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, pinninerved, 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 capitulate 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. (Usuri).

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 Malasia, 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 Aubreville (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 Claviipollenites 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).


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).


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.


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 cymes 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 placental appearance 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.


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 serialisation 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.


Palynology. Walker (1976) summarised the palynology of this very eurypalynous family as follows: “pollen grains anasulcate, inaperturate, with ‘colpoid complexes’ or colpoid streaks, polycolpoid or polycopate, heteropolar, apolar or isopolar; boat-shaped-elliptic, globose-oblote 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 polycopate/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 evitii (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 Albain 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. Lang (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.

Chromosomes. Ehrendorfer et al. (1968) compiled lists of numbers for primitive families and gave Hedyosmum arborescens n = 8; Sarcandra glabra 2n = 30; Ascarina cinnamomum 2n = 42; Chloranthus ericoides 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 x = 14 and 15 and continuing infragenus polyplody (4 x2). 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.


Phytochemistry. Even to the collector the aromatic smell suggests relationship with the Piperales. 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 Piperales. 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 flavone, quercetin and kämpferol, the former dominating. Shio & Higuchi (1981) have demonstrated the presence of a gymnospem type of lignin, guaiacyl lignin in Sarcandra glabra and Chloranthus spicatus.


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 Archichlamydaceae, 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.


Generic delimitation. This is very decisive. The genera with fully unisexual flowers or dioecious inflorescences with marked prostrandy, Ascarina (including Ascarinos) and Hedyosmum are clearly distinct from Chloranthus and Sarcandra in which the male floral parts are adnate to the ovary. In Ascarina both male and female flowers can be bracteate, but the male flower has only 1–5 anthers, whereas in Hedyosmum the male flowers have numerous anthers arranged in a cone with basal involucre and the female flowers are enclosed in highly developed cupular bracts. Morphologically Chloranthus and Sarcandra are more closely inter-related than the other two. Sarcandra is well characterised by its single stamen with anther cells on a club-shaped organ and particularly by its vessel-less xylem; Chloranthus can occasionally have a single stamen but then it is of different structure, e.g. as in C. multiistachys Pohl. Hutchinson and others maintained Tricercandra A. Gray distinct from Chloranthus on account of the fused male floral parts being produced into long narrow lobes ('connectives') but there are intermediates between this and the simple 3-lobed state found in typical Chloranthus which has been even more emphasised by new discoveries in China; it is not even possible to maintain it as a section. Ascarinos can on the other hand be kept as a section of Ascarina there being some distinctive characters such as 2–5 stamens and the curious disposition of two leafless nodes between the leafy ones.

Uses. The Chinese grow Chloranthus spicatus in pots for its fragrant aromatic leaves and it was formerly grown on a large scale in Java in one montane locality and used for imparting a scent to native tea and is apparently still used on a small scale for this purpose. Burkill (1935) reported that leaves and flowers are left in contact with the tea whilst it is drying; they are later discarded or left to add bulk to the tea. Its use has been claimed to be delerious. Among medicinal uses are as a poultice on carbuncles and boils, as a diaphoretic and excitant, as a cure for malaria but said to be poisonous in overdose, for back-ache and as a tea-like drink for treating coughs. Chloranthus erectus (= officinalis) is also used medicinally and as a tea, both the leaves and the roots being used. Heyne (1927) gives extensive medicinal uses for the latter. It has a sudorific effect and is used in cases of fever and as a restorative during some phases of venereal disease; also as a stimulant and mixed with Cinnamomum bark as an antispasmodic during parturition.

Dosedla reported (Gill, 1979) that formerly the leaves of Chloranthus erectus (= officinalis) were eaten together with pork as an offering in House Tambaran in the Hagen area of New Guinea. Areas where the plant grew were avoided; today the whole plant which stains the hands green on touching is taboo. Veldkamp (in sched.) reported that in S. Borneo the branches are boiled and the slightly peppery tasting concoction drunk by women to prevent conception.

Sarcandra glabra has also been used to scent tea or add bulk and used in Indonesia for the same purposes as Chloranthus erectus. In the Philippines an infusion is said to be useful in treating headaches, asthma and 'internal pains'. It is also used in Chinese medicine for bone fractures, contusions and in the form of a leaf-decoction as an astringent treatment for vomiting. Frake reported (PNH 37989 & 38204) that on Mindanao the leaves are pounded and applied to ulcers and Chai (S 35411) that the warm leaves are used for sprains. Heyne also mentions that when tea-planting started in Java the cultivation of Chloranthus was forbidden by the Dutch.


