APONOGETONACEAE (H. W. E. van Bruggen, Heemskerk)

1. APONOGETON

LINNÉ *f.* Suppl. (1781) 32; ENGLER & KRAUSE, Pfl. R. Heft 24 (1906); STEEN. Fl. Mal. I, 4 (1948) 11; BRUGGEN, Blumea 18 (1970) 457–486. — **Fig. 1–5.**

Perennial waterplants with a tuberous, elongate or cylindrical and often branched rootstock or rhizome which produces a tuft of leaves and the inflorescences. *Leaves* submerged and/or floating (very seldom emerged), with a mostly distinct midrib and one or more pairs of parallel main nerves, connected by numerous cross-veins. *Inflorescence* long-peduncled, emerging above the water surface, in bud enveloped by a caducous or rarely persistent spathe, composed of 1 (in Mal.) or 2–11 spikes. Flowers (in Mal.) bisexual, spirally arranged, turned towards all directions. *Tepals* 2, mostly persistent, rarely caducous. *Stamens* 6, in 2 whorls. *Ovaries* 3(–4–5), free, sessile, narrowed into the style with a stigmatic ridge on the inner side; ovules 2–8 per carpel. *Fruits* with a mostly distinct, lateral or terminal, often curved beak. *Seeds* without endosperm; testa mostly a single envelope, sometimes, however, split into two envelopes, the inner one, brown and closely fitting the embryo, the outer loose, transparent and reticulately veined; embryo with the plumule fitting in a groove or not, or without plumule (the embryos of all species with a double testa seem to have no plumule).

Distr. About 40 *spp.* described, from Africa (Ethiopia to the Cape), Madagascar, India & Ceylon, through SE. Asia (to *c.* 30° NL) and Malesia to SW., N. and E. Australia (to 34° SL), centering in Africa and Madagascar.

Ecol. In stagnant and running, shallow water, mostly in the lowlands, ascending to *c.* 1000 m; *A. crispus* THUNB. in Ceylon 1000–2300 m, also in Africa and Madagascar some species to *c.* 2500 m.

Phytochem. Very little is known about the chemistry of this highly interesting family. Since no recent chemical investigations were published, the reader is referred to the discussion of *Aponogetonaceae* in HEGNAUER, Chemotax. d. Pfl. 2 (1963) 70–73. — R. HEGNAUER.

Uses. In Malesia none. The starchy tuberous rootstock of most species is edible and seems to be in some areas an important food source in times of famine. The leaves and inflorescences can serve as a vegetable. Many species are in cultivation with aquarists.

KEY TO THE SPECIES

1. Tepals longer than 5 mm, caducous. Ovules 2. Plant stoloniferous. . . . . **1. A. undulatus**
1. Tepals shorter than *c.* 3 mm, persistent. Ovules 4–8. Plant not stoloniferous.
 2. Testa double. Tepals yellow. . . . . **2. A. lakhonensis**
 2. Testa simple.
  3. Cross-veins at a ± 50° angle. Tepals yellow. Filaments only slightly widening towards the base. Fruit with a terminal beak. . . . . **3. A. loriae**
  3. Cross-veins at a ± 70° angle. Tepals white or cream. Filaments strongly widened and applanate. Fruit with a short lateral beak. . . . . **4. A. womersleyi**

1. Aponogeton undulatus ROXB. [Hort. Beng. (1814) 26, *nomen*] Fl. Ind. ed. Carey 2 (1832) 211; ENGLER & KRAUSE, Pfl. R. Heft 24 (1906) 11, *pro nomen, excl. descr.*; BRUGGEN, Blumea 18 (1970) 465, f. 2^8, t. I–II. — *Spathium undulatum* EDGEW. Calc. J. 3 (1843) 534, f. 15. — *Ouvirandra undulata* EDGEW. in Hook. Lond. J. Bot. 3 (1844) 404, f. 18. — *A. microphyllum* ROXB. Fl. Ind. ed. Carey 2 (1832) 211; HOOK. *f.* Fl. Br. Ind. 6 (1894) 565. — *A. stachyosporus* DE WIT, Med. Landb. Hogeschool Wagen. 2 (1958) 96, f. 1–3. — *A. crispus* (*non* THUNB.) HOOK. *f.* Fl. Br. Ind. 6 (1898) 564, *pro parte*; TRIM. Fl. Ceyl. 4 (1898) 372; GAMBLE, Fl. Pres. Madras 3 (1931) 1597. — *A. monostachyon* (*non* L. *f.*) ANDR. Bot. Rep. 6 (1797) t. 406. — **Fig. 1[1], 2.**

