CHLORANTHACEAE (B. Verdcourt, Kew)

Erect or straggling herbs, shrubs or trees, sometimes monoecious or dioecious, the herbs sometimes rhizomatous; branches sometimes jointed at the nodes, sometimes without vessels (*Sarcandra*). *Leaves* simple, decussate or sometimes whorled in fours, serrate, crenate or dentate, the teeth often thickened at the apex, penninerved, usually petiolate; petioles more or less connected at the base at least by a transverse line or connate into a distinct sheath; in *Ascarina* often alternating with leafless internodes which have the petiolar sheath; stipules minute to fairly conspicuous, subulate, borne on the petiole bases or sheath, occasionally pectinate. *Flowers* much reduced, without perianth, fully unisexual or essentially bisexual with the reduced anther-bearing organ adnate to the side of the ovary; arranged in spicate, paniculate, or capitate axillary or terminal inflorescences. — *Male flowers* bracteate or not, apparently consisting of 1–5 stamens, or in *Hedyosmum* consisting of numerous anthers in a cone-like structure; if 3 then the whole forming a fused 3-lobed organ sometimes enveloping the female flower by its edges, the central anther with 2 or aborted loculi and the laterals with single loculi, simply lobed or with connectives slightly to considerably produced so that the whole organ is 3-fingered; if with only 2 anther locelli then these on either side of a thickened filament plus connective. — *Female flowers* naked or enclosed by a cupular bract, the perianth adnate to the ovary, often minutely or shortly dentate at the apex and the ovary thus inferior; ovary 1-locular; stigma sessile or style short; truncate, 2-lipped, depressed or subcapitate (or horseshoe-shaped in one species), rarely linear or clavate. *Ovule* solitary, orthotropous, pendulous, bitegmic and crassinucellate. *Drupes* fleshy, small, ovoid or globose, sometimes more or less 3-sided in *Hedyosmum*, free or united into a mass by the bracts; endocarp hardened and crustaceous. *Seeds* subglobose, exarillate, with copious fleshy or oily endosperm and minute embryo, the cotyledons divaricate or scarcely formed.

Distribution. Four genera with about 80 species. Since VESTER's (1940) small-scale map the family (*Ascarina*) has been found in Madagascar. It is mainly tropical but *Ascarina* extends south to North Island of New Zealand (fig. 6) and *Chloranthus* and *Sarcandra* extend north to Japan, China, Korea and the eastern U.S.S.R. (Ussuri).

Ascarina occurs in the Pacific and reaches New Guinea and the Philippines with a distinct section *Madascarina* in NE. Madagascar; *Chloranthus* and *Sarcandra* are widely distributed in Malesia, India, Indochina and China. *Hedyosmum* occurs in the New World from Mexico to Brazil and Peru and in the West Indies with one species occurring in the Old World in S. China, W. Sumatra, Borneo and Celebes (fig. 8).

The family is now absent from Africa, W. Asia, Australia, and much of America.

HUMBERT & CAPURON (1955) when describing *Ascarinopsis* (= *Ascarina* sect. *Madascarina*) speak of it as part of the most ancient floristic element in Madagascar, a survival from the Cretaceous flora and AUBRÉVILLE (1976) considers it as an Australo-Papuan element similar to *Hibbertia, Dillenia, Evodia, Protium* (& America), *Macadamia, Elaeocarpus, Weinmannia* (& America), *Bubbia, etc.*

The complete absence of *Chloranthaceae* from tropical Africa at the present time is paralleled in many other groups with trans-Pacific distributions. The discovery of the fossil pollen type *Clavatipollenites* there could indicate that something very like *Ascarina* once occurred in Africa. The

family might appear to owe its present distribution to a Gondwanaland origin in the Early Cretaceous or even earlier, the absence from Australia and Africa being attributed to climatic vicissitudes. *Clavatipollenites* (see later) is known from the Early Cretaceous of the U.S.A. (Maryland), England, Israel, Patagonia, South & Central Africa, Brazil, Australia, *etc.*; and probable Oligocene-Early Miocene deposits of South Africa (Cape Province) (COETZEE, 1981); and if all these refer to *Ascarina* or some closely allied genus then a different course of distribution is indicated. It seems the family may have been well distributed and common in the past but it is equally apparent that migrations involving any kind of stringent climatic deterioration are not feasible. *Ascarina lucida* for example was formerly (10,000–5,000 BP) abundant in New Zealand but is now much reduced due to increase of frost and drought (MCGLONE & MOAR, 1977).

