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ACORACEAE

(J. Bogner, Gersthofen, Germany)

Acoraceae Martinov, Tekhno-Bot. Slovar (1820) 6.

Perennial, glabrous, aromatic herbs, growing in marshes or as emergent aquatics; laticifers and raphides absent; aerenchyma present. *Rhizome* creeping, much branched, lacunose, with specialized aromatic oil cells; rooting on the lower side and bearing leaves at apex. *Leaves* distichous, bases overlapping, unifacial, ensiform, not differentiated into petiole and blade; intravaginal squamules present in leaf axils; venation parallel. *Inflorescence* solitary, terminal, borne laterally on leaf-like scape (usually interpreted as peduncle and spathe; peduncle with two separate vascular systems), peduncle triangular; continuation shoot arising in axil of leaf preceding inflorescence; the so-called spathe much longer than spadix, erect, persistent (appearing merely as a vertical leaf-like extension); spadix jutting out at an angle from peduncle, sessile, conoid, cylindrical and finger-like or slender and tail-like; flowering from the base to the top. *Flowers* bisexual, perigoniate, densely arranged, bractless, trimerous; tepals 6 in two whorls of 3, free, thin, fornicate; stamens 6 in two whorls of 3, free, filaments linear-oblong and flattened, anthers introrse, thecae rounded-ellipsoid, subopposite, dehiscing by longitudinal slit, connective inconspicuous; pollen monosulcate, ellipsoid, small (15–20 μm), exine shallowly and remotely or more densely foveolate, otherwise psilate, apertural exine subpsilate; gynoecium (pistil) obconic-cylindric, only slightly exceeding tepals, ovary 2- or 3-locular, ovules several per locule, orthotropous, pendent on apical placenta, both integuments bearing trichomes, inner integument longer than outer forming the micropyle; stigma minute (more or less punctate), subsessile (there is a broad stylar region visible in LS); fruit a few-seeded berry, oblong-obovoid with thin, leathery pericarp, enclosed by the tepals, more or less whitish with brownish stigma remnant when fresh, soon becoming straw-brown (*A. calamus*) or yellowish to yellow-white (*A. gramineus*) at maturity, 1–5(–9)-seeded; seed oblong to ellipsoid or ovoid, testa light brown, with small pits (slightly foveolate in *A. calamus*) or smooth (*A. gramineus*), long integumentary trichomes (bristles) present at the micropyle (*A. gramineus*) or absent (*A. calamus*); embryo axile, cylindric (*A. calamus*) or conoid (*A. gramineus*), with perisperm and abundant endosperm.

Chromosomes: 2n = (22) 24, 36, (44), 48.

Literature: Bogner, J. & S.J. Mayo, Acoraceae, in K. Kubitzki, The families and genera of vascular plants IV (1998) 7–11. Berlin, Heidelberg & New York. — Engler, A., Araceae-Pothoideae, in A. Engler (ed.), Pflanzenr. 21 (IV. 23B) (1905) 308–313. Leipzig. — Li Heng, Araceae (Acorus), Fl. Reipubl. Popularis Sin. 13, 2 (1979) 4–9. — Li Heng, Zhu Guanghua & J. Bogner, Acoraceae, Flora of China 23 (2010) 1–2. Beijing & St. Louis. — Mayo, S.J., J. Bogner & P.C. Boyce, Acoraceae, in The genera of Araceae (1997) 289–290.

DISTRIBUTION

Temperate, subtropical and tropical Asia and North America, introduced and naturalized in Europe and partly in North America, also at least in New Guinea. The genus *Acorus*

is mainly found in the northern hemisphere from the temperate zone to the tropics of Asia and in Malesia. *Acorus calamus* is distributed in the whole range of the genus, but *A. gramineus* only in East and Southeast Asia.

Literature: Hegi, G., Illustrierte Flora von Mitteleuropa, 3rd ed. II (1) (1979) 322–326. Berlin & Hamburg. — Wein, K., Die älteste Einführungs- und Ausbreitungsgeschichte von Acorus calamus. Hercynia 1 (1939) 367–450 & 3 (1942) 241–291.

ECOLOGY

The genus *Acorus* contains herbaceous helophytes in marshes, along the margins of streams and rivers, ponds, lakes, ditches, in standing or slow-running waters, swampy sites, pastures, meadows and wet rocky places. *Acorus gramineus* grows also in rock crevices or as a rheophyte along streams. Both species form large dense stands due to their extensively branched rhizomatous stems. This genus is found from sea level to an altitude of 1150 m in Central Europe and up to 2800 m in China. It grows in wetlands in temperate to subtropical (also in higher altitudes in the tropics) and tropical areas.

POLLINATION

The flowers of *Acorus* are proterogynous. The pollination was unknown until now (26/27 February 2011) when Luo Shixiao observed at night *Contarinia* spec. (Cecidomyiidae), a gall midge, as pollinator of *Acorus gramineus* in the Xianshan County, Guangdong Province, China (pers. comm., unpubl. data). The pollinator was determined by R. Gagné (pers. comm.). While depositing their eggs into the inflorescences the gall midges get sticky pollen onto their abdomen (see Plate 1), which they then transfer to the next plant's stigmas when laying their next egg. The larvae of many species of this very large genus live and feed in flowers or catkins (R. Gagné, pers. comm.).