Tuber globular, obovoid, or elongate, 6–25 mm ø, smooth. *Submerged leaves* 10–25 by ¾–4¼ cm, alternately transparent or opaque in an irregular pattern; base (narrowly) cuneate or rounded,

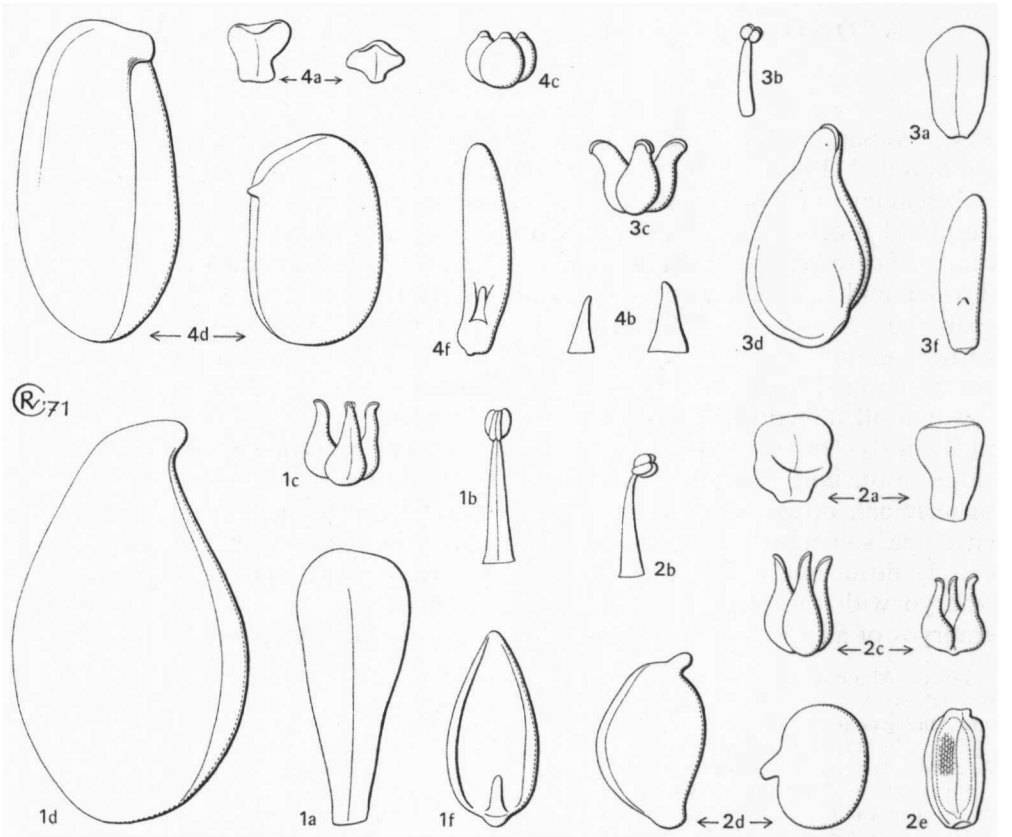

Fig. 1. Floral details of *Aponogeton*. — 1. *A. undulatus* ROXB. — 2. *A. lakhonensis* A. CAMUS. — 3. *A. loriae* MARTELLI. — 4. *A. womersleyi* BRUGGEN.
In all figures *a* = tepal(s), *b* = stamen, *c* = ovaries, *d* = fruit(s), *e* = seed, *f* = embryo. All ×7 (Courtesy Blumea).