Note: The drawings on the four plates were made by Mrs. Maureen Church, at Kew.
1. **Chloranthus**

Shrubs or perennial erect or straggling herbs, glabrous and aromatic; stems jointed at the nodes. **Leaves** deciduous or sometimes subverticillate in whorls of 4, serrate; petiole bases connected by a transverse line or shortly connate; stipules mostly small. **Spikes** terminal, slender, sometimes branched, sometimes leafy at the base, the flowers each in the axil of persistent mostly subopposite bracts along the spicate opposite side branches. **Flowers** essentially bisexual, the male part usually a 3-lobed organ adnate to the ovary and sometimes enveloping it forming a fleshy mass, the lobes ('connectives') short and broad or longer or distinctly narrow and elongate, in some species almost or quite free, or in one species not noticeably lobed and reduced to ± nothing but 1–3 anthers; anthers 1–3, the introrse locelli variously arranged, either 3 'anthers', one median with 2 approximate, or ± separated locelli and one on each lateral edge with single locelli, or 2 lateral 1-locellate anthers and usually no median one (but this can vary in a population), or 1–3 anthers joined and the lobed organ practically or quite obsolete with one 2-locellate anther and usually two lateral 1-locellate anthers. **Ovary** naked; stigma subsessile, truncate. **Drupes** usually white, fleshy. **Seeds** subglobose, minutely apiculate, narrowed below, invested by the thin fibrous endocarp, the seed-coat with a lignified endostomal palisade.

**Distr.** About 20 spp. extending from Japan, China and extreme East U.S.S.R. to India, Ceylon and *Malesia* as far as New Guinea.
Fig. 1. Chloranthus erectus (Buch.-Ham.) Verdcourt. a. Flowering branchlet, ×2/3, b. portion of young inflorescence, ×6, c. young flower, ×16, d. portion of older inflorescence, ×6, e. mature flower, ×16, f. anthers, ×20, g. ovary, ×30, h. LS ovary, ×30, i. fruiting branchlet, ×2/3, j. fruits, ×4 (a–c Anderson S 20818, d–h van Royen 3626, i–j Chai S 35523).
Taxon. Various authors have advanced subdivisions but there is no unanimity of opinion and this will have to wait for a monograph of the entire genus.

Palyn. Grains subspherical averaging about 22.5 by 30 μm, polycolpate with 3–8 colpi but often much modified reaching the poles in a few species but often short and appearing as slender unsculpted wavy meridional streaks and in some species only distinguishable as very faint tenuous short zigzag lines; exine with finely reticulate-pitted sculpture.

Floral morph. (see also general section). The staminal organ of Chloranthus has commonly been interpreted as 3 connate stamens and the available evidence suggests that it actually developed in this way from the concrescence of 3 stamens rather than the expansion of a single stamen and acquisition of supernumerary locelli (SWAMY, 1953). Where the central lobe of the male flower usually bears no anther cells, e.g. in C. japonicus, there is actually a good deal of variation showing an almost continuous range from rudiments to almost perfect anther cells in the same spike (MAEKAWA, 1970).

Key to the species

1. Perennial unbranched herbs or subshrubby herbs with ± subverticillate leaves in fours congested at top of stem. Anther-bearing organ with 3 distinct narrow lobes .............................. C. henryi
   2. Branched shrubs or shrubs with decussate leaves. Anther-bearing organ shortly 3-lobed or 3-crenate.
      2. Leaves usually long acuminate, 8–29 by 3–13 cm, usually finely shallowly glandular-serrate. Fruits and stamens white .......................................................... 1. C. erectus
         2. Leaves usually ± obtuse, 5–12.5 by 2–4 cm, crenate-serrate. Fruits and stamens green or yellowish (cultivated) .......................................................... 2. C. spicatus


Shrubby herb, subshrub or small shrub, 0.3–3 m, rarely epiphytic, ± aromatic when crushed; nodes distinctly swollen, sometimes purplish. Leaves bright green, glossy above in life, oblong-lanceolate to elliptic- or ovate-oblong, 8–29 by 3–13 cm, usually long-acuminate at the apex, cuneate at the base, rather thin, the margin rather finely shallowly (rarely more coarsely) glandular-serrate, with c. 9 pairs of nerves, sometimes purplish beneath; petiole 0.75–1.7 cm; stipules minute, subulate. Inflorescences scented, with 5–13 spikes 2.5–5 cm long; bracts sheathing; ovate, acute. Anther-bearing organ yellow, between green and white or violet-white, 3-lobed, 1.2–1.6 mm long; median anther 2-locellate; lateral anthers 1-locellate. Ovary enclosed by the male part. Fruit white, cream or rarely tinged violet or pinkish, the tip sometimes dark violet-purple, succulent, glossy, 5–7 mm ø. Seed yellowish white.

Distr. Continental SE. Asia from Nepal to Yunnan and Andaman Is., and throughout Malesia to New Guinea (incl. New Britain and New Ireland). Ecol. Primary and secondary forest, including Pandanus and palm, Araucaria, and Nothofagus-Castanopsis in montane forest, often on limestone, sometimes riverain or in boggy areas, mainly lowland, (20–)50–1450(–2535) m. Fl. Jan.–Dec. Ridley (Disp., 1930) stated that it is bird dispersed.
Taxon. The epithet elatior has come into wide usage but there is no Brown specimen at the BM or any Link specimen now extant at B, so it is not possible to be certain what was actually intended, since the description given by Link is fragmentary, his type being sterile. I agree with Van Steenis (in litt.) that the name is better discarded in favour of one which is unambiguous and of which the type is available.

Buchanan-Hamilton's faulty drawing and description have misled authors as to the identity of Cryphaea erecta, but the examination of the type (E) left no doubt.