DISPERSAL

Not much is known of dispersal ecology but seeds and parts of rhizomes must be transported by water, because the plants are always growing in or near water. The European plants of *A. calamus* are triploid and therefore sterile, but have been naturalized there widely by rhizome pieces since the 16th century; the triploid plant found today in the eastern United States of America were introduced by early settlers as a medicinal plant and later became naturalized widely. The native diploids are found further inland and in Canada.

MORPHOLOGY

Intravaginal squamulae are present in the leaf axils (as in almost all Helobiae and a few genera of Araceae). The leaves are distichous and unifacial (leaf blades), both surfaces being abaxial; only the base shows a bifacial development which can be interpreted as a sheath, and the upper part of the leaf clearly has the lower side completely connate

Plate 1. a. Spadix of *Acorus gramineus* with the pollinating gall midges (*Contarinia* spec.). Note the pollen on the abdomen of the insect; b. Flowering *Acorus gramineus* in the natural habitat. Photos: a by Luo Shi-Xiao; b by Gu Lei.

to form a unifacial blade. Aerenchyma is present. The peduncle is triangular. Axillary branches develop from proleptic buds and begin with a cataphyllary 2-keeled prophyll, followed by foliage leaves. The continuation shoot arises in the axil of the leaf preceding the inflorescence. The last leaf of the flowering shoot (article) is considered as a spathe (following Engler), although it resembles a foliage leaf morphologically. The lower part of the spathe appears to be congenitally adnate to the axis of the inflorescence proper. Two separate vascular systems occur in the peduncle, one corresponding to the spathe and the other to the inflorescence. Ray (1988) rejected the interpretation that the leaf associated with the spadix is a spathe, preferring to consider it as a sym-

podial leaf. According to him, the shoot of *A. calamus* shows anisophyllous sympodial growth; the continuation shoot arises sylleptically and has a prophyll that resembles a foliage leaf.

Reference: Ray, T., Survey of shoot organization in the Araceae. Amer. J. Bot. 75 (1988) 56–84.

FRUITS AND SEEDS

The fruit is a leathery berry, straw-brown at maturity (*A. calamus*) or yellowish to yellow-white (*A. gramineus*), and never capsular as reported in some literature (Bochenska & Koslowski 1974). The seed has perisperm and endosperm. The testa is foveolate (*A. calamus*) or smooth *(A. gramineus*), in the latter species trichomes are present as bristles (see also under Seed Anatomy).

Reference: Bochenska, I. & Koslowski, J., Comparative investigations of the structure of fruits of the family Araceae growing in Poland. Herba Polon. 20 (1974) 3–10.

SEEDLING MORPHOLOGY

The cotyledon of the genus *Acorus* is narrowly cylindric and unifacial; the distal part is haustorial as in other monocots and remains in the seed. The cotyledonary sheath is short and the hypocotyl is not visible externally. The root collar bears quite long, dense rhizoids ('root hairs'). The primary root elongates and remains simple, later aborting without branching. The first persistent roots arise on the sides of the cotyledonary sheath, each with a short coleorhiza. The primary leaf is ensiform and unifacial, closely resembling the adult form. After the appearance of the foliage leaf, the distal part of the cotyledon is pulled out of the seed. The germination type of *Acorus* is different from any of those known in the Araceae.

Literature: Seubert, E., Die Samen der Araceae (1993) 325–332. Königstein (Taunus). — Tillich, H.-J., Keimlingsbau und verwandtschaftliche Beziehungen der Araceae. Gleditschia 13 (1985) 63–73. — Tillich, H.-J., Seedlings and systematics in monocotyledons, in P.J. Rudall, P.J. Cribb, D.F. Cutler & C.J. Humphries (eds.), Monocotyledons: systematics and evolution 1 (1995) 303–352. Kew.

POLLEN MORPHOLOGY

Pollen grains are ellipsoid, monosulcate (to subulcerate), heteropolar, small, 15–20 μm, exine remotely or more or less foveolate, otherwise psilate (smooth), exine structure tectate-columellate.

Literature: Grayum, M.H., Comparative external pollen ultra structure of the Araceae and putatively related taxa. Monogr. Syst. Bot. Missouri Bot. Gard. 43 (1992) 1–167.

VEGETATIVE ANATOMY

Raphides and true laticifers are absent in the genus *Acorus*. Only irregular and tetrahedral crystals have been observed. Primitive vessels are present in the roots and rhizomes. The roots have large schizogenous intercellular spaces in the cortex. Idioblastic oil

cells are present in the root cortex. The inner boundary of the stem (shoot, rhizome) is delimited by an endodermis with Casparian strips. The endodermis encircles the central cylinder, interrupted only where the leaf traces depart. The rhizome also has aerenchyma. The vascular bundles in the rhizome and leaves are amphivasal.

The leaves have a central region of large air cavities (aerenchyma) beneath a chlorenchyma of 3–5 layers of isodiametric cells. A chlorenchyma-less hypodermis is present. The leaf venation is parallel, with minor transverse veins joining the main, longitudinally oriented, system. This corresponds to the typical monocot venation type. Leaf variegation due to periclinal chimeras occurs in *Acorus*. Stomata are present on both surfaces and are brachyparacytic with one pair of subsidiary cells, the guard cells oriented parallel to the longitudinal axis of the leaf. Secretory cells (oil cells) are common and tannin cells are scattered in the leaves and rhizomes, occasionally also in the roots. Crystals are present as druses and prisms. The cuticle of the leaves is smooth or occasionally striate.

