

A REVISION OF THE INDIAN APONOGETONACEAE

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A B S T R A C T

Unigeneric family Aponogetonaceae, represented by about 44 species of *Aponogeton* L. f. is distributed in tropics and subtropics of the Old World. The genus *Aponogeton* is represented by 7 species in India. Detailed taxonomic account including synonymy, morphology, phenology, distribution, ecology, taxonomic note if any, chromosome number and key to the Indian species of *Aponogeton* is presented in this paper.

I N T R O D U C T I O N

The genus *Aponogeton* was first erected by Linnaeus fil. in 1781. After the erection of the genus *Aponogeton* L. f., Mirbel (1802) created the new genus *Uvirandra* with a species *U. madagascariensis* Mirbel mainly characterized by the fenestrate leaves. Edgeworth (1848) maintained both the genera viz. *Aponogeton* characterized by the persistent tepals and the inconspicuous plumule and the genus *Ouvirandra* by the caducous tepals and the large two leaved plumule. However, some of the species of the genus show persistent tepals and large well developed plumule while few others have caducous tepals with inconspicuous plumule. Therefore, *Ouvirandra* does not stand as a separate genus. Thus, the family Aponogetonaceae is represented by a genus *Aponogeton* with 43 species mainly confined to the Old World namely Africa (17), Madagascar (11), Asia inclusive of New Guinea (11) and Australia (4) (Bruggen, 1985). During last decade, one new species *A. bruggenii* Yadav & Govekar from India has been added to the list. Most of the species have restricted distribution. All species of *Aponogeton* seem to be endemics and do not occur outside their continent or sometimes

even Island (Sculthrope, 1967; Bruggen, 1985).

The Aponogetonaceae received the attention of several workers (Planchon, 1844; Edgeworth, 1848; Teighem, 1870-71; Duval-Jouive, 1873; Teighem and Dauliot, 1888; Costanin, 1886; Engler, 1887 & 1889; Dutailly, 1875; Minden, 1899; Gibson, 1905; Krause & Engler, 1906; Chrysler, 1907; Sergueeff, 1907; Lagerthem, 1913; Reide, 1921; Afzelius, 1920; Arber, 1921 & 1922; Verdoon, 1922; Camus, 1923; Gluck, 1924; Czaja, 1930; Saunders, 1929; Solereder and Meyer, 1933; Eber, 1934; Drawert, 1938; Sane, 1940; Uhl, 1947; Hutchinson, 1959; Singh, 1965; Obermeyer, 1966; Shah, 1972; Zhilin, 1974; Yamashita, 1976; Lye, 1986 and Pneva, 1988), however, the major works on the taxonomy of the Aponogetonaceae are that of Bruggen (1968, 1969, 1970, 1973, 1982, 1985, 1987 & 1990), who has made significant contributions to the understanding of Aponogetonaceae.

Important literature on anatomy of Aponogetonaceae include that of Teighem (1870-71), Dutailly (1875), Duval-Jouive (1873), Teighem and Dauliot (1888), Minden (1899), Sergueeff (1907), Meyer (1915), Reide (1921), Afzelius (1920), Arber (1921 & 22), Gluck (1924), Czaja (1930), Solereder & Meyer (1933), Drawert (1938), Kaul (1976), Paliwal (1976), Singh (1965), Singh and Sattler (1977), Tomlinson (1982) and Mujawar (1992). Based on older literature and own original observations, Tomlinson (1982) has summarized anatomical features of Aponogetonaceae. On the basis of anatomical evidence combined with information from embryology, shoot construction, and floral morphology, Tomlinson (1982) concluded that *Aponogeton* clearly belongs to the Helobiae, and can best be placed between the group of Alismataceae, Butamaceae and Hydrocharitaceae on the one hand and the Scheuchzeriaceae, Juncaginaceae and Liliaceae group on the other.

Although several botanists have studied embryology of Aponogetonaceae (Wettstein, 1906; Sergueeff, 1907; Palm, 1915; Suessenguth, 1919; Tisechler, 1915; Afzelius, 1920; Riede, 1921; Netolitzky, 1926; Clausen, 1927; Sane, 1940; Davis, 1966; Shah, 1970 & 72; Yamashita, 1976; Mujawar, 1992 and Gaikwad, 2000), our present knowledge regarding the embryology and seed structure of the family is still far from

complete (Bouman, 1985). The most reliable reviews of the literature have been given by Krause and Engler (1906) on the life history in general, by Netolitzky (1926) on the seed coat structure and by Davis (1966) on the embryology. The principal embryological features and anatomical seed characters are summarized by Bouman (1985), which fit very well in with those of the Alismatiflorae (sensu Dahlgren & Clifford, 1982).

Extensive light microscopic studies on pollen grains of Aponogetonaceae were carried out by Thanikaimoni (1972, 1973, 1976, 1980). Scanning and transmission electron microscopic studies on pollen grains (Meyer, 1966; Thanikaimoni, 1985; Mujawar, 1992) revealed that the pollen grains are monosulcate, foveolate with tectate and collumellate pollen wall.

Although number of workers have studied cytology of Aponogetonaceae (Sergueeff, 1907; Suessenguth 1919; Harada, 1956; Sharma and Chatterjee, 1967; Misra, 1972; Davidse, 1981; Raven, 1975 and Ghosh and Bhattacharya, 1980), somatic chromosome number is known for only few species viz. *A. distachyos* $2n = 16$ (Sergueeff, 1907); $2n = 24$ (Harada, 1956); $2n = 32$ (Suessenguth 1919); *A. crispus* $2n = 24$ (Davidse, 1981); $2n = 26, 52$ (Ghosh and Bhattacharya, 1980); *A. natans* $2n = 78, 92$ (Misra 1972); *A. distachus* $2n = 38, 68$; *A. crispus* $2n = 114$ [Liebenberg in Obermeyer (1965); *A. natans* $2n = 70, 2n = 78, 2n = 92$; *A. satarensis* $2n = 26$ (Yadav & al., 1989), $2n = 16$ (Sundararaghavan, 1996) and *A. appendiculatus* $2n = 30$ and *A. undulatus* $2n = 70$ (Gaikwad & al., 1998)]. Based on previous observations on cytology of the Aponogetonaceae, Bruggen (1985) concluded that the interspecific polyploidy in some cases in combination with aneuploidy is a common feature in the members of the family. Small size and high number of chromosomes in some species suggest advanced degree of development. Similarly, closely graded size of the chromosomes in the species of *Aponogeton* suggest the symmetrical nature of the karyotype.