References: AUBRÉVILLE, Adansonia II, 15 (1976) 302; COETZEE, S. Afr. J. Sc. 77 (1981) 341; COETZEE & MULLER, Ann. Mo. Bot. Gard. 71 (1984) 1092, f. 11; HUMBERT & CAPURON, C. R. Ac. Sc. Paris 240 (1955) 28, fig.; MCGLONE & MOAR, New Zeal. J. Bot. 15 (1977) 485–489; VESTER, Bot. Arch. 41 (1940) 349, f. 144.

Fossils. As far as I am aware no undoubted fossils of parts of the plants other than pollen are known, but leaves with chloranthoid characters have been found in the Lower Cretaceous Potomac Group (UPCHURCH, 1984). Several Lower Cretaceous pollen types have been referred to the family, but can hardly refer to the recent genera. Pollen of recent genera is also known from various strata. These are dealt with elsewhere (see p. 126 and 143).

Reference: UPCHURCH, Amer. J. Bot. 71 (1984) 192–202.

Ecology. The species are all moist evergreen forest species, many ascending into submontane forests. They occur from 0 to 3300 m in Malesia.

Dispersal. The white-fruited *Chloranthus erectus* (= *officinalis*) is dispersed by birds according to RIDLEY (Disp. 1930: 410) and the red-fruited *Sarcandra glabra* must also be.

Pollination. VAN DER HAMMEN & GONZÁLEZ (1960) have shown that *Hedyosmum* is wind-pollinated and has a high pollen production, but it has usually been assumed that the forest-dwelling *Chloranthus* and *Sarcandra* are insect-pollinated but I have traced no recorded observations. Some collectors mention scent.

Reference: VAN DER HAMMEN & GONZÁLEZ, Leidse Geol. Meded. 25 (1960) 261–315.

Floral morphology. PAYER as long ago as 1857 investigated the floral morphology of *Chloranthus spicatus* and found that during the early stages of development the median lobe of the anther-bearing organ appears first, soon followed by the two laterals which are distinct in origin but immediately join up to form the 3-lobed organ and later still the ovary arises as a half-moon-shaped outgrowth with the curved side towards the bract. ARMOUR (1906) investigated the morphology of the flower. The minute scale at the base of the anther-bearing organ on the ovary in some species has been looked on as a perianth but it is not vascularised and probably simply an outgrowth. The anther-bearing organ in *'C. chinensis'* (probably *C. erectus* = *officinalis*) has been described as bearing four anther-lobes each composed of two pollen-sacs, usually regarded as corresponding to three stamens, of which the median one has two anther-lobes and the lateral ones reduced to one and the traces are consistent with this, but development gives no evidence of reduction of the lateral stamens, nor whether the flowers are to be regarded as reduced or the reverse. In *Sarcandra glabra* the anther-bearing organ is usually described as a single stamen, the position of the two anther-lobes resembling that of a normal Angiosperm stamen but the presence of two traces suggests a derivation from an organ similar to that of *Chloranthus* by total reduction of the median anther-lobes and reduction in width.

These curious structures have been looked on as separate male and female flowers joined and simulating a bisexual flower, *e.g.* by HOOKER *f.*, but most authors (*e.g.* ARMOUR) have considered the flowers to be bisexual and SWAMY & BAILEY's (1950, 1953) studies of the vascularisation of the structure support this. They could, however, be considered as very reduced inflorescences derived from mixed cymules of male and female flowers such as occur in *Ascarina*, but there is no evidence from vascularisation to support this.

In *Sarcandra* the bract has a single trace; the carpel a double or single median strand and ventral strands close or separated; staminal trace double and joining median traces or single and free to below the bract or one free and one joined.

ENDRESS (1971) investigated the female flowers of *Hedyosmum mexicanum* and the following is taken from his own summary. The flowers are free and not partly fused with each other nor with the inflorescence axis. The perianth region extends not only to the free 3-lobed perianth-tube and three double wings on the flower ridges, but also to the periphery of the whole flower below the style. The 3-lobed perianth is initiated as the first floral organ, contrary to the occasional small protrusions below the stamen attachment in *Chloranthus*. The fruit is a kind of drupe, the wings of the flowers forming the outer subfleshy part and the periphery of the flower body the inner hard part. The ovary wall tissue degenerates around the growing and ripening seed, the fruit wall thus consisting mainly or completely of perianth tissue. The gynoecium lacks distinct signs of pseudomonomery and seems to be truly monocarpellate. It is distinctly ascidiform at least up to the style-base with an oblique or transverse ventral slit, the stylar canal and with ventral median placentation appearing markedly laminar at anthesis. Except for the 3 bundles of the atropous bitegmic and crassinucellate ovule there are no independent ovary bundles.