Literature: French, J., Vegetative anatomy, in S.J. Mayo, J. Bogner & P.C. Boyce, The genera of Araceae (1997) 9–24. — Keating, R.C., Acoraceae and Araceae, in M. Gregory & D.F. Cutler, Anatomy of the Monocotyledons 9 (2002) 46–49. Oxford, England.

FLOWER ANATOMY

The inner integument forms the micropyle and is much longer than the outer integument. The endothecial thickenings have a unique, stellate pattern (French 1985). The ovary wall lacks vascular bundles and the vascular supply of the gynoecium is restricted to an axile system which supplies the placentae (French 1986).

References: French, J., Patterns of endothecial wall thickenings in the Araceae: subfamilies Pothoideae and Monsteroideae. Amer. J. Bot. 72 (1985) 472–486. — French, J., Ovular vasculature in Araceae. Bot. Gaz. 147 (1986) 478–495.

SEED ANATOMY

The seeds are ovoid to elongate ovoid or more or less ellipsoid-oblong, 4 by 1 mm (*A. calamus*) or 1.5 by 1 mm (*A. gramineus*); testa smooth to somewhat scabrous and with small pits (*A. calamus*) or more or less smooth without small pits but with bristles (stiff hairs) at the micropyle (*A. gramineus*), these trichomes are multicellular (see SEM micrographs of the seeds, Fig. 1). The perisperm is 78 μm (*A. calamus*) to 126 μm (*A. gramineus*) thick and appears transparent; endosperm copious and with lipids. Raphides lacking. Embryo cylindrical (*A. calamus*) and c. 1/3 of length or conoid (*A. gramineus*) and 4/5 of length of the endosperm; starch present in immature seeds in the peripheral tissue but lacking in the mature stage or starch completely lacking (*A. gramineus*).

Literature: Seubert, E., Die Samen der Araceen (1993) 325–332. Königstein (Taunus).

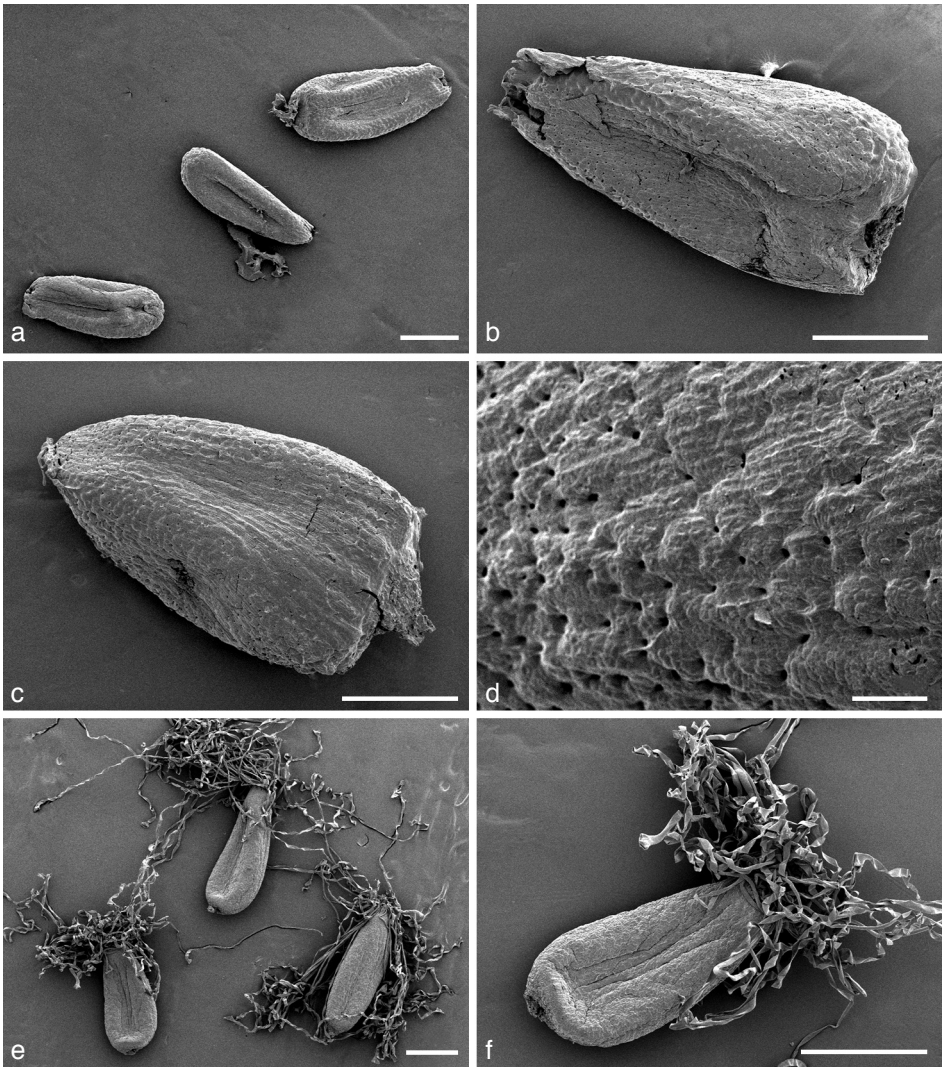

Fig. 1. a–d: *Acorus calamus* L. a. Three seeds; b, c. single seed; d. testa with small pits. — e, f. *Acorus gramineus* Sol. ex Aiton. e. Three seeds, with bristles; f. single seed, with many bristles (a: *Bogner 2098*, M, diploid plant from Quebec, Canada; b–d: *Jiangpu team no. 8031* [= MO 04128113]; e, f: *Wei Zhaofan no. 120042* [= MO 04130080]). — SEM micrographs by M. Hesse & H. Halbritter. — Scale bars: a–c, e, f = 1 mm; d = 0.1 mm.