apex (narrowly) cuneate or rounded, seldom emarginate, tip blunt; margin undulate, midrib wide with (2–)3(–4) main nerves on either side; petiole 10–35 cm. *Floating leaves* rather rare, up to 20 by 3½ cm; base rounded or cordate, apex cuneate with a blunt tip; main nerves 5 or 7; petiole up to 70 cm. *Peduncle* up to 55 cm, thickening towards the inflorescence. Spathe up to 17 mm, persistent or caducous. Spike up to 10 cm, laxly flowered. *Tepals* (1–)2(–3), caducous, spathulate or obovate, 1(–2–3)-nerved, white or pinkish, (2–)3½–6(–12) by 1–2½(–4) mm. *Filaments* slightly widening towards the base, white or pinkish; anthers light yellow, pollen yellow. *Ovaries* 3(–4), light pink, 1¼–2 by ½–1 mm; ovules 2. Infructescence up to 16 cm. *Fruit* 5–7 by 4 mm with a short, terminal, curved beak. *Seeds* with a simple testa; embryo up to 5 by 2 mm; plumule attached near the base of the embryo and lying in a very wide groove.

Runners resembling peduncles, ascending, up to 35 cm, not or slightly thickened towards the tip. The plantlet is developed at the tip of the runner, in an early stage it is enveloped by a persistent spathe of up to 20 mm. The young plant itself may also put forth one or two short runners, and by repeating this up to 7 plantlets may be produced.

Distr. NW., N. and NE. India, E. Pakistan, Burma, ?Thailand; in *Malesia*: ?Malay Peninsula (Johore: Sg. Sedili at Mawai).

Ecol. Ponds and ditches, 300 m. *Fl.* July–Aug. and Nov.

Notes. There are no specimens which specimens proved to come from Malaya. The only have been I have seen were collected in the Van Cleef Aquarium at Singapore. They are said to have been collected in the Sg. Sedili at Mawai, but I am not convinced that this record is reliable. These specimens have been described as *A. stachyosporus*. Also the occurrence in Thailand has not yet been proved. Yearly many thousands of corms are exported from Bangkok for aquarium purposes. They are claimed to have been collected near Chanthaburi and Haadyai (close by the Ma-

Fig. 2. *Aponogeton undulatus* ROXB. Drawn at Singapore after a living specimen in the Van Kleef Aquarium, said to have been collected originally in the Sg. Sedili, Johore, by ERNEST TOFT, × ½.

layan frontier), but up till now I have not seen herbarium specimens collected in Thailand either.

It is remarkable that *A. undulatus* flowers very seldom in cultivation. I have been cultivating specimens from different localities for more than twelve years, but up till now only once an inflorescence has developed.

It seems that in the eastern part of its range the leaves are more narrow than in the western part; moreover, the eastern populations seem not to tend to develop floating leaves.

2. Aponogeton lakhonensis A. CAMUS, Not. Syst. 1 (1909) 273, f. 18; Fl. Gén. I.-C. 6 (1942) 1226; BRUGGEN, Blumea 18 (1970) 479, f. 2[12], 3a. — *A. pygmaeus* KRAUSE, Bot. Jahrb. 44 (1910) Beibl. 101: 8; A. CAMUS, Fl. Gén. I.-C. 6 (1942) 1227. — *A. luteus* A. CAMUS, Not. Syst. 2 (1911) 204; Fl. Gén. I.-C. 6 (1942) 1227. — *A. monostachyon* (*non* L. *f.*) A. CAMUS, Fl. Gén. I.-C. 6 (1942) 1225; LARSEN, Dansk Bot. Ark. 20, 2 (1962) 134. — *A. loriae* (*non* MARTELLI) STEEN. Fl. Mal. I, 4 (1948) 11, *pro descr.* — **Fig. 1[2], 3.**