Chemical works on the members of Aponogetonaceae were summarized by Hegnauer in 1963. Some additional phytochemical analysis has been done by Bate and Smith (1968) and Harris and Hartely (1980), however, the family is still poorly known chemically and the available data is of little taxonomic value.

There is no doubt about close affinities of Aponogetonaceae with the families of Alismatidae (Helobiae). Apocarpy and monosulcate pollen grains are indicative of its primitiveness among monocots. It is one of the most primitive families of monocots. According to Cronquist (1981) Aponogetonaceae represent a line of reduction from Alismatales characterized by a progressive adaptation to aquatic habit.

Engler treated the family Aponogetonaceae under order Helobiae. Hutchinson (1973) placed Aponogetonaceae and Zosteraceae under Aponogetonales. Takhtajan (1966) and Cronquist (1968) included Aponogetonaceae under Najadales, Thorne (1968) under Zosterales and Dahlgren (1975) under Alismatales. Thus, although the affinities of families of Aponogetonaceae are well established with families of Alismatidae, its position among Alismataceous taxa is uncertain obviously because of great reduction and progressive adaptation to aquatic habit.

Aponogeton is represented by 7 species in India of which *A. appendiculatus* Bruggen, *A. bruggenii* Yadav & Govekar and *A. satarensis* Raghavan & al. are endemic to the country (Ahmedullah and Nayar, 1986; Nayar and Sastry, 1987; Yadav and Govekar, 1994; Nayar, 1996 and Sundararaghavan, 1996). Other species, viz., *A. crispus* Thunb., *A. natans* (L.) Engl. & Krause and *A. undulatus* Roxb., are widely distributed in tropical and subtropical parts of the country. *Aponogeton lakhonensis* A. Camus is reported from the eastern part of the country i.e. Assam, Meghalaya and Nagaland. Some exotic species viz. *A. distachyos* L. f. and *A. abyssinicus* Hochst ex A. Rich. are cultivated in aquaria. Apomictic female plants of *A. decaryi* Jumelle from Madagascar have been maintained in the botanical garden of the Shivaji University, Kolhapur since 1993. Except for *A. lakhonensis*, all other Indian species of the genus were collected, and maintained in botanical garden of the University. The present paper is an outcome of extensive fieldwork and constant observations on living plants of *Aponogeton* for last two decades. The available species were thoroughly studied to understand their morphology, anatomy, cytology, relationship and utilization in aquaria.

APONOGETONACEAE

J. Agardh, Theor. Syst. Pl. Phan. 44. 1858 (Aponogetonaceae), *nom. cons.*

Type : Aponogeton L. f.

Perennial aquatic plants with a tuberous, elongate or cylindric, often branched rootstock or rhizome; roots fibrous from top of tuber. Leaves submerged and / or floating (very rarely emergent), with distinct petiole, sheathing at base; lamina oblong - elliptic, lanceolate, linear, margins undulate, midrib distinct with one to more pairs of parallel nerves, connected by transverse cross veins. Inflorescence spike, on long peduncled scape, solitary or 2-10 spikes, enclosed in a caducous or persistent spathe when young, simple or forked, much elongating in fruits. Flowers sessile, more or less spirally arranged along rachis and turned towards all directions or secund, hypogynous, bisexual or if unisexual then plants dioecious. Tepals (1) 2 (6), absent in female flowers of dioecious species, mostly persistent, sometimes caducous, 1-3 veined. Stamens 6 in two whorls or more, absent in female plants of dioecious species and in apomictic specimens, free, persistent; filaments unequal, filiform or subulate, persistent; anthers didymous, extrorse, 2-loculed, basifixed; pollen grains subglobose or ellipsoid, monosulcate; pollination entomophilous. Carpels 3, 4 or (rarely) 5, superior, free, sessile, one loculed; ovules 1-8 per carpel, basal, anatropous; style short; stigma discoid or decurrent with stigmatic ridge on ventral suture, persistent. Follicles distinct with lateral or terminal curved beak. Seeds without endosperm, testa single or double, if double outer one loose, transparent, reticulately veined, inner one brown and closely fitting the embryo; embryo with a single terminal cotyledon.

Monotypic. The genus *Aponogeton L. f.*, is confined to the tropics and subtropics of the Old World.

APONOGETON L. f.

Suppl. Pl. 214. 1781; Planch. in Ann. Sci. Nat. Bot. Ser. 3, 1: 107. 1844; Edgew. in London J. Bot. 3: 402. 1844; Hook. f. in Benth. & Hook. f., Gen. Pl. 3: 1013. 1883; Engl. in Bot. Jahrb. Syst. 8: 261. 1887; Engl. & Prantl. in Nat. pflanzenfam. 2, 1: 218. 1889; Engl. & Krause in Engl. Pflanzenr. 24 (IV, 13). 1906; A. Camus, in Bull. Soc. Bot. France 16: 670. 1923. Type : *Aponogeton natans* (L.) Engl. & Krause. *Amogeton*