Note. Judging by dried material specimens from New Ireland have larger fruits but the constancy of this needs checking in the field. Sterile material of Chloranthus erectus (= officinalis) with more toothed leaves than usual can be difficult to distinguish, but Sarcandra glabra usually dries with more reddish brown coloured foliage.


Small glabrous shrub, 0.5–1.5 m, with ascending or ± spreading branches. Leaves oblong-ovate or ovate-elliptic to elliptic, 4–13.5 by 2–8.5 cm, rather obtuse or at least not or scarcely acuminate at the apex, cuneate at the base, rather coarsely crenate-serrate, nerves 4–6 pairs; petiole 0.4–1.2 cm; stipules membranous, linear, 2–3 mm, mucronate. Inflorescences terminal with 10–20 ascending spikes 2–5 cm long; peduncles 3–8 cm; bracts 1.5 mm; bracteoles 1 mm. Anthers 3, the central with 2 locelli and the laterals 1-locellate, the cells ± 0.5 mm long. Fruit green or yellowish, 4 by 2 mm, narrowed at the base.

Distr. China but widely cultivated elsewhere in eastern Asia; in Malesia cultivated in Java (e.g. Parakansalak) and Sumatra (West Coast); 700–920 m. Fl. Jan.–Dec.


Herb 20–40 cm; stem simple, glabrous or pubescent towards the apex, with 3–5 leafless nodes bearing paired scales 6–9 mm long, which are caducous or perhaps not developed in some specimens; rootstock said to be aromatic. Leaves in whorls of (?3–4) at apex of stem, elliptic to broadly elliptic or obvate-elliptic, 8–15.5 by 3.5–9.5 cm, narrowly long-acuminate at apex, cuneate at base, margin sharply serrate, serrations terminated by prominent thick glands, glabrous, or shortly pubescent on the 5–9 pairs of nerves beneath; petiole 2–7 mm, glabrous or pubescent. Inflorescence terminal; peduncle slender, 7.5–13 cm long with 2–3(–4) spikes 2–6 cm long; secondary peduncles 0.5–1.2 cm, sparsely pubescent; bracts ovate, ± 1.5 mm long. Male part attached about the middle of the ovary, white; central lobe 2.2–3 by 1 mm (4 by 1.2 in original description of C. verticillatus), lateral lobes 1.5–1.8 by 0.6–0.8 mm, all rounded at apex; anther cells about half as long as lobes, 2 on central lobe, one on each lateral lobe, 0.8–1 mm long. Ovary ± ovoid, narrowed from near middle to ± triangular apex, 1.5(–2?) by 1 mm. Fruits white?

Distr. China; in Malesia: Philippines (Luzon: Ifugao, Mt Polis; Bayninan, Banaue, Cagayan, Abulug R.).


Note. When describing C. verticillatus MERRILL suggested it might be nearest to C. henryi, but later MERRILL and QUSUMBING synonymised it with C. oldhamii SOLMS-LAUB. MERRILL also compared C. philippinensis with C. henryi but stated the former had much smaller flowers. Chloranthus henryi is variable particularly in regard to the ratio of the length of the anther cells to that of the lobes of the male part which vary from about a 1/2 to more usually 1/4 to
1/3, but some Chinese material is very similar to that from the Philippines and for the present I am content to consider them conspecific. The above description does, however, refer only to Philippine material. A better range of material from China and the Philippines may show constant differences and that subspecies may be recognised.

2. SARCANDRA


Shrubs or shrublets with nodose jointed branchlets. Primary and secondary xylem without vessels. Leaves decussate or sometimes appearing subverticillate where nodes are congested, pinnately nerved, usually coarsely serrate, serrations thickened at apex; petiolar sheath short, with short setaceous stipules on its margin. Flowers essentially bisexual, in lax terminal spikes with c. 3 main branches, each with up to c. 12 flowers; bracts boat-shaped. Male part reduced to a club-shaped or ± discoid organ usually interpreted as a filament and connective of a single stamen bearing 2 locelli, adnate about 2/3 of the way up the abaxial side of the ovary and with a cushion-like fold below the point of attachment; locelli latrorse or introrse, opening lengthwise, usually separated but sometimes touching at their tips. Ovary ovoid, 1-locular; ovule pendulous, bitegmental, crassinucellate; stigma sessile depressed and subcapitate. Drupe nearly invariably red, 1-seeded, obvoid, bearing the scar of the fallen male part on its anterior face; pericarp succulent, the epidermis without stomata. Seed pendulous with membranous testa; innermost cell layer of outer integument developing into a lignified palisade of radially elongate cells with 1—several crystals, the cell cavity becoming filled with an internal reticulum of lignin.

Distr. Two species in Ceylon, India, Burma, Indochina to China and Japan, one of which in Malesia: Malay Peninsula, Sumatra, Java, Borneo, Lesser Sunda Is., Philippines, New Guinea. A map (now out of date) was published by SUSSENGUTH & GALL, Mitt. Bot. Staatsamml. München 1 (1953) 351.

Taxon. There is no doubt that SWAMY is correct in maintaining this genus, well-characterised by the vesselless xylem, characteristically shaped male part of the flower with 2 locelli and with 1 or 2 traces rather than 3, presence of stone cells, dorsal carpel traces, characteristic pollen, nearly invariably red fruits etc. Confusion has occurred in the nomenclature of the species occurring in S. India and Ceylon (VERDCOURT, 1984).