LEROY (1981, 1983a, 1983b) considers the male structures, formerly universally interpreted as inflorescences of bractless flowers much reduced to single stamens, to be strobiloid male flowers, each bearing several hundred spirally arranged stamens and closely resembling a gymnospermous cone-like male flower. This reinterpretation considered in conjunction with monosulcate pollen similar to pollen known from the Lower Cretaceous and adaptation to wind pollination suggests that the male *Hedyosmum* flower is one of the most primitive Angiosperm flowers still existing. Male *Ascarina* flowers with either 3–5 stamens or 1–3 stamens and *Hedyosmum* male flowers with very numerous stamens are homologous and it is suggested easily derived from a common ancestor.

References: ARMOUR, New Phytol. 5 (1906) 49–55, pl. 3–4; ENDRESS, Bot. Jahrb. 91 (1971) 39–60; LEROY, XIII Int. Bot. Congr. Abstr. (1981) 136; Taxon 32 (1983) 169–175; C. R. Ac. Sc. Paris 296 (1983) 747–752; PAYER, Traité d'organogénie comparée de la fleur, Paris 1 (1857) 422; SWAMY, J. Arn. Arb. 34 (1953) 385–399; SWAMY & BAILEY, J. Arn. Arb. 31 (1950) 121–125.

Anatomy. This has been very thoroughly investigated by SWAMY (1953) and SWAMY & BAILEY (1950). An outstanding feature is the lack of vessels in the xylem in *Sarcandra*. The other genera have vessels but they are relatively unspecialised, *Chloranthus* being the least advanced. In *Sarcandra* tracheary elements in the secondary xylem are arranged in ± undisturbed radial seriations as seen in transverse section; tracheids in the region of the first year's growth measure nearly 1.9 mm and have very extensive overlapping ends similar to other vesselless dicotyledons indicating a cambium of very primitive type, and unusually long fusiform initials. The wood in *Hedyosmum* is of a very unspecialised type; parenchyma paratracheal as incomplete sheaths around the vessels; rays sometimes up to 1 mm wide, multiseriate rays composed of almost entirely upright cells; fibres with simple pits and occasionally septate wall rather thin; in *Ascarina* the parenchyma is apotracheal and the multiseriate rays of square to procumbent cells. *Ascarina* and *Hedyosmum* have nodes typically of the unilacunar type with 2 vascular strands in the leaf of *Ascarina* and 5 in *Hedyosmum*, the lateral pairs larger; *Chloranthus* and *Sarcandra* have modified unilacunar nodes with 5 vascular strands in the petiole, 2 much larger and extending most of the length of the midrib, the intermediate small trace disappearing about half-way but formed by the fusion of 2 minor branches of the larger traces at nodal level; the two small lateral strands come from a different gap. In *Hedyosmum* the stipular sheath formed from the connate petiole bases consists of collenchymatous tissue and supports the stem during intercalary growth. Lateral branches are initiated in the leaf-axils but are attached to the parent axis above the node at maturity; cork formed on the inner surface of the sheath brings it into intimate contact with the stem. There is a pulvinus on the stem at the upper margin of the sheath. In *H. arborescens* and related species the nodal sheath develops by pushing beyond the apical growing point and surrounding it, tightly

closed above the bud and affording it protection. In *Sarcandra* and *Chloranthus* the stomata have 1–2 subsidiary cells oriented parallel to the guard cells whilst in *Ascarina* and *Hedyosmum* there is a rosette of 4–6 ordinary epidermal cells.

BARANOVA (1983) reported that the laterocytic type of stomatal apparatus occurs in *Chloranthus, Sarcandra* and sometimes *Hedyosmum* along with other types. This type is known from a very heterogeneous mixture of families.

MELVILLE (1962) stated the 2 leaf traces in *Ascarina* can unite at various levels in the petiole or lamina and form a single vein, but in *Chloranthus* and *Sarcandra* each of the initial pair of traces forks, resulting in bundles, the middle pair reuniting to give a final triple trace. In *Hedyosmum* a trace of 5 bundles results from the bifurcation of the two outer bundles of such a triple trace. He points out these types are also to be found in both the Pteridosperms and *Cordaitales*.