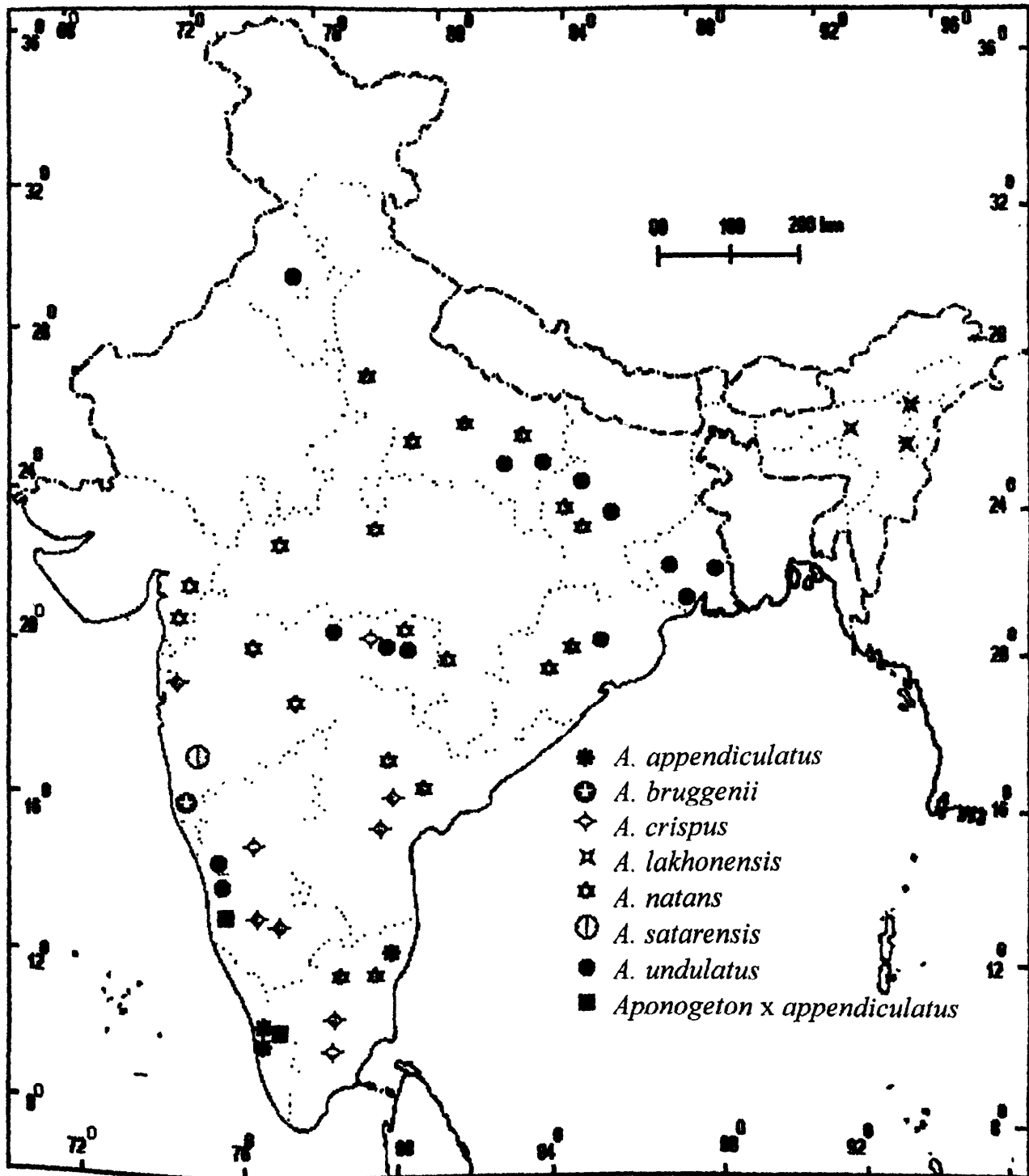
Necker, Elem. Bot. 3: 276.1790, *nom inval.*, also a new name of *Aponogeton* L. f. *Uvirandra* Mirbel, Hist. Nat. Pl. 4: 117. 1803 = part 41 of Buffon, Hist. Nat., ed. Sonnini ('*Urirandra*'). - Type : *Urirandra madagascarensis* Mirbel. *Spathium sensu* Edgew. J. Asiat. Soc. Bengal 11: 145. 1842; Calcutta J. Nat. Hist. 3: 533. 1843 (*non* Lour.).

The generic characters are the same as that of the family.

Distrib. : Species 44, distributed in Africa (17), Madagascar (11), Asia inclusive of New Guinea (12) and Australia (4 species). Seven species in India (Map-I).

KEY TO THE SPECIES

- | | |
|--|------------------------------------|
| 1a. Plants producing propagules (young plants
being developed on inflorescence-like axis) ... | 2 |
| 1b. Plants not producing propagules ... | 3 |
| 2a. Tepals 3 - 6 mm long, caducous ... | A. undulatus |
| 2b. Tepals 1 - 2 mm long, persistent | Aponogeton x appendiculatus |
| 3a. Dioecious; inflorescence a forked spike | A. satarensis |
| 3b. Monoecious; inflorescence a simple spike ... | 4 |
| 4a. Flowers yellow ... | A. lakhonensis |
| 4b. Flowers pink, white or lilac ... | 5 |
| 5a. Ovules more than 2 (4 - 8) per carpel;
seeds with double testa ... | A. natans |
| 5b. Ovules 2 (rarely 1) per carpel; seeds
with single testa ... | 6 |
| 6a. Leaves submerged, embryo with 4 - 6,
linear, subulate, tortuous appendages ... | A. appendiculatus |



Map - I : Distribution of APONOGETON species in India.

- 6b. Leaves emergent or both submerged as well as floating, embryo without tortuous appendages ... 7
- 7a. Leaves erect and emergent; embryo 3 times as long as wide, pointed at one end; plumule small, not lying in a groove ... **A. bruggenii**
- 7b. Leaves floating as well as submerged; embryo at the max 2 times as long as wide, not pointed; plumule large, lying in a groove ... **A. crispus**

1. *Aponogeton appendiculatus* H. Bruggen in Blumea 16: 265, f. 5. 1968; 18: 461, f. 2: 1970; in Biblioth. Bot. 45. 1985 & in Aqua Planta. 2: 20. 1990; S. Karthikeyan & al. Fl. Ind. Enum. Monocot. sr. 4. 4. 1989; C. D. K. Cook, Aquat. Wetl. Pl. India 47. 1996; Sundararagh. in Hajra & Sanjappa, Fasc. Fl. India 22: 126. 1996. Type : *Lawson* 113 (K, holo, isotype CAL, K). (Plate - I & Fig.1)