Morph. It is logical to treat the flowers as bisexual flowers since the two staminal traces usually join with the median carpal traces although flower is really a vague term for combinations of structures of different origins; variants exist, however, which have a single staminal trace free at least to below the bract.

Fig. 4. *Sarcandra glabra* (Thunb.) Nakai. a. Flowering branchlet, ×2/3, b. part of inflorescence, ×6, c. flower, back view, ×10, d. flower, front view, ×10, e. stigma, ×16, f. LS ovary, ×16, g. fruiting branchlet, ×2/3, h. fruits, ×2 (a–f Purseglove 4097, g Kalkman 5319, h Nooteboom & Chai 1825, spirit material).
For further references and synonymy see under ssp. brachystachys.

Glabrous shrub or half-woody herb, 0.6—3 m tall; stems up to 1.5 cm in diameter, longitudinally ridged when dry; bark ± smooth. Leaves elliptic-oblongaceous, lanceolate or narrowly oblanceolate, 2—20 by 1—8 cm, long-acuminate, cuneate at the base, ± subcoriaceous, coarsely or shallowly very sharply serrate or dentate-serrate, the teeth with thickened points; lateral nerves in 5—10 pairs; stipules small, linear-subulate, c. 1.5 mm long; petiole 0.4—1.7 cm. Inflorescences greenish or ± white, 3—8 cm long, the spikes rather dense, 1—3.5 (—5) cm long; paired bracts 3 mm long; bracteoles oblong, 1 mm long, sometimes ± trilobed. Male part 1.3—2 mm long, 1—1.3 mm wide, the anther cells extending from half to the whole length or almost so, c. 1.3 mm long. Female part flask-shaped or subglobose, 1—1.5 mm long; stigma up to 1 mm wide. Fruit at first yellow, becoming red or bright orange, very rarely black, 4—7 mm Ø (dry), shining. Seed pale, yellowish or cream.

Dist. Continental SE. & E. Asia, throughout Malesia.

Note. The typical ssp. glabra occurs in N. & Central China, Korea, Japan and the Ryukyu Islands. Some specimens from NW. India and S. China are somewhat intermediate.

KEY TO THE SUBSPECIES

1. Male structure with anther cells about as long as the structure itself, the non-antheriferous part much reduced .............. ssp. brachystachys

1. Male structure with anther cells much shorter, the non-antheriferous part (i.e. apparent 'filament') well-developed. E. Asia ............. ssp. glabra


Male structure with anther cells almost equalling it, i.e. the non-antheriferous part much reduced.

var. brachystachys

Fruits red.

Dist. NE. India (Assam, Manipur, Naga Hills), Bangladesh, Burma, Thailand, N. Vietnam, S. China (incl. Hainan), and throughout Malesia.

Ecol. Evergreen, both lowland and lower montane forest, secondary forest, heath forest, moist ground ridge forest, sometimes by water, also eroded limestone slopes with thin 'mos' soil, ridge podsolized soil, shingle banks and stream beds, shaly slopes; 135—2550 m. Fl. Feb., April—June; fr. Jan.—May, Aug.—Nov.


Notes. Field notes and spirit material show that the fruit is much larger in life, e.g. 9—15 by 7—10 mm.

Sterile material of Chloranthus erectus with much more coarsely toothed leaves than usual can be difficult to distinguish, but Sarcandra glabra usually dries with more reddish brown coloured foliage rather than a grey-green colour.


Differ in having black fruits.

Dist. Malesia: N. Sumatra (Berastagi, West Hill; Lake Toba, Gunung Batu, Lopang, 10 km ESE of Prapat).

Ecol. Montane rain-forest, 1400—1500 m.

Note. I had dismissed Ridley's variety as a casual variant, but its recollection in the same general
area suggests a population of black-fruit specimens exists; since the fruit is uniformly described as red throughout its range the occurrence of such a variety seems worth emphasising.

3. ASCARINA


Shrubs or small or sometimes quite large trees, usually apparently dioecious or monoecious, glabrous, aromatic, the branches jointed at the nodes and the bases of the internodes sometimes swollen. Leaves decussate, often coriaceous, obtusely serrate, the serrations often gland-tipped; petiolar sheath very short; stipules very small, subulate; in sect. Madascarina Jérémié and some species of sect. Ascarina there are two intermediary aphyllous nodes with eventually deciduous sheaths 2–6 mm long between successive pairs of leaves the stipular collar made up of the petiole-bases bearing 2 pairs of small teeth under 5 mm long. Flowers basically in much condensed biparous sessile cymes borne in the axil of a bract with an abaxial male flower and 1 or 2 adaxial female flowers with bracts and bracteoles (if 2-flowered), essentially representing a bisexual flower; sometimes 1–2 stamens are associated with 1–2 rudimentary or functional adaxial carpels which develop much later; but mostly inflorescences reduced to single male flowers or 1–2 female flowers and appearing monoecious or dioecious. — Male flowers bracteate, reduced to 1–2 sub sessile anthers with parallel linear locelli opening lengthwise or in sect. Madascarina with 2–5 (usually 3) sessile stamens with bilocular anthers. — Female flowers consisting of a naked sessile ovoid-globose ovary without outer bracts or with 2 often caducous inner bracts and if flowers paired then with bracteoles also; stigma sessile, truncate or 2-lipped or in sect. Madascarina horseshoe-shaped. Fruits purplish grey turning black, obovoid, with thin succulent exocarp and stony smooth or verrucose un specialised endocarp; epidermis without stomata. Seeds ovoid, flattened, with smooth testa, the seed coat with un lignified endotestal palisade but with lignified fibrous exotegmen.