Mucilage canals are present in the petiole, larger veins and also in the margins of the pith in *Hedyosmum*, in some species also containing sphaerocrystalline masses. Small clustered crystals are recorded in the inner part of the cortex. Stone cells are scattered in the cortex of younger stems of *Sarcandra* with larger groups in the pith; in older pith these cells form conspicuous transverse diaphragms alternating with plates of parenchymatic cells, but these diaphragms are absent from *Chloranthus*. Ethereal oil cells occur in the mesophyll of the leaf.

References: BARANOVA, Brittonia 35 (1983) 93–102; MELVILLE, Kew Bull. 16 (1962) 39–40; SWAMY, J. Arn. Arb. 34 (1953) 385–399; SWAMY & BAILEY, J. Arn. Arb. 31 (1950) 121–125.

Palynology. WALKER (1976) summarised the palynology of this very eurypalynous family as follows: "pollen grains anasulcate, inaperturate, with 'colpoid complexes' or colpoid streaks, polycolpoidate or polycolpate, heteropolar, apolar or isopolar; boat-shaped-elliptic, globose-oblate or globose, tectate or semi-tectate; more or less psilate, fossulate, scabrate, rugulate or reticulate; monads; medium-sized to small". He noted that polycolpate grains derived from monosulcate ones occur only in this family and in *Aristolochiaceae*, stating that the polycolpate/polyporate pollen found in the two families must be considered unique in its clear monosulcate derivation. KUPRIANOVA (1981) has given much data on the pollen of several species. Grains of *Chloranthaceae* are remarkably similar to those of the oldest known fossil Angiosperm pollen: *Clavatipollenites* COUPER at first known only from the Lower Cretaceous of England, Israel (N. Negev), Maryland (U.S.A.), and Patagonia. KUPRIANOVA (1967) was the first to claim that *Clavatipollenites* and *Ascarina* are congeneric; COUPER (1960) had earlier noted the strong similarity, and it is clear that there is at least close relationship. A very strong case has been made for the conspecificity of *Clavatipollenites evittii* (California, Maestrichtian) and *Ascarina lucida*. MULLER (1981) summarised the fossil pollen records of the *Clavatipollenites-Ascarina* complex. In New Zealand there are records from the Maestrichtian to the present day, bridging the gap between Cretaceous and recent. A virtually continuous record from the Albian to the Eocene has recently been discovered in Australia where elimination from the continent may have been due to increasing aridity. A record has also been published from the 90° ridge in the Indian Ocean from Oligocene deposits. In Europe there are records from the Aptian, Albian and Cenomanian with probably extension to the Barremian. LAING (in Ferguson & Muller, 1970) gave a Barremian record from England. Apart from the eastern U.S.A. record there have been finds from California and Chile (Maestrichtian), Bahamas (Cenomanian), Falkland Plateau (Palaeocene), Central Africa (Albian, Aptian and possibly Barremian), South Africa (probably Oligocene to early Miocene), and Brazil (and once again possibly eliminated from the latter three by climatic deteriorations). DOYLE (1977) commented on the various types of *Clavatipollenites* pollen and compared the finely clavate-retipilate forms from the Lower Cretaceous with *Ascarina*, the coarser clavate irregularly aperturate ones with *Hedyosmum* and the reticulate nearly inaperturate type with *Sarcandra*. Considered in conjunction with the distribution of the recent species, a purely Gondwanaland distribution does not cover all the main facts of fossil distribution and either some of the latter are misidentified or a Pangaea type theory now largely discarded by most workers must be resorted to. The family must have been widespread and common in the Lower Cretaceous, only a few species lingering on to the present day.

References: COETZEE, S. Afr. J. Sc. 77 (1981) 341; COETZEE & MULLER, Ann. Mo. Bot. Gard. 71 (1984) 1092, f. 11; COUPER, New Zeal. Geol. Surv. Palaeont. Bull. 32 (1960) 1–87; DOYLE, Bull. Cent. Rech. Explor. Prod. Elf-Aquitaine (1977) 451–473; KUPRIANOVA, Pollen et Spores 9 (1967) 95–100; Bot. Zhurn. USSR 26 (1981) 3–15; LAING in Ferguson & Muller, Linn. Soc. Symp. Ser. 1 (1976) 15–25; MULLER, Bot. Rev. 47 (1981) 9–12; WALKER in Beck, Origin & Early Evolution of Angiosperms (1976) 269.