Monoecious, tuberiferous, perennial, submerged, aquatic herb, c. 90 cm in height; rootstock tuberous; tubers c. 4 × 2 cm, elongate, often narrow below; roots slender, fibrous, from top of tuber. Leaves submerged, petiolate; petioles up to 30 cm long, sheathing at base; lamina c. 55 × 4.2 cm, flat or slightly undulate, narrowly tapering at base and apex, obtuse or acute; main nerve prominent with 6 parallel nerves on either side. Spathe 1.5-6 cm long, attenuate, membranous, caducous, enclosing inflorescence when young. Peduncles c. 65 cm long, thickened above, cylindric; spike c. 25 cm long, simple, sturdy, densely flowered with flowers arranged in all directions. Tepals 2, persistent, c. 2.4 × 2.5 mm, obovate, obtuse, concave, 1-nerved, often wider than long, white-lilac. Stamens 6, included; filaments c. 1.5 mm long, narrow above, yellow; anther 2-celled, pale yellow; pollen yellow, c. 18.30 µm in diam. Carpels 3, c. 1.4 mm long; stigma decurrent; ovary c. 0.7 × 0.7 mm; ovules 1-2 per carpel. Follicles 0.9-1.3 × 0.5-0.9 cm, beaked, often spiculate; seeds 0.8 × 0.3 cm, tapering at both ends; embryo obovate, tuberous, crowned with 4-6 linear tortuous appendages, up to 5 mm long, obtuse or subacute.

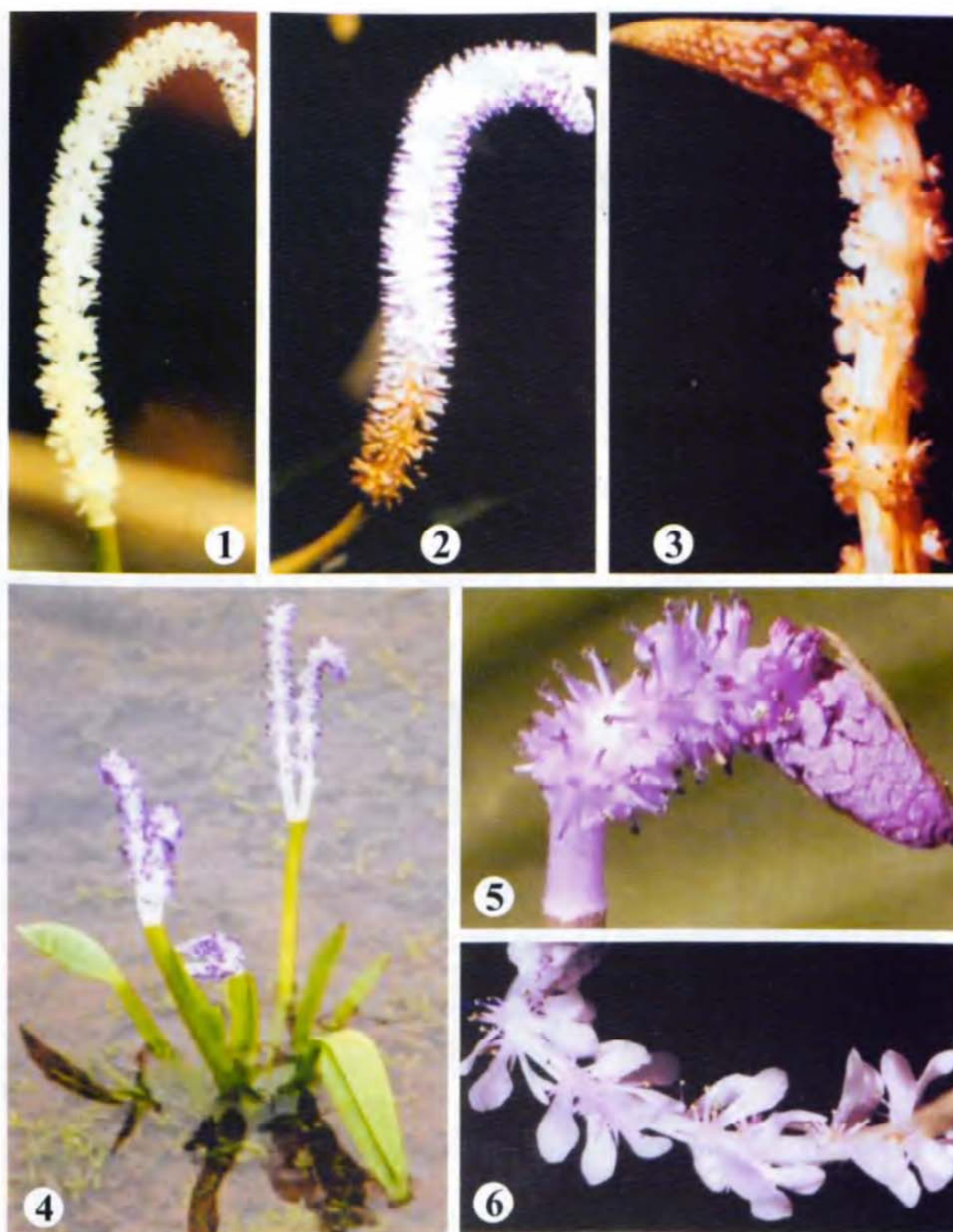


Plate 1.(1-6) : 1. *Aponogeton crispus*; 2. *A. natans*; 3. *A. appendiculatus*;
4. *A. satorensis*; 5. *A. bruggenii*; 6. *A. undulatus*