EMBRYOLOGY

Endosperm formation is cellular and unlike those types found in the Araceae. There is no chalazal basal apparatus. The anther tapetal cells are 2–4-nucleate.

Literature: Grayum, M.H., Systematic embryology of the Araceae. Bot. Rev. 57 (1991) 167–203.

CYTOLOGY

Acorus gramineus is known only in diploid populations (2n = 22, 24) and *A. calamus* in diploids (2n = 22, 24), reported from North America and rarely from Asia (Mongolia, middle Siberia), triploids (2n = 36) in Europe, Near East, India (Himalaya region) and Sakhalin, and in the eastern United States of America (introduced by early settlers there) and tetraploids (2n = 44, 48) which occur only in Asia. A plant from Borneo (Sarawak) has been shown to have 2n = 44 chromosomes (c. 44, certainly tetraploid, unpublished count); pollen of some specimens from New Guinea was studied and turned out to be sterile, suggesting that these plants were triploid and introduced, but it is possible that others are tetraploid (it is practically impossible to distinguish both cytotypes morphologically). The examined Bornean plant of *A. calamus* had somewhat narrower leaves (1 cm wide) and was formerly distinguished as var. *angustifolius* (Engler 1905), but a range of intermediates exist leading to the typical form. Triploid *A. calamus* is sterile and therefore never sets fruit. The triploid cytotype probably originated in the Himalayan region of India; it is widespread there and may have originated there from a cross between diploid and tetraploid cytotypes. The triploid *A. calamus* was brought to Turkey by people and in the 16th century to Central Europe as a medicinal plant, later to eastern North America; it was probably also taken to the Island of Sakhalin along with human migration.

Literature: Engler, A., Araceae-Pothoideae, in A. Engler (ed.), Pflanzenr. 21 (IV. 23B) (1905) 308–313. Leipzig. — Evstatieva, L.N., M.N. Todorova, I.V. Ognyanov & L.V. Kuleva, Chemical composition of the essential oil in Acorus calamus L. (Araceae). Fitologija (Bulgarian Academy of Sciences) 48 (1996) 19–22. — Petersen, G., Cytology and systematics of Araceae. Nordic J. Bot. 9 (1987) 119–166.

PHYTOCHEMISTRY

Dried rhizomes of *A. calamus* have been used for centuries as a source of medicinal compounds. Substances extracted from the rhizome have sedative, analgesic, insecticidal and antibacterial properties. Compounds which were identified from the rhizome include acorin and polyphenols localized in specialized idioblasts, and varying concentrations of ethereal oils. The precise composition of the ethereal oils varies according to the geographical source and cytotype of the plant material (Wulff 1954, Wulff & Stahl 1960); phenylpropanoids (asarone, methyleugenol), monoterpenes and sesquiterpenes have been identified from the ethereal oils. The composition of ethereal oils in the leaves of *A. calamus* differs from that of the rhizome, but also shows a clear correlation with the cytotype. The rhizomes of *A. gramineus* also contain ethereal oils, in which asarone is the main component (Hegnauer 1963, 1986). Bruised leaves give a strong sweet odour, which is why it is called in English ‘sweet flag’; leaves of *A. calamus* have been used as a floor strew in former times to give a pleasant aroma to living areas.

References: Hegnauer, R., Chemotaxonomie der Pflanzen 2 (1963) 73–99, 475–476 & 7 (1986) 581–591. — Wulff, H.D., Zur Zytologie, geographischen Verbreitung und Morphologie des Kalmus. Arch. Pharm. Ber. deutsch. pharm. Ges. 287 (1954) 529–541. — Wulff, H.D. & E. Stahl, Chemische Rassen bei Acorus calamus. Naturwissenschaften 47 (1960) 114.

FOSSILS

Acorus spitsbergensis Golovn. & Budantzev was described from Spitsbergen (Svalbard) of the Late Eocene from a spadix with a short piece of the peduncle (axis) and the lower part of the spathe (Budantsev & Golovneva 2009). *Acorus brachystachys* Heer (Bogner 2001) was also described from Spitsbergen of the Eocene epoch (in the original publication it was said erroneously to be from the Miocene), but in fact is a synonym of *Nordenskioeldia borealis* Heer (Trochodendraceae); the structure which was interpreted as a spadix is a short shoot with spirally arranged bud scales rather than flowers as suggested by Heer (1870). *Acorus heeri* E.W.Berry was transferred by Crepet (1978) to the genus *Acorites* as *Acorites heeri* (E.W.Berry) Crepet; it consists of a single spadix and a second spadix with a piece of a peduncle (axis) from North America of the Eocene epoch. Fruits and seeds as *Acorus procalamus* Nikitin from Quaternary deposits of the former Soviet Union were reported (Katz et al. 1965), and these are very similar to those of the extant *Acorus calamus* L. Katz et al. (1965) described also fossil seeds of the extant *Acorus calamus*. *Acoropsis eximia* (Göpp. & Menge) Bogner (syn. *Acoropsis minor* Conw., *Carex eximia* Göpp. & Menge) from the Eocene of the Baltic Amber represents a well-preserved infructescence of the Araceae-Monsteroideae, tribe Monstereae (Bogner 1976); it lacks tepals and is therefore not related to *Acorus* as suggested by Conwentz (1886). The infructescences of *Acorus* always clearly show the presence of tepals.

