into *Diospyros*, however, seems not to be warranted.

Selected flora treatments: **Africa**: Central Africa (WHITE 1987); tropical East Africa (WHITE & VERDCOURT 1996); Southern Africa (WINTER 1963; WHITE 1983); Madagascar and Comoros (PERRIER DE LA BÂTHIE 1952a, 1952b); Rwanda (TROUPIN 1985); Swaziland (COMPTON 1976).

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