Tuber elongate or obovoid, up to 2 cm ø. *Submerged leaves* very variable in shape and size, narrowly oval to linear, up to 25 by 6 cm (*e.g.* 25 by 6 cm, 15 by 0.9 cm); base (very) narrowly cuneate, apex narrowly cuneate with a blunt tip or rounded; main nerves 7 or 9; petiole 7–35 cm. *Floating leaves* (not seen in Mal.) up to 17 by 4 cm, base cordate or (seldom) rounded; apex cuneate with a blunt tip or rounded; main nerves 7 or 9. *Peduncle* only slightly thickening towards the inflorescence. Spathe *c.* 17 mm, caducous, rarely persistent. Spike up to 8 cm, rather laxly, sometimes densely flowered. *Tepals* 2, obovate, 1–2 by ¾–1½ mm, yellow, 1-nerved. *Stamens* 6, 1½–3 mm, filaments widened towards the base. *Ovaries* 3–4(–5), 1–1¾ by ¾–1 mm; ovules 4–8. Infructescence up to 17 cm. *Fruits* up to 3 by 2 mm, with a terminal or lateral beak. *Seeds* 2–3 by 1 mm; testa double; embryo 1¼–2½ by ½ mm; plumule absent.

Fig. 3. *Aponogeton lakhonensis* A. CAMUS. Habit, with submerged leaves (HARMAND *s.n.*), × ½ (Courtesy Blumea).

Distr. SE. Asia (India: Assam, Thailand, Cambodia, Vietnam, China); in *Malesia*: SW. Celebes (Maros; Pangkadjene), two collections.

Ecol. Slow running streams, flooded rice fields and ponds, in Celebes in a stream in limestone country, not frequent but rather abundant locally, 200–800 m. *Fl.* March, May, Sept. and Oct.

Note. The Malesian specimens are very fragmentary with regard to their generative parts, and have only some almost ripe fruits. Therefore, I can not be completely certain that these specimens belong indeed to the continental *A. lakhonensis*. They share with this species the shape of the tepals and the structure of the seed, which has a double testa. This last characteristic distinguishes them from *A. loriae* from Papua, which has a single testa and with which they were confounded before. It is highly desirable to have fresh material from Celebes for further study.

3. Aponogeton loriae MARTELLI, Nuova Giorn. Bot. Ital. 2, 3 (1897) 472, t. 8; ENGLER & KRAUSE, Pfl. R. Heft 24 (1906) 12; RENDLE, J. Bot. (1923) Suppl. 58; STEEN. Fl. Mal. I, 4 (1948) 11, *excl. descr.*; BRUGGEN, Blumea 18 (1970) 473, f. 2[9], 5b. — *A. crispus* (*non* THUNB.) F. v. M. Descr. Not. Pap. Pl. 8 (1886) 51; RIDL. J. Bot. 24 (1886) 359. — *A. monostachyon* (*non* L. *f.*) HEMSL. Kew Bull. (1899) 113. — **Fig. 1[3], 4b, 5.**

Tuber up to 2½ cm ø. *Leaves submerged,* very hard in texture, greenish red, 15–65(–80) by 1–3¾ cm; base narrowly cuneate, apex (narrowly) cuneate with a blunt tip; main nerves 7–9, connected by numerous cross-veins at a 50° angle; margin flat, waved or slightly crisped; petiole 2–15(–30) cm. *Peduncle* up to 60 cm, *c.* 3½ mm ø, not or slightly thickening towards the inflorescence. Spathe up to 22 mm, persistent, seldom caducous; spike up to 12 cm, densely or rather laxly flowered, scentless. *Tepals* 2, obovate, (greenish) yellow, 1–2 by 1–1¾ mm, 1-nerved. *Stamens* 6, 1½–2 mm, filaments not or slightly widened towards the base; filaments, anthers, and pollen yellow. *Ovaries* 3, 1¼–1½ by ¾–1 mm, yellow; ovules 4–8. Infructescence cylindrical, very dense. *Fruits* up to 6 by 3½ mm, with a terminal beak, greenish brown. *Seeds* with a simple testa; embryo 2½–4 by ¾–1 mm, greenish brown; plumule very small, completely covered