The recent discovery of *Acorus spitsbergensis* from Spitsbergen (northern Europe) proves that the genus *Acorus* was present in Europe already in the Eocene epoch and later died out. Modern populations of *Acorus calamus* in Europe are introduced.

References: Bogner, J., Die systematische Stellung von Acoropsis Conwentz, einer fossilen Aracee aus dem Bernstein. Mitt. Bayer. Staatssamml. Paläontologie hist. Geologie 16 (1976) 95–98. — Bogner, J., What is Acorus brachystachys Heer? Aroideana 24 (2001) 100–101. — Budantsev, L.Yu. & L.B. Golovneva, Florulae fossiles arcticae II, Paleogene flora of Spitsbergen (2009) 178–179, t. 95, 1–3. Russian Academy of Sciences, Komarov Botanical Institute (St. Petersburg) [in Russian]. — Conwentz, H., Die Flora des Bernsteins II. Die Angiospermen des Bernsteins (1886) 12, t. 1, f. 14–17. Danzig. — Crepet, W.L., Investigations of Angiosperms from the Eocene of North America: an aroid inflorescence. Rev. Palaeobot. Palynol. 25 (1978) 241–252. — Heer, O., Die miocene Flora und Fauna Spitzbergens. Kongl. Svenska Vetensk. Acad. Handl. 8, 7 (1870) 1–98, t. I–XVI. — Katz, N.Ja., S.V. Katz & M.G. Kapiani, Atlas and keys of the fruits and seeds occurring in the Quaternary deposits of the USSR (1965) 1–367. Moscow [in Russian].

USES

Both species, *A. calamus* and *A. gramineus*, are used as medicinal and ornamental plants. Dried rhizomes of *A. calamus* (rhizoma calami) have been used for a very long time and were already known to ancient Egyptians, Greeks and Romans. Calamus oil (tinctura calami, extractum calami) was used for medicaments and is still today of some importance. The chopped rhizomes are still used as a tea to treat stomach ailments. Further use mainly of the rhizomes are for treatments of neurasthenia, chronic bronchitis, diarrhoea, abdominal distension, chills, colds, externally for abscesses, liver disturbance, antiulcer remedy, kidney and stomach as well as gut diseases; these uses are mainly reported from Chinese medicine. It is also said that β-asarone is cancerogenic

(Keller & Stahl 1983). The rhizomes were also formerly used for perfume and are still used today to make a liqueur. Mostly the rhizomes of *A. calamus* are used, because the content of the ethereal oil is highest there, but the leaves are also used. Other reported uses are as an aromatizer for wine and tobacco and also as an insecticide. The bitter rhizomes of *A. gramineus* have also been used medicinally. Both species are commonly cultivated as ornamentals for wet sites, such as bog gardens, ponds and aquatic gardens and *A. gramineus* 'Pusillus', with leaves only up to 10 cm long, is used as an aquarium or terrarium plant. Cultivars of both species with variegated leaves are popular in gardens. Both species are hardy in temperate regions.

Reference: Keller, K. & E. Stahl, Zusammensetzung des ätherischen Öles von ß-asaronfreiem Kalmus. Pl. Med. 47 (1983) 71–74.

RELATIONSHIPS

The genus *Acorus* L. was early treated as a separate family, the Acoraceae, described in the year 1820. Later authors, like Schott 1858, 1860 and Engler 1889, 1905, treated this genus within the Araceae and for long afterwards it was considered as a member of this family until DNA analyses showed that *Acorus* is not related to the Araceae at all. It is the only genus of the family Acoraceae and the only family of the order Acorales. According to the DNA data, *Acorus* has a basal position within the monocots and is considered as the most ancient member of the monocots living today (Duvall et al. 1993).

Grayum (1987) pointed out morphological and anatomical characters which distinguish *Acorus* from the Araceae. These are: All Araceae (including the Lemnaceae = subfamily Lemnoideae) have raphides in their tissues, but *Acorus* lacks them. In *Acorus*, the flowering shoot consists of a peduncle adnate to a leaf as it is shown in two separate vascular bundles and the upper part of the leaf has been interpreted as the spathe which is different from the Araceae where the last leaf is modified into a spathe and the spadix is situated above it. The ensiform leaves of *Acorus* are unifacial, which is unknown in Araceae. In the Australian endemic, monotypic genus *Gymnostachys* R.Br. the leaves resemble those of *Acorus* in being ensiform, but they are bifacial; all other Araceae have leaves divided into a petiole and a well-developed blade. *Acorus* has seeds with perisperm and endosperm, but Araceae never have a perisperm. Other characters distinguishing *Acorus* from the Araceae are: bud trace patterns , presence of ethereal oil cells, stellate pattern of endothecial thickenings, introrse anthers dehiscence (but also introrse anthers in *Zamioculcas*), apical-axile placentation, exclusively axile vascular supply to the placentae, location and organisation of ovule hairs, 2–4 nuclei per tapetal cell, secretory anther tapetum, cellular endosperm development (Grayum 1987); Grayum also reported that the rust-fungus *Uromyces sparganii* Cooke & Peck, occurs in both *Acorus calamus* (in North America) and *Sparganium*.