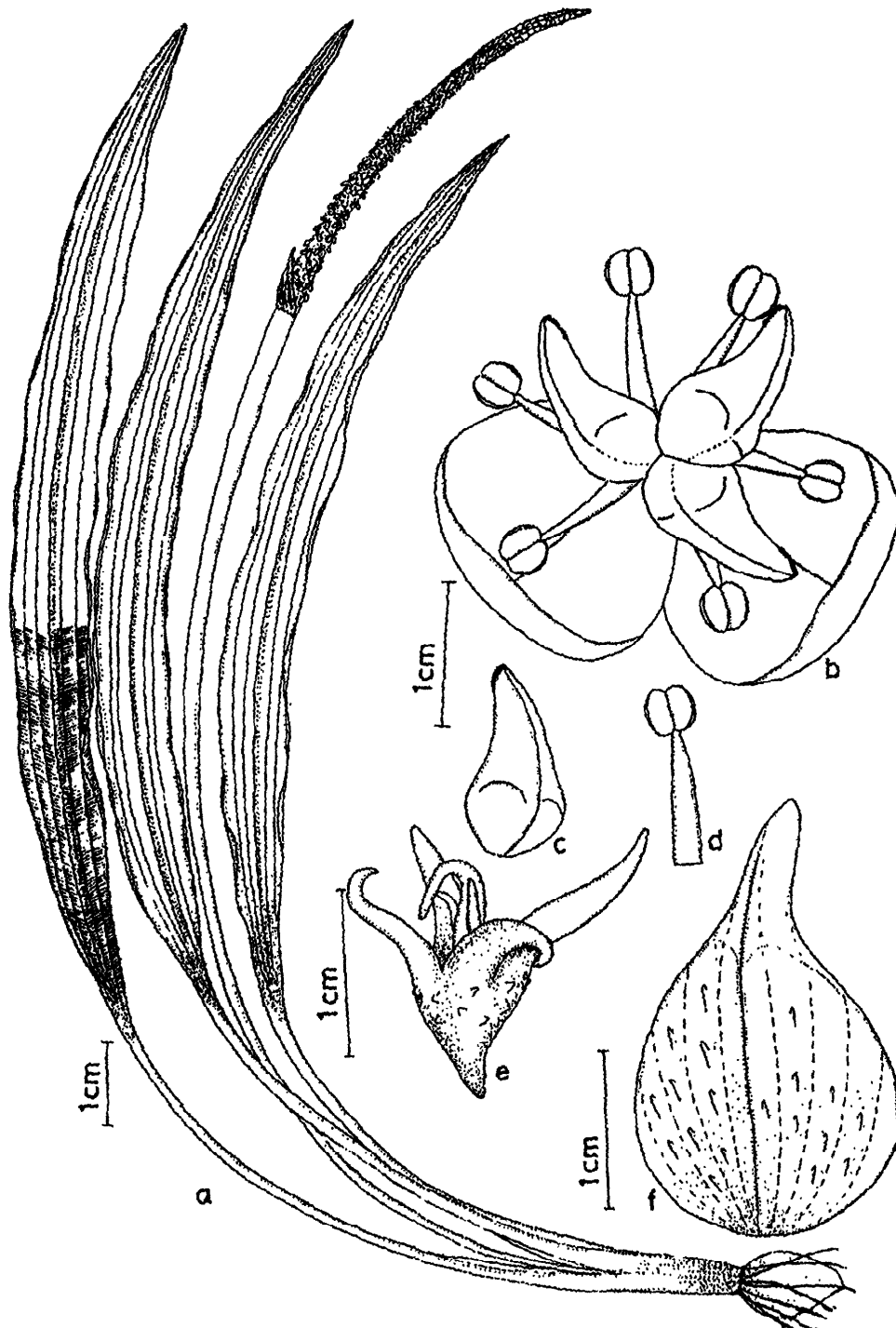


Fig.1. *Aponogeton appendiculatus* Bruggen ($2n = 30$)
 a. Plant, b. Flower, c. Carpel, d. Stamen, e. Seed, f. Fruitlet.

Fl. & Fr.: July - October.

Distrib. : Reported from peninsular India, viz. Alleppy; Vembanad lake between Cochin and Alleppy; Spure tank Egmore (Madras) and Chorla ghat in Goa State (Bruggen, 1985). During the present work, it was collected in North Paravoor on way to Alwaya in Trichur district, Kerala [10° 32' N/76° 140'E].

Ecology : Grows in brackish and or backwaters of the depth of 1-1.5 m in streams in vicinity of sea.

Note : Among Indian species, it is distinct from the rest in its brackish water habitat, submerged leaves and seeds with 4-6 linear tortuous appendages.

Chromosome number : $2n = 30$ (Gaikwad & al. 1998).

Specimens examined : Kerala: North Paravoor on way to Alwaya in Trichur dist., 04.09.1997, Gaikwad 5126 (SUK).

During the present survey of the west coast, populations of *Aponogeton* species were observed at Pudbudri in Karnataka and Khodungullor in Kerala showing many flower abnormalities and sexual sterility. These populations showed combination of characters of *A. appendiculatus* and *A. undulatus*. They are probably the result of hybridization of these two species. (Gaikwad & al., 1998).

2. *Aponogeton* x *appendiculatus*

2.1. Population from Pudbudri, Udupi Taluka, S. Kanara district, Karnataka. (Fig. 2)

Tuberiferous, perennial, robust, submerged aquatic herbs, up to 2 m high. Tubers globose to elongate, c. $2-3 \times 2$ cm; roots fibrous, slender, from top of tubers. Leaves submerged, up to 150 cm long, petiolate; petioles up to 1 m long, sheathing at base; lamina lanceolate, c. 50×6.5 cm, 5-7 nerved, rounded at apex, undulate with opaque areas between veins. Spathe c. 5 cm long, persistent or semipersistent, membranous, acuminate, enclosing inflorescence when young. Inflorescence up to 2.2 m long;