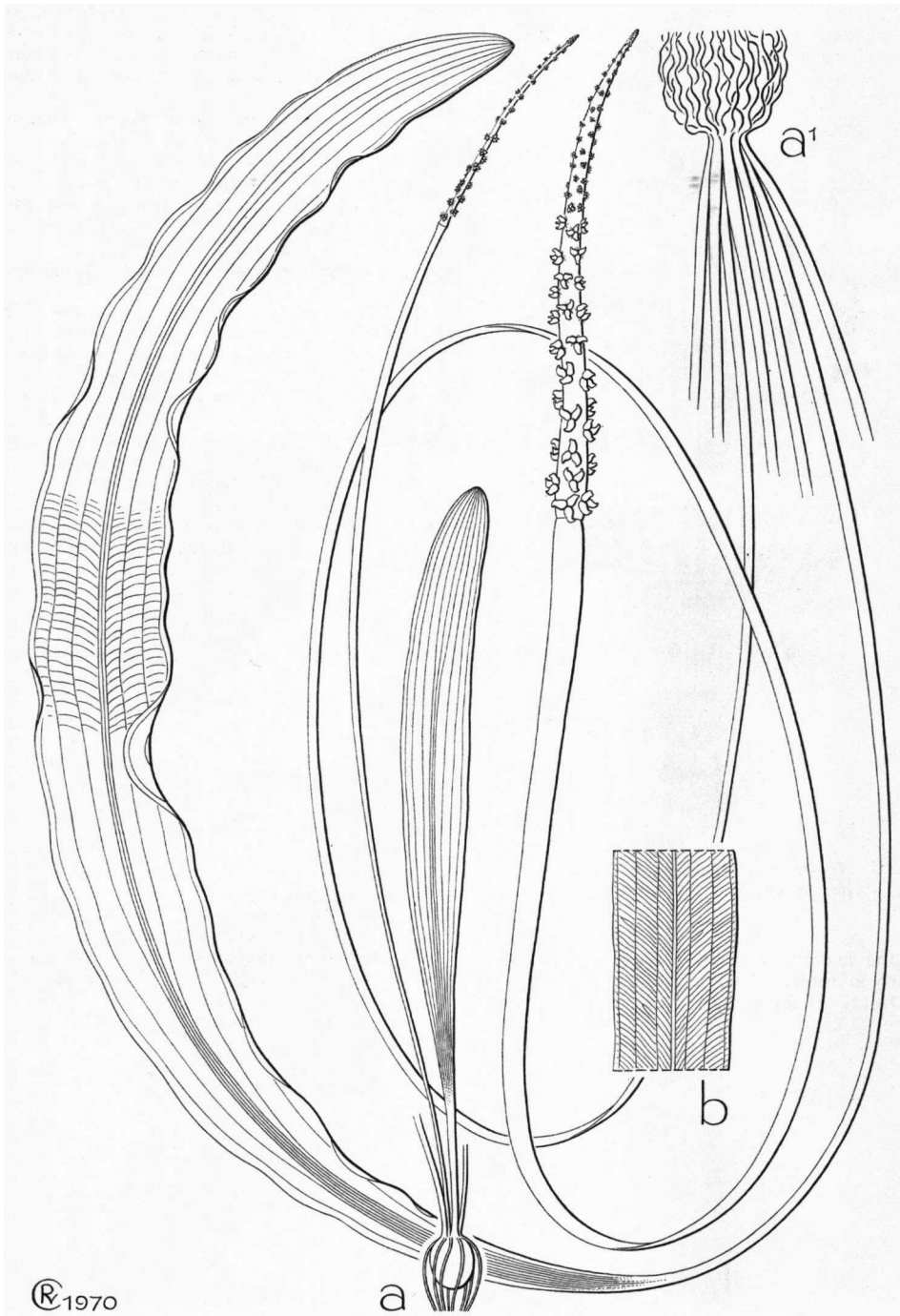

Fig. 4. *Aponogeton womersleyi* BRUGGEN. *a–a'*. Habit. — *A. loriae* MARTELLI. *b*. Fragment of leaf showing venation. All × ½ (*a* BRASS 8671, *a'* NGF 17717, *b* BRASS 5567) (Courtesy Blumea).