References: Duvall, M.R., M.T. Clegg, M.W. Chase, D.W. Clark, J.W. Kress, H.G. Hills, L.E. Eguiarte, J.F. Smith, B.S. Gaut, E.A. Zimmer & G.H. Learn Jr., Phylogenetic hypotheses for the monocotyledons constructed from rbcL sequence data. Ann. Missouri Bot. Gard. 80 (1993) 607–619. — Duvall, M.R., G.H. Learn Jr., L.E. Eguiarte & M.T. Clegg, Phylogentic analysis of rbcL sequences identifies Acorus calamus as the primal extant monocotyledon. Proc. Nation. Acad. Sci. USA 90 (1993) 4641–4644. — Engler, A., Araceae, in A. Engler (ed.), Pflanzenfam. II, 3 (1887–1889) 102–153.

Leipzig. — Engler, A., Araceae-Pothoideae, in A. Engler (ed.), Pflanzenr. 21 (IV. 23B) (1905) 308–313. Leipzig. — Grayum, M.H., A summary of evidence and arguments supporting the removal of Acorus from the Araceae. Taxon 36 (1987) 723–729. — Schott, H.W., Genera Aroidearum (1858) t. 1–98. Wien. — Schott, H.W., Prodromus systematis Aroidearum (1860) 1–602. Wien.

CONSERVATION

Both species of *Acorus* are vigorous plants and tend to naturalize, therefore they are not threatened. They are easy to grow and especially *A. calamus* is prone to naturalize and under favourable conditions can become quite weedy.

Only one genus:

ACORUS

Acorus L., Sp. Pl. 1 (1753) 324. — Type: *Acorus calamus* L.

Description, distribution and further notes as for the family.

2 species, both in Malesia.

Etymology — From *akoron*, an ancient Greek plant name.

KEY TO THE SPECIES

1a. Leaves with a distinct midrib, 70–100(–150) by (0.7–)1–2(–2.5) cm; rhizome stout, (0.8–)1–1.5(–3) cm diam.; spadix 4.5–5.6(–8–10) cm long and 0.6–1.2(–1.5) cm diam.; seed without long bristles, testa slightly foveolate (with small pits) . . . . . **1. A. calamus**

b. Leaves without distinct midrib, 20–45(–55) by (0.3–)0.5–1 cm; rhizome slender, 0.4–0.6(–0.8) cm diam.; spadix (3–)5–10(–14) cm long and (0.3–)0.4–0.6(–0.7) cm diam.; seed with long bristles, testa smooth . . . . . **2. A. gramineus**

1. Acorus calamus L.

Acorus calamus L., Sp. Pl. 1 (1753) 324. — Lectotype (Suresh et al., Taxon 32: 130): Herb. Linn. No 447.1 (LINN).

Acorus angustifolius Rumph. ex Schott, Ann. Mus. Bot. Lugduno-Batavi 1 (1864) 284. — *Acorus calamus* L. var. *angustifolius* (Schott) Engl., in A.DC. & C.DC., Monogr. Phan. 2 (1879) 217. — Type: Rumphius 5, t. 27-1.

Acorus rumphianus S.Y. Hu, Dansk Bot. Ark. 23 (1968) 416. — *Acorus terrestris* Rumph. ex Schott, Prodr. (1860) 579, non Sprengel 1825. — Type: Thomson in herb. Hook.f. (K) Kumaon.

(For full synonymy see: R. Govaerts & D.G. Frodin, World Checklist and Bibliography of Araceae (and Acoraceae) (2002) 545–553.)

Rhizome stout, 4–10(–20) cm long, (0.8–)1–1.5(–3) cm diam., aromatic; roots at the lower side of the rhizome. *Leaves* several, ensiform, mid-green, (60–)70–100(–150) by (0.7–)1–2(–2.5) cm (mostly 1–1.5 cm wide), base green to reddish or red, apex acuminate, midrib conspicuous on both sides. Peduncle compressed-triangular, (15–)40–50 cm long. *Spathe* leaf-like, mid-green, 30–50 cm long, acute, also with conspicuous mid-

rib. *Spadix* straight or slightly curved, erect, oblique, narrowly conic to subcylindrical (tapering towards apex), 4.5–8(–10) cm long, 0.6–1.2(–1.5) cm diam., densely flowered. *Flowers* perigoniate, yellowish green, c. 1.8–2 mm diam. seen from above; tepals oblong, keeled, apex triangular-hooded, membranous, (2–)2.5–3 by 1–1.2(–1.4) mm; filaments oblong, flat, 2–2.5 by 0.3–0.5 mm; anthers 0.4–0.5 mm diam., cream coloured; pollen grains c. 20 µm long, exine shallowly and remotely foveolate; gynoecium obconic-cylindric, 2.5–3.5(–4) mm long, (0.8–)1–2.3 mm diam., with conical, spongy apex and very small stigma; ovary 2- or 3-locular, ovules several, orthotropous, placentation apical. *Infructescence* 1.5–2 cm diam., straw-brown at maturity, berries densely arranged; berry oblong-obovoid, 1–few-seeded, (3.5–)4–4.5 mm long, c. 2–3(–3.5) mm diam.; seed oblong-ellipsoid to ovoid, 2.5–3(–4) mm long, 1–1.2(–1.8) mm diam., without bristles, testa nearly smooth and covered with very small pits (slightly foveolate), light brown. — **Fig. 2a–k.**

Distribution — North Temperate Europe (except Greece and the Mediterranean), North Asia extending to subtropical as well as tropical Asia, eastward to the Himalayas, North America; in *Malesia*: Sumatra, Singapore (one coll.), Borneo (one coll. from Sandakan District, Sabah and two from Sarawak), Java, Philippines, Celebes, Lesser Sunda Is. (Lombok, Flores, Timor), New Guinea.