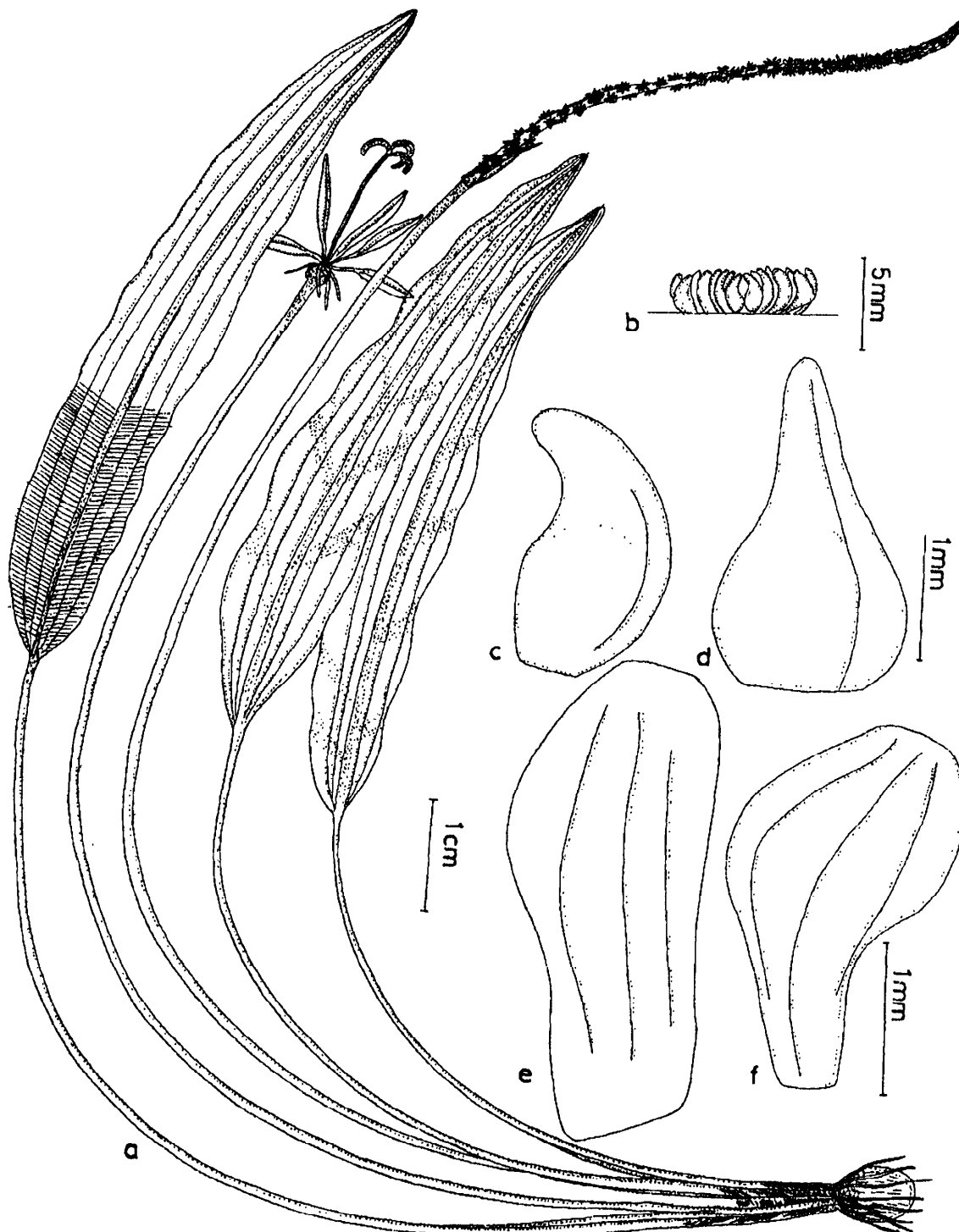


Fig.2. *Aponogeton* hybrid [*A. appendiculatus* x *A. undulatus* ($2n = 84$)]
a. Plant, b. Flower unit, c & d. Carpels, e & f. Stamens modified into tepal like structures.

peduncles c. 1.8 m long, cylindrical, thickened above; spike simple, densely flowered, 10 cm long, flowers arranged in all directions, old spike elongate at maturity, 45 cm long, turning green with age. Tepals 2, obovate, 2-3 mm long, additional tepals 6-many (20), spathulate, 3-nerved, liliac, persistent. Stamens absent (probably modified into tepal like structures ?). Carpel 3-many; ovules 2, basal, abortive.

Fl.: September - October.

Distrib. : Stream bed in vicinity of sea at Pudbudri (13°, 23' N / 74°.40') near Udupi in S. Kanara district of Karnataka.

Ecology : The stream possesses luxuriant growth of hybrid population. The water depth of the stream ranged between 1-2.5 m in September. The plants grow in slow moving water of the stream. The stream moves through the paddy fields in vicinity of sea. *Cryptocoryne crispatula* and *Nymphoides parviflorum* were mainly found to be associated with the population.

Note : The plants are robust and produce only submerged leaves. Though the plants produce many inflorescences, the carpels fail to develop. The plants reproduce by vegetative means through formation of young plants on the inflorescence like-axis as seen in *A. undulatus*. Additional tepal-like structures in the flower probably represent modified stamens and carpels. With age, the inflorescence elongates enormously, floral parts of the inflorescence turn green and finally decay.

The hybrid nature of the population is evidenced by morphological characters. It is like *A. undulatus* in possessing opaque areas in an irregular pattern between the veins in submerged leaves and formation of plantlets at the tip of inflorescence-like axis for vegetative propagation. It resembles with *A. appendiculatus* in its habitat preference, geographical distribution, submerged leaves, inflorescence and flower characters. Thus, among the Indian species, population shares characters with *A. appendiculatus* and *A. undulatus*.

Chr. No.: $2n = 84$ (Gaikwad & al., 1998).

Specimens examined : Karnataka: Pudbudri near Udupi in S. Kanara dist., 07.09.1997, Gaikwad 5324 (SUK).

2.2. Population from Khodungullor in Eranakulam district of Kerala. (Fig. 3)

Tuberiferous, perennial, submerged aquatic herbs. Rootstock tuberous; tubers 0.5-2.5 × 0.5-1.6 cm, globular, often pink-brown in colour; roots fibrous, slender, from the top of the tuber. Leaves submerged, petiolate; petiole up to 65 cm long, sheathing at base; lamina c. 22 × 4.6 cm, lanceolate, obtuse, narrow at apex, rounded at base, margin flat or slightly undulate, main vein prominent with 6 parallel nerves on the either side. Spathe up to 3.5 cm long, membranous, acuminate, semipersistent. Inflorescence up to 80 cm long; peduncles c. 65 cm long, cylindric, thickened above. Spike simple, up to 22 cm long, densely flowered, flowers arranged in all direction, white-lilac, turning green with maturity. Tepals 2, 3-3.5 × 2-2.3 mm, obovate, spathulate, obtuse, 1-nerved, persistent. Stamens 6, exserted; filaments 1-3 mm long, narrow above, yellow; anthers 2 - celled, dehiscence longitudinal, pale yellow; pollen yellow, 14.6 - 32 × 10.95 - 36.5 µm. Carpels 3, c. 1.4 mm long; stigma decurrent; ovary 1 × 1 mm; ovules 2, basal, abortive.