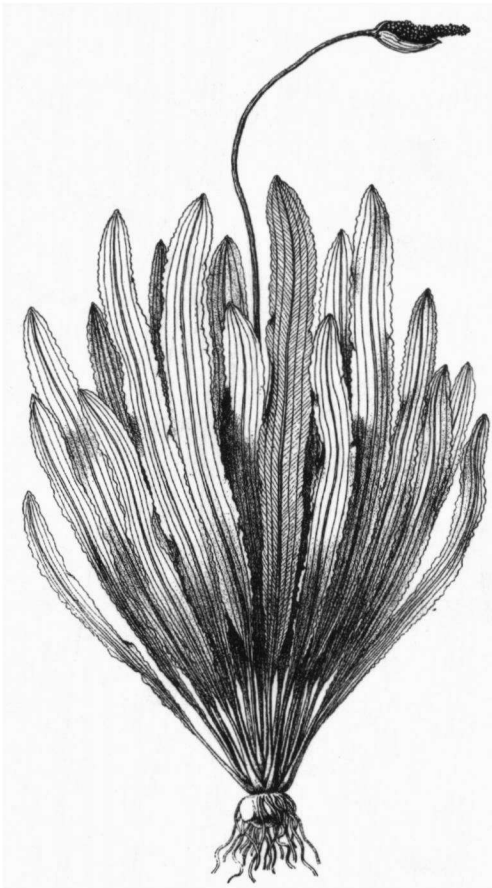

Fig. 5. *Aponogeton loriae* MARTELLI. From the type, after MARTELLI, × *c.* ½.

by the margin of the cotyledon, and therefore nearly invisible.

Distr. *Malesia*: East New Guinea (Papua, Central District: Laloki R., *c.* 3 miles E of Sogeri patrol station, 147°25′ E, 9°30′ S; Sogeri: Sirinumu area, *c.* 3 miles S of Sogeri; Kubuna; Koitaki; Magibiri; affluent of Laragi; stream near Ower's Corner).

Ecol. Common in swiftly flowing, shallow, stony streams, 100–600 m. *Fl.* June–Jan.

Note. The description is partly based on cultivated specimens from Sirinumu, I received thanks to the co-operation of Dr. ROBBINS and Mrs. PULSFORD of the University at Pt. Moresby.

4. Aponogeton womersleyi BRUGGEN, Blumea 18 (1970) 477, f. 2[10] 5a. — **Fig. 1[4], 4a.**

Tuber up to 2½ cm ø. *Leaves submerged*, 20–50 by 1½–3½ cm; base very narrowly cuneate, apex narrowly cuneate with a blunt tip; main nerves 7 or 9, connected by numerous cross-veins at a ± 70° angle; margin flat or waved; petiole 5–35 cm. *Peduncle* up to 1½ m, strongly thickened towards the inflorescence. Spathe unknown, caducous. Spike up to 15 cm, very laxly flowered. Flowers very small. *Tepals* 2, white to cream, broadly obovate or wedge-shaped, ¾–1 by 1–1¼ mm, 1-nerved. *Stamens* 6, ¾–1¼ mm, filaments strongly widened towards the base and applanate. *Ovaries* 3, up to 1 by ¾ mm, ovules 4–6. Infructescence very dense. *Fruits* greenish brown, 7–8 by 2–3 mm, laterally beaked. *Seeds* with a simple testa; embryo 4–5 by ½ mm; plumule *c.* ½ mm, attached at ± 1/6 of the length of the embryo and partly covered by the margins of the cotyledon.

Distr. *Malesia*: East New Guinea (Papua, Western District: Oriomo R., mouth of Yakup Creek, *c.* 64 km from sea, 143° E, 8°50′ S; Penzara, between Morehead and Wassi Kussa R.), 2 collections.

Ecol. Usually rooting on muddy bottoms in the shallower parts of lowland rivers in savannah forests. *Fl. fr.* Sept. and Dec.

Vern. *Zo-inge*, Penzara.

Note. *A. womersleyi* is clearly different from *A. loriae* from the Central District and even in a sterile state they cannot be confused, as its cross-veins are at a 70° angle (in *A. loriae* at a ± 50° angle).