Habitat & Ecology — Growing in swamps, pond sides, standing water, also cultivated. Altitude: up to 2800 m. Flowering: from (February to) April to September.

Chromosome numbers — 2n = (22) 24, 36, (44) 48; mostly unknown from the southern part of its distribution (one count of 2n = c. 44 from Sarawak (*P.C. Boyce s.n.*), from *A. calamus* L. var. *angustifolius* (Schott) Engl. sensu A. Engler).

Vernacular names — Chang pu, Xi gen chang pu, Yuan bian zhong (Chinese), Le-ep (in Enga language in New Guinea).

Etymology — *Acorus calamus*: Calamus (Latin) was used for Reed or Common Reed or Reed Grass (*Phragmites australis* (Cav.) Trin. ex Steud.) and then derived for this species as ‘calamus aromaticus’ for its aromatic odour.

Note — *Acorus calamus* with its three cytotypes, diploid, triploid and tetraploid, in different geographical regions shows great morphological variability and also a wide variation in the chemical composition of the ethereal oils in the rhizome and leaves. The different cytotypes have been considered as separate species or varieties: var. *calamus* (or var. *vulgaris*) for the triploids (2n = 36), var. *americanus* for the diploids (2n = 22, 24) and var. *angustifolius* (2n = 44, 48), the latter well documented from Asia. However, *A. calamus* is considered in this treatment as a variable species and infraspecific taxa are not recognized, because there is overlap in the width of the leaves from 0.8–1.5(–2) cm in Asian collections of different geographical regions, and the length of the spadix is also variable. It is true that most of the Asian plants look somewhat weaker and have narrower leaves, e.g. plants from Borneo (Sarawak) with c. 1 cm wide leaves, but there are also broader ones from Asia and a continuous series of forms exists. Sometimes the leaf margins are more or less undulate. The berries are straw-brown at maturity and never reddish as also reported in literature. The two cytotypes, European and North American (wild plants from Quebec, Canada), are not distinguishable when grown under the same conditions in cultivation, therefore *Acorus americanus* (Raf.) Raf. or *Acorus calamus* L. var. *americanus* Raf. is not accepted as a different taxon. Hand-pol-

