



Fig. 1. *Isoetes habbemensis* ALSTON, tufted in marginal shallows of Habbema Lake, c. 3225 m, with *Libocedrus papuana* F. v. M., on ridge in background (Archbold Expeditions, BRASS, 1938).

ISOETACEAE (A. H. G. Alston †, London)

1. ISOETES

LINNÉ, Sp. Pl. (1753) 1100; Gen. Pl. ed. 5 (1754) 486.—Fig. 1.

Herbaceous, perennial, submerged aquatics or marsh plants, usually with annual grass-like leaves arising in a tuft from a lobed, flattened, corm-like stock. *Stock* divided into stem and rhizophore, 2–4-lobed, with black dichotomous roots arising from the furrows between two lobes. *Roots* monarch, with the stele attached to one side of a central cavity, vascular system protostelic, 2–4-lobed at base. *Leaves* distichous, crowded, with overlapping bases, terete or flattened above, with a broad spoon-like base. Blades with a simple trace and median, unbranched vein, accessory peripheral strands often present; mesophyll chambered with four longitudinal cavities divided by transverse diaphragms, which give the leaf a muriform appearance when seen in transmitted light. Stomata present on one or both surfaces in some species and absent in others. Leaf-bases usually membranaceous and hyaline but in some species persistent as hard, brown, 2-lobed, horny structures. Ligule present near the base of the leaf above the sporangium, arising from a cavity called the ligular pit, cordate-triangular or subulate, 2–15 mm long, without chlorophyll or cuticle, secreting mucilage at least when young. All leaves potentially sporophyll with a sporangium seated in a pit (fovea) on the adaxial surface below the ligule. *Megasporophylls* normally arising below the *microsporophylls*; opening of fovea often wholly or partly covered by a membrane (velum) extending downwards from the apex. *Sporangia* large, 4–7 mm long, oblong, thin-walled (walls with 3–4 layers of cells), subdivided irregularly and incompletely by oblique sterile plates (trabeculae); of two kinds, megasporangia and microsporangia, sessile and broadly adnate. Sporangia with both megaspores and microspores have been reported and the megaspores often vary considerably in size. Megasporangium containing 50–300 trilete spores, 250–900 μ in diam., white, grey or black, smooth or with warts, spines, or ridges. Microspores monolete, elliptic, 20–45 μ long, smooth or papillose, 150,000–1,000,000 in each sporangium. Annulus wanting, spores released by the decay of sporangial walls. Some species may be aposporous with young plants taking the place of the developing sporangia. *Gametophytes* dioecious. Female prothallus green, development starting within and the prothallus remaining attached to the wall of the megaspore. Archegonia one or more up to 30, deeply sunken. Rhizoids present, projecting beyond the spore wall. Male gametophyte arising within the microspore, consisting of only a single prothallial cell and an antheridium, with 4 peripheral cells and 4 central cells, each giving rise to a single antherozoid with 15 flagellae.

Distribution. About 75 *spp.*, in all parts of the world except the Pacific Islands (present in Tasmania and New Zealand), but mainly temperate, scarce in Asia, in *Malaysia* 3 *spp.*, one in the hills and two in the high mountains.

Ecology. The Malaysian species are submerged aquatics in hill and mountain lakes or streams. Outside Malaysia tropical species may also occur in temporary pools, rice-fields, and on damp ground at low altitude. The spores are sometimes dispersed by being carried by detached floating sporophylls; also earthworms have been reported as dispersing both megaspores and microspores in their excreta (DUTHIE, Ann. Bot. 43, 1929, 411–412).

Morphology and taxonomy. The most recent comparative survey of the family *Isoetaceae*, regarded as sole family of an order *Isoetales*, is by RAUH & FALK (Sitz. Ber. Heidelb. Ak. Wiss. 1959, 1, 1959, 3–160). Three genera are included: *Isoetes* (worldwide), *Stylietes* (Peru), and *Nathorstiana* (fossil

of lower Cretaceous, Germany). *Stylites*, with its elongate stem and unbranched roots, shows some resemblances to *Nathorstiana*, which has been considered to be a possible link between *Isoetes* and the Triassic fossil *Pleuromeia*. *Isoetes* has a very short stem of complex structure, and is generally regarded as reduced and specialized. The fossil genus *Isoetites*, differing from *Isoetes* in the relative size of megaspores and microspores, in the shape of leaf-tips and in having an unlobed stem, has been most recently discussed by R. W. BROWN (J. Wash. Acad. Sci. 29, 1939, 261-269) who described two species from N. America, ranging from lower Cretaceous to early Tertiary; he considers that a Portuguese fossil from the lower Cretaceous probably belongs to the same genus, though the specimens are imperfect.