Distr. 12 species in Madagascar, Pacific Islands (widespread from Solomons to the Marquesas), New Caledonia and New Zealand; in Malesia 4 spp.: Borneo, Celebes, Philippines, New Guinea. Fig. 6.

Ecol. Mostly in montane or submontane rain-forest, 450–3300 m; in both lowland and montane rain-forest in New Zealand and at lower and medium altitudes elsewhere in the Pacific.

Palyn. Grains spherical, about 30 μm diameter, monocolpate, with fine faint pitted-reticulate sculpture.
Fig. 5. *Ascarina philippinensis* C.B. Rob. a. Male flowering branchlet, ×2/3, b. stipules, ×4, c. portion of male inflorescence, ×8, d. base of anthers showing bract, ×16, e. apiculate apex of anther, ×14, f. TS anther, ×16, g. female flowering branchlet, ×2/3, h. female inflorescence, ×4, i. portion of older female inflorescence, ×6, j. female fruiting branchlet, ×2/3, k. LS ovary, ×16, l. fruits, ×4, m. seed, ×6, n. leaf, ×2/3 (a–f van Royen & Sleumer 6075, g–h Ramos & Edaño BS 30647, i van Royen & Sleumer 8127, j–m van Royen & Sleumer 5898, n van Balgooy?).
The species of sect. Ascarina fall into two groups, a predominantly western Pacific group with a single bract subtending the flower and male flowers with two stamens and the other mostly eastern Pacific group with 3 bracts and 1 stamen.

Floral biology. Ascarina species have usually been assumed to be dioecious but A.C. Smith (1976) pointed out that he had seen specimens which were monoecious with male and female inflorescences on the same branchlet. Rawlings (1974) published an observation made in 1972 by J. Don that a solitary tree of *Ascarina lucida* produced copious pollen and later was loaded with drupes thus disproving that the genus is dioecious. It was noted that flowers were produced in the early spring, developing very slowly during August and September and that the drupes did not mature until the following spring and did not fall until after new flowers had formed. Even earlier in 1971 J. Godley studied a plant in flower and suspected it might be a hermaphrodite with very strong protandry. Moore (1977) showed that *Ascarina lucida* exhibits a peculiar type of monoecism where a male flower is represented by a single stamen and commonly accompanied by two female flowers which mature distinctly later or in other compound inflorescences a stamen and single accompanying ovary mature almost simultaneously. In essence there is a reduced biparous sessile cyme which resembles a bisexual flower and has in fact been accepted as a single flower. Corde moy (1863) long ago suggested that the 'single flower' of *Chloranthus* is in reality a little glomerulus, a biparous sessile cyme. Jérémie (1980) also comments on this subject and states that generally male and female flowers are on different plants but exceptionally certain specimens present flowers of 1 or 2 stamens and one or two rudimentary but sometimes functional carpels in an adaxial position i.e. falsely hermaphrodite with ± marked protandry but true monoecism also occurs. Smrtn (1981) has accepted that this condensed biparous cyme with male and female flowers is the basic inflorescence in the genus. A survey of the herbarium material of *Ascarina philippinensis* has not revealed anything but dioecious plants.

**KEY TO THE SPECIES**

1. Leaves rounded or only very shortly acuminate at the apex. Flowers with a single subtending bract; male flowers with 2 stamens. Endocarp smooth.
2. Leaves subsessile, the petiole short and thick, about 2 mm long; blades narrowed to rounded or subcordate at base ................................................................. 3. *A. subsessilis*
3. Leaves distinctly petiolate, the petioles slender, 0.4–1.5 cm long; blades cuneate at base.
4. Fruits 1.2–2 mm long, with thinner more finely wrinkled exocarp (dry material), in more lax terminal and axillary inflorescences, the distances between the fruits greater and inflorescence-branches more slender ................................................................. 2. *A. maheshwarii*
5. Fruits 2–3 mm long, with thicker more coarsely wrinkled exocarp, in lax usually very densely congested terminal inflorescences, the distances between the fruits shorter and inflorescence-branches usually much stouter ........................................................................ 1. *A. philippinensis*

Endocarp warty-papillate ................................................................. 4. *A. diffusa*