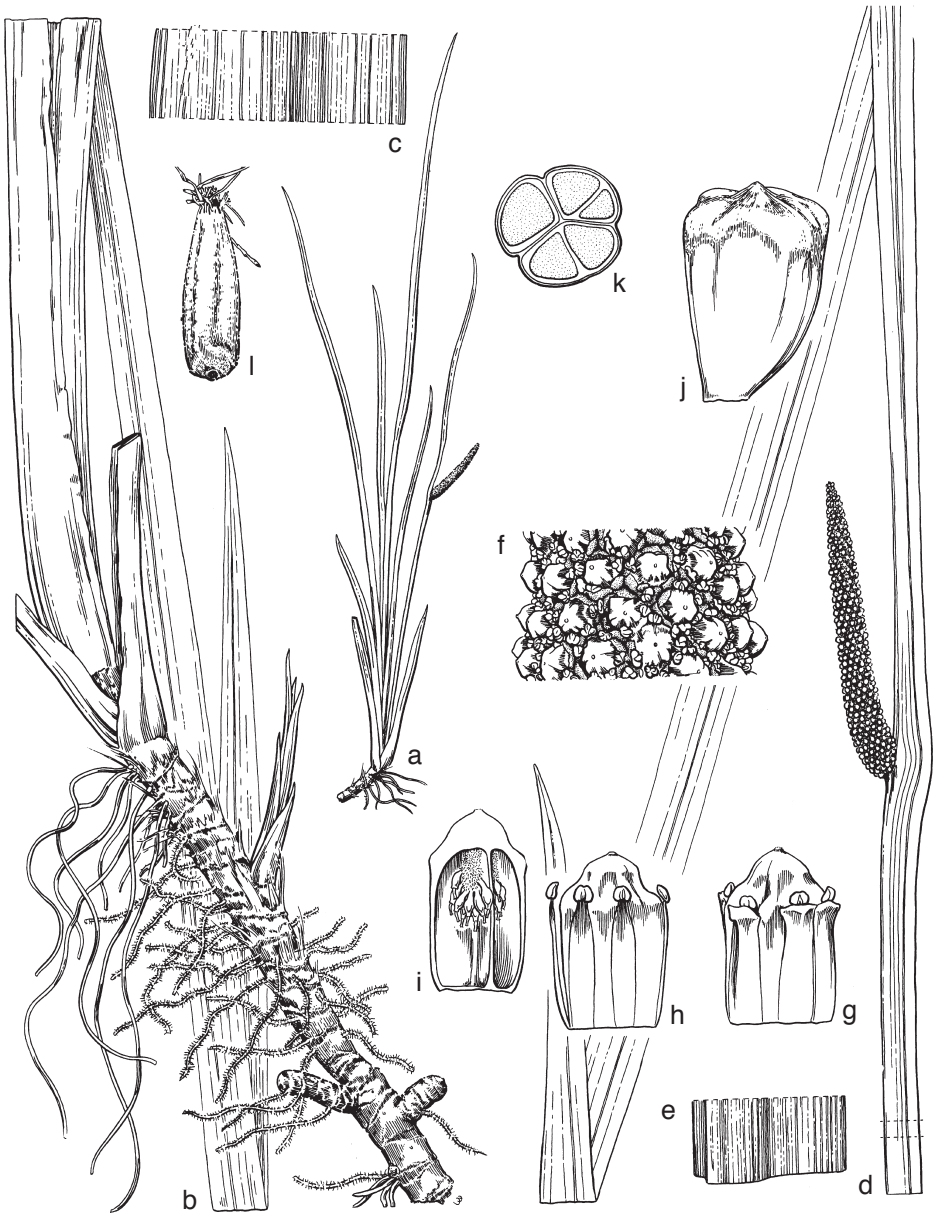

Fig. 2. a–k: *Acorus calamus* L. a. Habit ×0.1; b. base of plant and rhizome ×0.5; c. detail of venation ×2; d. inflorescence ×0.5; e. detail of peduncle ×2; f. detail of spadix ×3; g. flower with perigone, side view ×8; h. flower, perigone removed, side view ×8; i. gynoecium in longitudinal section ×8; j. berry ×8; k. berry in cross section ×8. — l: *Acorus gramineus* Sol. ex Aiton. Immature seed, with bristles ×10 (a: *Birch Wolfe Herb.*; b: *Turrill s.n.*; c, d: *Mitchell 1143*; e–j: *Barnes 1629* [= Kew spirit collection 6913]; k: *Licent 1473*; l: *Anonymous s.n.*, all from K). — Drawing by Eleanor Catherine, reproduced from Mayo, Bogner & Boyce, The Genera of Araceae (1997).

linated inflorescences of the diploid plants set 100 % fruits and seeds, but the flowers are not visited by any insects and without artificial pollination no fruits are produced. Asian tetraploid plants also set fruits in nature, but still no pollinator is known.

2. Acorus gramineus Sol. ex Aiton

Acorus gramineus Sol. ex Aiton, Hort. Kew (1789) 474. — Lectotype (here chosen): *Hort. Kew. 1788* (BM). Introduced by Allan Cooper in 1786.

Rhizome slender, 5–10 cm long, 0.4–0.6(–0.8) cm diam., aromatic. *Leaves* several, ensiform, dark to mid-green, (15–)20–45(–55) by (0.3–)0.5–1(–1.4) cm, apex acuminate, midrib lacking. *Peduncle* compressed-triangular, (4–)9–20(–24) cm long. *Spathe* leaf-like, green, (8–)10–24(–25) by 0.2–0.4(–0.5) cm. *Spadix* straight or slightly curved, narrowly cylindrical to subcylindrical, (3–)4–10(–14) cm long, (0.3–)0.4–0.6(–0.7) cm diam., densely flowered. *Flowers* perigoniate, yellowish, yellow-green to somewhat whitish, 1.8–2 mm diam. seen from above, tepals more or less oblong, keeled, rounded at apex or acute, membranous, 1.5–2 by 0.7–1 mm; filaments oblong, flat, c. 1.5 mm long, anthers 0.4–0.5 mm diam., yellow; pollen grains c. 15 µm long, exine more densely foveolate; gynoecium obconic-cylindric, (2–)2.5–3 mm long, (1.2–)1.8–2 mm diam., with conical, spongy apex and very small stigma. *Infructescence* yellowish to yellow-white at maturity, 1–1.5 cm diam., berries arranged densely, obovoid-globose, few- to several-seeded, 3–3.5 mm long, 2.2–2.5 mm diam.; seed ellipsoid, (2–)2.5–3 mm long, (0.8–)1–1.2 mm diam., with many long (3–4 mm) bristles (longer than seed itself), testa more or less smooth, light brown. — **Fig. 2l; Plate 1.**

Chromosome numbers — 2n = 24.

Distribution — Throughout China, Taiwan, East Siberia (Russia) and from northeast India to Myanmar, Thailand and Indo-China (Vietnam, Laos, Cambodia), Korea, Japan; in *Malesia*: Philippines (Luzon, Province Laguna, San Antonio).

Habitat & Ecology — Dense forests, moist rocky stream banks, meadows. Altitude: up to 2600 m in China; often in crevices between rocks in or along streams (the seed bristles are perhaps an adaption to rheophytic life form). *Acorus gramineus* is a facultative rheophyte (Van Steenis, C.G.G.J., Rheophytes of the World (1981) 163–164). Flowering: February to July; fruiting: July to August.

Etymology — *Acorus gramineus* means ‘grass-like’ (from Latin).

Note — *Acorus gramineus* is a variable species; there is a continuous series of measurements which overlap between different forms. Plants with shorter spadices were described with a leaf width of 7–13 mm and it is even said that the leaves are smaller than 6 mm wide; some collections have quite long spadices. However, there are many collections with spadices of intermediate length. The flowers of these different types can hardly be distinguished. The size of the plants also depends on growing conditions, especially on the available nutrients. If infraspecific taxa are to be distinguished, perhaps as varieties, then it must be emphasized that intermediates always exist. In the horticultural literature several cultivars are recognized, which is a good way to distinguish different forms. There are also variegated cultivars and these are often preferred in gardens. The dwarf form, described as *A. pusillus* or *A. gramineus* var. *pusillus*, is considered as a cultivar, ‘Pusillus’, today and which is known only from cultivation.