Fl. : July - September.

Distrib. : Khodungullor [10° 32' N/ 76° 140' E] in Ernakulam district of Kerala, in roadside canal.

Ecology : It grows in stagnant, 0.5-1 m deep water in canal with *Ottelia olismoides*.

Note : Though the plants of the population produce normal flowers, the carpels fail to develop. Similarly, the pollen grains showed great sterility (70-80 %). Plants of this population also have adopted vegetative means of propagation as in *A. undulatus*.

Plants of this hybrid population can be easily confused with *A. crispus* due to superficial similarities in flower structure but they can be easily distinguished by the presence of propagules on inflorescence-like axis for vegetative propagation which is absent in later species.

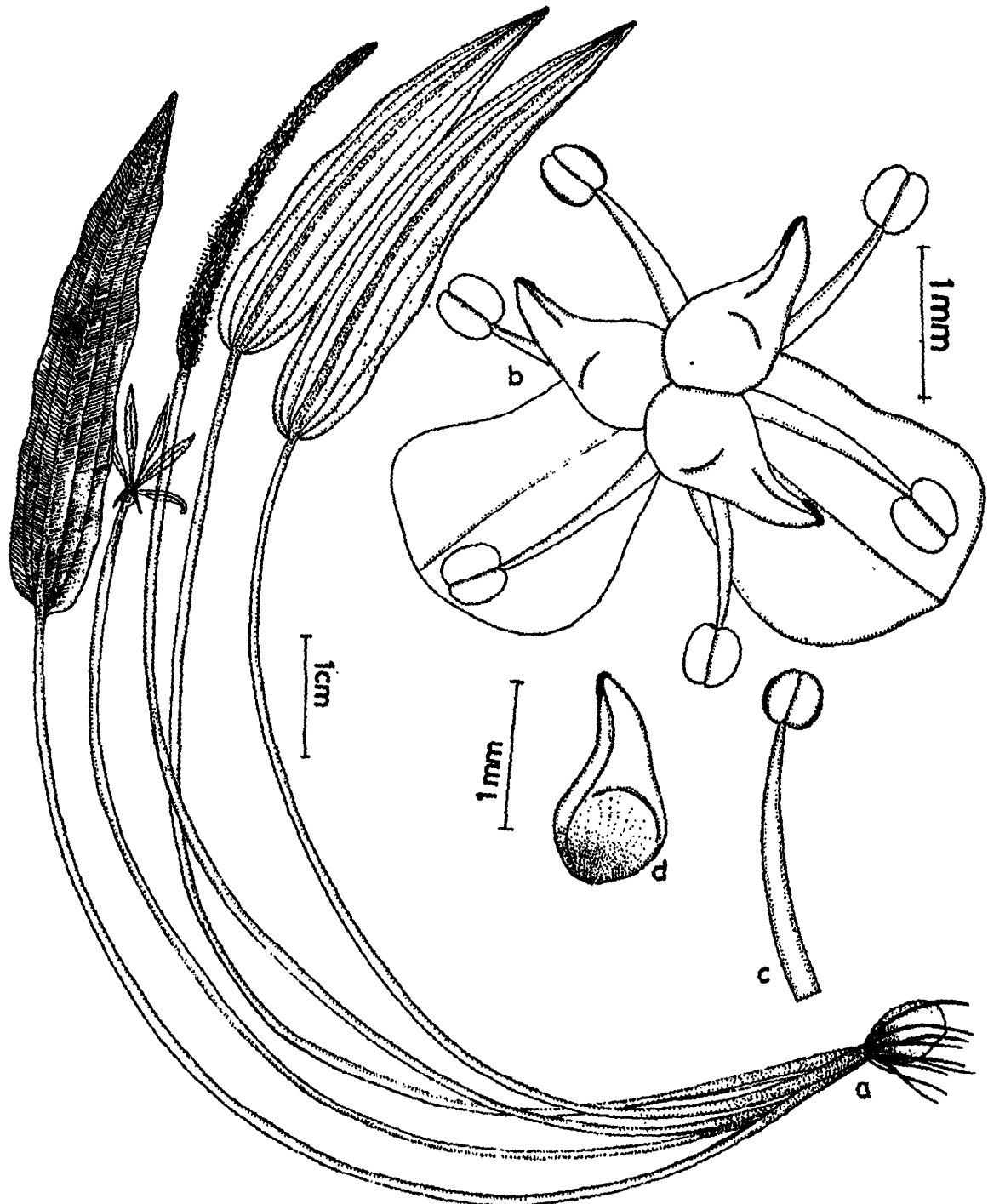


Fig.3. *Aponogeton* hybrid [*A. appendiculatus* x *A. undulatus* ($2n = 74$)]
a. Plant, b. Flower, c. Stamen, d. Carpels.

Chr. No.: $2n = 74$ (Gaikwad & al., 1998).

Specimens examined : Kerala: Khodungullor in Eranakulam dist., 04.09.1997. Gaikwad 5131 (SUK).

- 3. *Aponogeton bruggenii*** Yadav & Govekar in *Rheedea* 4: 34. 1994; Yadav, *Aqua Planta* 1: 3. 1995; C. D. K. Cook, *Aquat. Wetl. Fl. India*: 47. 1996; Lakshmin. in B. D. Sharma & al. *Fl. Maharashtra* 1: 237. 1998. Type : India, Maharashtra, Sindhudurg dist. Nerurpar about 9 km west to Kudal, 10.09.1992, Yadav 1 (holo! CAL, iso! BSI). (Plate - I & Fig. 4)