Small to medium-sized tree, 7.5–24 m, ø to c. 35 (–60) cm, sometimes a shrub or treetop 2–4 m at high altitudes; twigs very brittle; bark very variable, white, grey or dark reddish brown, very rough and flaky to slightly to distinctly fissured, the fissures widely spaced, deep, bordered with yellowish scar tissue; inner bark straw to orange or pale brown, fibrous; blaze off-white to pale brown; cambium yellow; wood pinkish straw, turning ± orange, the rays well marked, with no exudate or sapwood described as yellow or straw-coloured and heartwood purplish or dull brownish. *Leaves* very variable, elliptic, oblong, ovate or obovate, 3.2–14 (–18) by 1.5–8.5 (–10) cm, rounded or obtuse to very shortly acuminate at apex, cuneate at base, rather fleshy or leathery, glossy, ± paler beneath, crenate with thickened tips to crenations; nerves 8–11 pairs; petiole 0.4–1.5 cm; stipules linear to ovate-boat-shaped, 1–2.5 mm long, often caducous; intermediate leafless nodes often present, with sheaths up to 6.5 mm long. *Inflorescences* terminal compound spikes with several branches usually spreading from a central axis, 1.5–3 cm long, the final branches spiciform with 4–8 flowers; bracts ovate, up to 1.5–3 by 1–2 mm. — *Male flowers* whitish or pale greenish yellow with
2 collateral stamens and rarely a third adaxial one; anthers c. 3 by 1–1.5 mm, the projecting connective subacuminate. — Female flowers and fruits congested, the inflorescence-branches usually 0.5–2 cm long, the flowers usually not separated by more than 2 mm; ovary green; stigma brownish. Fruits with spicly aroma, green turning purple-black. Endocarps straw-coloured, sublenticular, 2.5 by 2 by 1.3 mm, keeled.


Small to medium-sized, dioecious tree 3–15 m, with broad trunk 15–55 cm Ø; rarely with thick buttresses to 1 m; bark pale grey to dark brown, smooth or fissured; blaze dull brown; wood soft, white or straw-coloured. Leaves elliptic to somewhat obovate, 6–14 by 3–8 cm, shortly acuminate at the apex, narrowly cuneate at the base, crenate or crenate-dentate, the tips of the crenations with brown to black thickenings (hydathodes), dark green and shiny; nerves 12–20 pairs; petiole 0.4–2 cm; stipules triangular-subulate, 0.5–1.5 mm long from a narrow sheath; leafless nodes with short to cylindrical sheaths 3–10 mm long bearing leaf vestiges about 1 mm long. Inflorescences green, terminal but often also borne in axils of upper leaves (up to 4 nodes below apex); branches 5–8, slender, (1–)2.5–3.5 cm, each unbranched or again branched, the flowers well spaced with internodes 2–8 mm; lower bracts of inflorescence similar to sheaths at leafless nodes, the upper longer, 0.5–1.5 mm long; bracteoles supporting the flowers deltoid, 0.5 mm long or almost obsolete. — Male flowers with 2 yellowish anthers 2–3 mm long. — Female flowers with cream ovary and unequally bilobed sessile stigma. Fruits drying yellow-brown but said to be black (WHITMORE), translucent green or greenish cream, ovoid, 1.2–2

Fig. 6. The disjunct distribution of the genus Ascarina Forst. The single species in Madagascar (not indicated here) is the sole representative of the sect. Madascarina Leroy & Jérimie (Ascarinopsis Humb. & Capuron).

Localities of sect Ascarina after Pacific Plant Areas 2, map 64.
mm long, exocarp thin and finely wrinkled (dry state); endocarp ± discoid, straw-coloured, smooth.

**Distr.** Solomon Is.; in **Malesia**: Papua New Guinea (Milne Bay, Morima Range), incl. Manus & Bougainville Is.

**Ecol.** Primary rain-forest, also open forest and hillside forest, 450–750 m. **Male fl.** July, **fr.** June, Oct.

**Note.** Although Smith (1976) speaks of this 'very distinct species' characterised particularly by having additional axillary inflorescences, slender long inflorescence branches with spaced flowers and smaller fruits with less wrinkled exocarp, examination of extensive material of *A. philippinensis* which is very variable over its wide range; small fruits are found for instance in **RAU** 158 (Onim) and **Vinas & Wiakabu LAE** 59447 but both have typical *philippinensis* foliage; long inflorescence branches occur in some material from the Cycloop Mts which have, however, larger more wrinkled fruits and foliage of *philippinensis*.


Medium-sized, dioecious tree 15–24 m, 8–35 (–50) cm d.; bark pale grey-brown to dark brown, fissured; wood straw-coloured or light brown. Leaves elliptic or oblong-elliptic, rarely narrowly obovate, 5–14 by 3–9 cm, rounded at the apex, narrowed, rounded or subcordate at the base, shallowly crenate, rather fleshy in life, drying thick and with minutely rugulose surface, the costa sometimes dividing the leaf somewhat asymmetrically, subsessile; nerves 10–15 pairs; petiole thick, c. 2 mm; stipules minute, c. 1 mm long; leafless nodes present with sheaths 2–6 mm long bearing lateral leaf-vestigies 0.8–1.5 mm long, rugulose in dry state. Inflorescences terminal, branched and occasionally a simple unbranched one from a lower node. **Male** 2 cm long, 3-branched at the base, the main branch with side branchlets c. 5 mm long; anthers c. 3 mm long. — **Female** 1.5–4 cm long with 3–5 main branches each with 5–7 rather thick branchlets 1.5–2.5(–3) cm; lower bracts similar to the leaf-vestiges at leafless nodes, the upper again similar but with the lateral projections longer, lanceolate, longitudinally folded, 4.5 mm long; bracteoles supporting flowers deltoid, scarcely 1 mm long; female flowers not seen. **Fruits** greenish white (presumably becoming dark when ripe?), ovoid, ± congested; exocarp strongly wrinkled in the dry state; endocarp c. 1 mm long (mature?), smooth.