There has been no recent monograph of the whole genus *Isoetes*, and estimates of the number of species vary. C. F. REED has published a very full list of names, with bibliography, in Bol. Soc. Brot. 27 (1953) 5-72.

Cytology. MANTON records chromosome numbers as follows for *Isoetes*: *I. hystrix* DURIEU, n = 10; *I. lacustris* L., n = 54-56 (Problems of Cytology and Evolution in the Pteridophyta, 1950, 254-259). RAUH & FALK (l.c.) record 2n = c. 50 for *Stylites gemmifera* W. RAUH.

Uses. Leaves of *I. philippinensis* are said to be eaten.

KEY TO THE SPECIES

- 1. Megaspores smooth on inner surfaces.
- 2. Leaves up to 50 cm. Stock 3-4-lobed. Microspores minutely scabrous . . . 1. *I. philippinensis*
- 2. Leaves up to 14 cm. Stock 2-lobed. Microspores densely spinulose . . . 2. *I. habbemensis*
- 1. Megaspores warted on inner surfaces. Stock 3-4-lobed. Leaves up to 7,5 cm 3. *I. neoguineensis*

1. *Isoetes philippinensis* MERRILL & PERRY, Am. Fern Journ. 30 (1940) 19, fig.

Submerged aquatic. Stock apparently 3-4-lobed. Leaves numerous, elongate, up to 50 cm, slender, rather flaccid, 3 mm broad in the middle, c. 7 mm broad at base, with membranaceous wings. Accessory peripheral strands wanting. Foveae 3-4 cm long, narrow, 1½-2 mm broad, gradually narrowed upwards, with hyaline margins. Velum none. Ligule elongate, ovate-triangular. *Sporangia* oblong, c. 9 by 3 mm, pale. Megaspores above 420 µ in diam. with a prominent triradiate marking, usually smooth on the inner surfaces, sometimes sparingly and minutely rugose; reticulate on the outer surface. Microspores 25-30 by c. 22 µ, very minutely scabrous.

Distr. *Malaysia*: Philippines (Mindanao: Lanao Prov. near Momungan, vicinity of Olangu).

Ecol. Bottom of a stream, 400-500 m, once found.

Vern. *Kabauingbauing*, Lanao.

2. *Isoetes habbemensis* ALSTON, J. Arn. Arb. 26 (1945) 180.—Fig. 1.

Submerged aquatic. Stock apparently 2-lobed, appressed-semiglobose c. 3½ by 1½ cm across, 1 cm high, with numerous short, brownish-black roots 2 mm in diam. arising from the lower surface. Leaves numerous, up to 14 cm, stout, more or less recurved, c. 3 mm broad in the centre, semicircular in transverse section, rounded on the back and flattened above; central vascular strand rather prominent; margins slightly winged. Upper part of the leaves green, apices caducous. Lower part of leaves c. 3 cm long, pale reddish-brown,

up to 1 cm broad and winged at base. Stomata none. Ligule deltoid. Velum none. *Sporangia* obovate-oblong, c. 1 cm by 4 mm, pale brown. Megaspores c. 575 µ in diam., almost smooth, with a prominent triradiate marking, pale greyish-white when dry. Microspores c. 43 µ long, densely spinulose, brown when dry.

Distr. *Malaysia*: West New Guinea (Mt Wilhelmina; Lake Habbema), twice found.

Ecol. Abundant in marginal shallows of Lake Habbema and also on Mt Wilhelmina, 3225-3660 m.

3. *Isoetes neoguineensis* BAKER [ex F. v. M. Ann. Rep. Brit. N. Guinea 1897-8 (1898) 149, *nomen*]; Kew Bull. (1899) 122; SADEBECK in E. & P. Pfl. Fam. 1, 4 (1901) 776; PFEIFFER, Ann. Mo. Bot. Gard. 9(1922) 211.

Submerged aquatic. Stock 3-4-lobed. Leaves numerous, 5-7½ cm by 3 mm, recurved, terete towards the apex, flattened lower down, abruptly dilated at base. Dilated base hyaline, c. 1 cm long and broad. Upper part of leaves dark green. Stomata few. Ligule broadly cordate. Velum none. *Sporangia* oblong, 6 by 4 mm, pale brown. Megaspores c. 800 µ in diam., deeply and irregularly warted and reticulate on the outer face, warted on the inner faces, with a strongly marked triradiate marking.

Distr. *Malaysia*: E. New Guinea (Mts Scratchley and Albert Edward), twice found.

Ecol. Shallows of an alpine lake, 3000-3680 m.

Note. BAKER's statement that the megaspores are smooth between the triradiate ridges is incorrect.