Chromosomes. EHRENDORFER *et al.* (1968) compiled lists of numbers for primitive families and gave *Hedyosmum arborescens* n = 8; *Sarcandra glabra* 2n = 30; *Ascarina rubricaulis* 2n = 28; *Chloranthus serratus* n = 14 & 2n = 30; *C. spicatus* 2n = 30; *C. japonicus* 2n = 30; *C. fortunei* 2n = 60. He stated that from these data it can be seen that there are still true diploids in the family: x = 8, further secondary polyploid base numbers x2 = 14 and 15 and continuing infrageneric polyploidy (4 x_2). EHRENDORFER stated (in Beck, 1976) that "*Chloranthaceae* demonstrate progressive elimination of diploids (n = 8), major representation on the 4 x level (n = 14 and 15, the latter from 7 + 8?) and occasional origin of 8 x (n = 30)", corresponding in part with the *Piperales*.

References: EHRENDORFER *et al.* Taxon 17 (1968) 337–468; in Beck, Origin & Early Evolution of Angiosperms (1976) 228–229.

Phytochemistry. Even to the collector the aromatic smell suggests relationship with the *Piperaceae*. In 1964 HEGNAUER complained that the chemistry of this family had scarcely been touched. BATE-SMITH (1962) found in the hydrolysed leaf-extract of *Chloranthus erectus* (= *officinalis*) none of the otherwise very widespread phenols save for β-coumaric acid and in this respect it resembles many *Piperaceae*. The ethereal oils which undoubtedly exist have so far not been chemically investigated.

KUBITZKI & REZNIK (1966) in their investigation of flavonoids as systematic characters investigated 4 species of *Chloranthus*, 7 of *Hedyosmum* and 5 of *Ascarina* and found them to contain traces to massive amounts of the two derivatives of flavanole, quercetin and kämpferol, the former dominating. SHIO & HIGUCHI (1981) have demonstrated the presence of a gymnosperm type of lignin, guaiacyl lignin in *Sarcandra glabra* and *Chloranthus spicatus*.

References: BATE-SMITH, J. Linn. Soc. Bot. 58 (1962) 95–173; HEGNAUER, Chemotaxonomie der Pflanzen 3 (1964) 428; KUBITZKI & REZNIK, Beitr. Biol. Pfl. 42 (1966) 445–470; SHIO & HIGUCHI, Wood Res. Kyoto Univ. 67 (1981) 43–46 [from For. Prod. Abstr. 5 (1982) *no* 2121].

Taxonomy. Early placings of *Chloranthus* were various and mostly wide off the mark. LINDLEY, who first recognised the family (1821) placed them in *Piperales* and his clear view has been supported by many authors (BENTHAM & HOOKER, 1880, 1883; ENGLER, 1894; ARMOUR, 1906; SWAMY, 1953; HOWARD, 1970; BEHNKE, 1975; BURGER, 1977) with arguments from various disciplines (morphology, anatomy, phytochemistry, pollen). After digesting a wholesale literature on the subject (1985), I believe this comes at least close to the correct affinity. The most probable conclusion from the floral structure appears to be that *Chloranthaceae* is a group of *Piperales* presenting in some points, especially in the structure of the ovary, primitive characters in common with the majority of the *Archichlamydeae*, while in other aspects modifications of the flowers are shown. A.C. SMITH (1972) found them more primitive than other elements of the *Laurales* and repeated (1981) that *Chloranthaceae* is best assigned to its own order, *Chloranthales*, validated by LEROY (1983). HUTCHINSON (1973) and CRONQUIST (1981) retain the family in *Piperales*, but this then remains a matter of choice.

It is certainly clear that the small, insignificant family *Chloranthaceae* is one of great importance in the study of primitive flowering plants whose ancestry points to high age, probably even to the Early Cretaceous, judging from the affinity of the pollen to *Clavatipollenites*. Unusual generic ranges also point towards early time, *viz.* one species of otherwise neotropical *Hedyosmum* in Indo-Malesia and one species of *Ascarina* in Madagascar even representing a separate section.

References: ARMOUR, New Phytol. 5 (1906) 49–55, pl. 3 & 4; BEHNKE, Ann. Mo. Bot. Gard. 62 (1975) 647–663; BENTHAM & HOOKER *f.*, Gen. Pl. 3 (1880) 133–135, (1883) 1220–1221; BUR-