**Ecol.** Montane rain-forest, partly secondary forest on limestone ridge, 1830–3200 m. **Male fl.** Aug., **fr.** Nov., **Jn.**, Jan., June–Sept.


Shrub to small or medium-sized tree, dioecious or monoecious, 4–15(–25) m tall with open spreading crown; trunk 7–10 cm d.; young stems reddish; bark light grey to brown, smooth; blaze red and wood white, soft. Leaves elliptic-lanceolate to lanceolate, 4–17 by 1.5–4.5 cm, distinctly acuminate at the apex, cuneate at the base, minutely to coarsely serrate, save near the base, thinly coriaceous; nerves 12–25 pairs; petioles slender, 0.5–2.7 cm; stipules 1–3 mm long on leaf sheaths 1–5 mm long; leafless nodes occur. Inflorescences green, yellowish or purple, many-flowered, lax, terminal and in the upper axils; main axis 3-branched, the central branch again 2–3-branched but some axillary inflorescences simple; individual branches slender, 3–12 cm long, the flowers closely placed, each subtended by 3 bracteoles scarcely 1 mm long; lower main bracts of inflorescence up to c. 1 cm long consisting of a sheath with lateral projections; upper bracts ovate-acuminate, 3 mm long. Inflorescences glomerules consisting basically of an abaxial male flower and adaxial female flower but more usually unisexual. — **Male flowers** with 1 stamen; anthers 2–4 mm long, scarcely 1 mm wide (reported purple in Fiji specimen), with a minute deltoid apical projection. — **Female flowers:** ovary green, ovoid, 1.5 mm long; stigma between translucent and white or purple, 0.8–1.3 mm wide. **Fruit** ellipsoid, 2–3 by 1.2–2.5 mm; exocarp thin and slightly wrinkled in dry state; endocarp rounded ellipsoid, ± 1.5 by 1.2 mm, compressed, the margin keeled, surfaces warty-papillate.

**Distr.** Solomon Is., New Hebrides, Fiji, Samoa, Cook Is.; in **Malesia**: Papua New Guinea (New Britain: Mt Talawe; Bougainville).

**Ecol.** Rain-forest, cloud-forest with *Pandanus*, 900–1800 m. **Male fl.** Feb., **Aug.**, **fr.** May.

**Vern.** New Britain: **pot**, Talasea.

**Note.** There is considerable difference between the foliage and inflorescence length of the single New Britain specimen seen and those from Bougainville (3 specimens), but bearing in mind the variation throughout its range this seems of no significance. **Frodin** observed flower buds (young fruits?) red-violet whitish at tip and inflorescence purple but elsewhere the inflorescence is described as yellowish.
Fig. 7. Hedyosmum orientale MERR. & CHUN. a. Female flowering plant, × 2/3, b. female inflorescence, × 4, c. female flower and bract, × 6, d. female flower, stigma removed, × 8, e. perianth spread out, × 10, f. ovary, × 10, g. ovary opened to show ovule, × 16, h. TS ovary, × 10, i. stigma, × 10, j. portion of stigma lobe to show multicellular hairs, × 24, k. part of male plant, nat. size, l. young male flower, × 2, m. portion of expanded male flower, × 8, n. front view of anther, × 12, o. side view of anther, × 12, p. TS of anther, × 16 (a–j S 16539, k–p BURTT 12775, spirit material).
4. HEDYOSMUM


Herbs, shrubs or trees, monoecious or dioecious; branches often jointed at the nodes, often exuding a gelatinous aromatic exudate when cut. Leaves decussate, mostly serrate, the serrations often tipped with glands (? hyathodes); petiolar sheath mostly with marginal subulate or pectinate stipules. Inflorescences axillary or terminal, sometimes united with the stem near their base; flowers truly unisexual; individual inflorescences unisexual but the compound inflorescences often with female flowers above and male flowers on lower branches. In some species the flowers are partly fused amongst themselves and with the axis. — Male flowers cone-like, solitary or paniculate, with involucres and very numerous bilocellate anthers, filaments absent or very short; locelli parallel opening lengthwise, at first 2-celled; connective shortly appendaged or subpeltate above the loculi. — Female flowers variously capitate or paniculate, distinctly bracteate; perianth-tube adnate to the ovary, limb very short, 3-toothed; style very short, stigmatose at apex or stigma sessile, rarely linear or clavate, often caduceous; outer and inner integuments of ovary 3 cells thick. Drupes free, or united by the bracts into a dense mass, globose or ovoid, often 3-sided or 3-ribbed, sometimes crowned with persistent perianth lobes, the fleshy wall formed partly by the accrescent perianth; exocarp juicy; endocarp hard; seed coat unspecialised.

Distr. About 35 spp., almost entirely in the New World from Mexico to Peru and Brazil and West Indies, a single species in SE. Asia, extending into W. Malesia.

P a l y n. ERDTMAN (1952) described the pollen of *H. brasiliense* as 1-sulcate or 1-sulcoideate (?), sometimes provided with a number of thin branched and irregularly placed apertural areas, which in optical section can convey the impression of a polycolpoidate grain. According to SWAMY (1953) the grains tend to be larger than in other genera of the family up to 35 μm and are generally polycolpate resembling *Chloranthus* but the furrows are often localised at a pole or other locus and the ends joined or reduction in number of the furrows resulting in acolpate grains occurs in some species; the exine is finely reticulate-pitted. MULLER (1981) reported that pollen grains of this genus have been found in Upper Miocene deposits in Mexico, Guyana and Colombia and suspects DOYLE may have been correct in comparing irregularly aperturate forms from the Lower Cretaceous with this genus.


Floral morph. LEROY (1981, 1983) has suggested that what has usually been considered to be an inflorescence of unistaminate, naked, ebracteate, male flowers is in fact itself a strobiloid male flower bearing several hundred spirally arranged stamens, an extremely primitive structure which correlates with the 'Lower Cretaceous' type monosulcate pollen and adaptation to wind pollination. I have accepted this interpretation as being the more plausible.

Dr P. RUDALL of the Jodrell Laboratory (Kew) has cut sections of the axis of material collected by B.L. BURTT in Sarawak. It contains 8 bundles and only single bundles enter the stamens, which is not at variance
with the theory. ENDRESS' comments (1971) on the female flower have already been mentioned in the general section (see p. 125).

BURGER (1977) considered that both the female flower (the most complex in the family) and the male (the most reduced) were derived from simple flowers resembling those of Chloranthus and Sarcandra, an idea of course totally at variance with that of LEROY. The 3-lobed covering of the female flowers of Hedyosmum truly suggests reduction and fusion from an ancestor with a 3-parted perianth. In some species this tissue becomes succulent and white in fruit, an aril-like adaptation for dispersal by birds. It may have arisen by modification of 3 adnate staminodes and the dorsal and lateral positions of the ribs and alternation of the vascular bundles of the ribs with those of the ovary supports this idea.


1. Hedyosmum orientale MERR. & CHUN, Sunyatse- 
Nia 5 (1940) 36, t. 5; Wu Kuo-Fang, Fl. Reipubl. 
P. Sin. 20 (1982) 95, f. 30. — H. nutans (non Sw.) 

Diocious glabrous herb or subshrub, 1–2.5 m tall; stems long, often straggling at the base, brittle and juicy above, up to 2 cm Ø, smelling like ginger-root; branches often drooping; upper internodes often condensed, particularly in young plants so that petiolar sheaths overlap. Leaves lanceolate to linear-oblong, 9–22 by 1.5–4 cm, thin, long acuminate at the apex, narrowly cuneate at the base, the margins rather closely serrate, the serrations apically thickened, more or less obtuse; lateral nerves 20–30 pairs, fine, ± raised; petioles 0.6–2(–3.5) cm, longer on one side, each pair joined to form a sheath 6–15 by 
6–8 mm. — Male flowers few in panicles, the floral 
axes 2–4.3 cm, the stalks c. 1 cm; very young flowers 
cone-like, about 1 cm long with a basal oblique ring 
6 mm wide of c. 13 acute or bifid bractlets; stamens 
about 300, anther locule 1.2 mm (2 mm in vivo) long, 
the connective appendage compressed, acute, 0.5–1 
mm long, asymmetrically incurved. — Female inflor-
encescs green, paniculate, c. 5 by 2 cm, the few 
branches 1–1.5 cm, ± few-flowered; bracts rounded 
ovate, c. 5–6 by 5 mm with a long caudate apex 3–6 
mm long, c. 1 mm wide; sepals 3, triangular, 1–1.2 
mm long and wide, entire, crenate or ± dentate. Ovary 
somewhat 3-angled, genuinely monocarpellate; stigma greenish with red tips, essentially lanceolate 
in outline, 2–2.2 mm long, irregularly lobulate, 
covered with several-celled hairs; tip of ovary with 
triangular impressed area with mammillate centre. 
Fruit ellipsoid, 3–4 mm long, ± 3-angled, crowned 
by the calyx.

Distr. S. China (Hainan; Kwangsi-Tonkin border; S. Vietnam: Kontum); in Malesia: Sumatra Westcoast Residency (Lubuk Sulasi; Laras Talang), N. Bencoolen (B Taun), Borneo (West: B Tibang; Sarawak: Hose Mts, base of B Kajang, B Sarpandai; Bt Kenawang: Usun Apau), and Central Celebes (Palu Distr.: near Lake Lindu, G. Njilalaki, and west slope of Mt Poroka, Timbu). Fig. 8.

Fig. 8. Localities of Hedyosmum orientale MERR. & 
CHUN.

ECOL. Forest on dacite hillside, in ridge forest and 
foot of wet cliff, with conifers and Fagaceae, 1000– 

Note. In the BM there is a HORSFIELD specimen 
of the genus, labelled in sched. H. sumatranum, 
which is the earliest collected specimen from the Old 
World.