Monoecious, tuberiferous, perennial, semiaquatic herbs, 10-30 cm high. Tubers globose to elongate, 2-3 cm across; roots slender, fibrous, from top of tuber forming a crown over tuber. Leaves semierect, emergent; petioles stout, brittle, 5-25 cm long, acutely triangular; lamina $2-7.5 \times 1.8-3.3$ cm, thick, amphistomatic, dark green, brittle, shiny, ovate-oblong, cordate or rounded at base, acute or rounded at apex, entire, 7-9 nerved. Spathe c. 1.5×0.6 cm, conical, acute, membranous, cauducous. Peduncles 20-30 cm long, thickened above, slender. Spike simple, 6-7 cm long, dense flowered, dark pink with flowers in all directions, elongate and turns green at maturity. Tepals 2, dark pink, obovate, obtuse, c. 1.5×1.5 mm in flowering, c. 2×2 mm in fruiting, persistent, 1-nerved. Stamens 6, exserted; filaments 2-2.2 mm long, narrow above; anthers 2-celled, violet; pollen monocolpate, elliptic, $21-27 \times 15-19.5 \mu\text{m}$ with reticulate ornamentation. Carpels 3, c. 1×0.5 mm; stigma decurrent; ovules 2, basal. Follicles $5-7 \times 2-3$ mm, beaked, smooth; seeds with simple testa; embryo $5-6.5 \times 1.5-1.8$ mm, cylindric; plumule basal, not in a groove.

Fl. & Fr.: July - September.

Distrib.: Originally, the species was collected from paddy fields along the Tarcarli river at Nerurpar-Dhamapur [$73^\circ 41' \text{ N} / 37^\circ 30' \text{ E}$] about 9 km west to Kudal in Sindhudurg district of Maharashtra at about 15-20 m above mean sea level. Later, it has also been collected from Sathose near Sawantwadi, a locality about 50 km south to type locality.

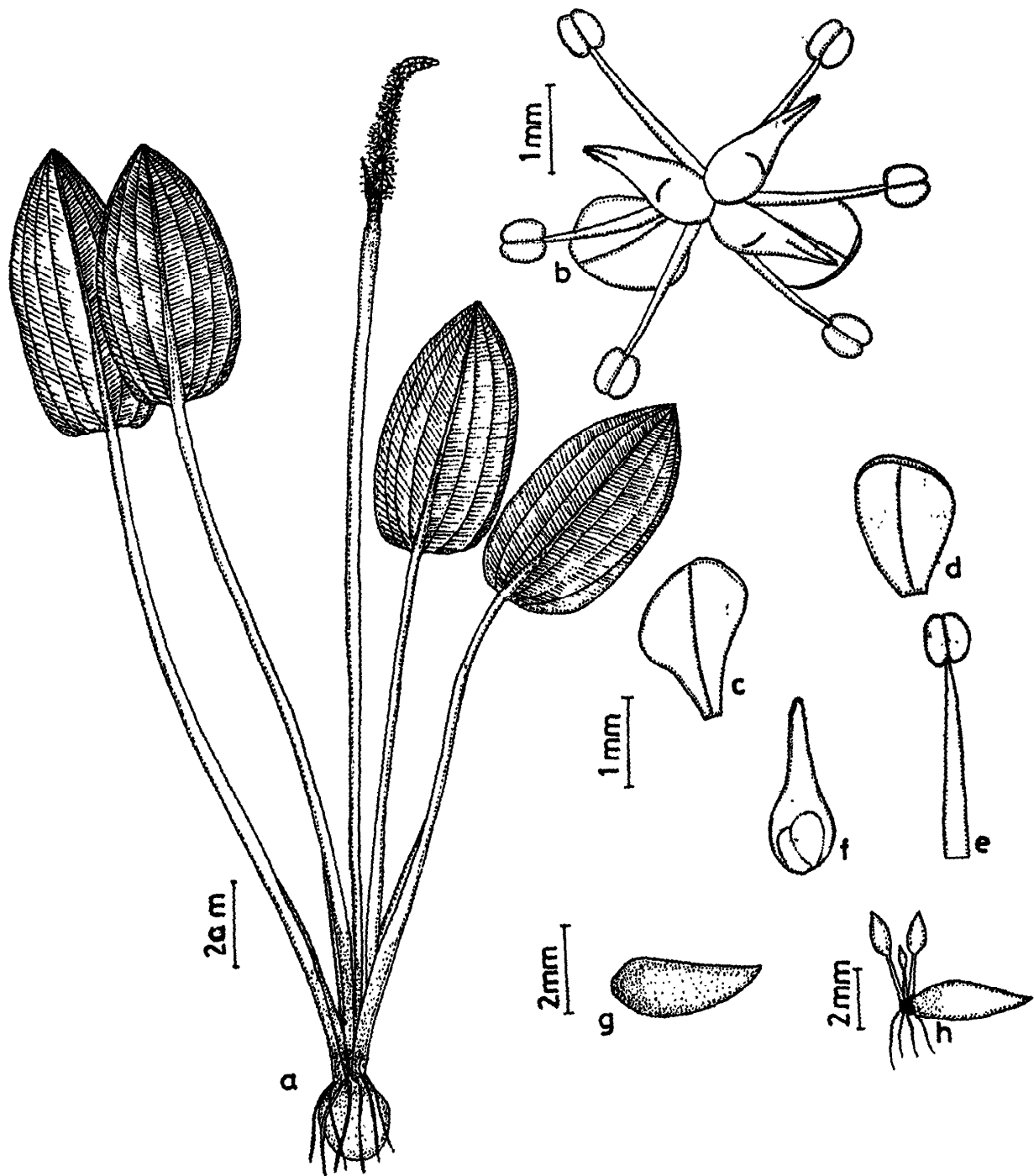


Fig.4. *Aponogeton bruggenii* Yadav & Govekar
 a. Plant, b. Flower, c. & d. Tepals, e. Stamen, f. Fruitlet & g. Seed.

Note : In natural habitat, this species perpetuates the dry summer in the form of dormant tubers. With the on set of the monsoon the dormant tubers sprout in June and start producing leaves and inflorescences from July to September. The aerial parts die during October heat on drying of paddy fields and the tubers enter into the dormancy till the next monsoon season.

Although a number of healthy inflorescences were produced in nature, no fruit and seed setting was observed except for development of one or two follicles on few spikes. In natural habitat as well as under cultivation, the inflorescences after their emergence stand erect in water for 10-15 days, gradually turn green and finally decay without setting seeds. In spite of self and cross-pollination, the plants failed to set seeds. During the present studies, only about 15 seeds were obtained out of the several inflorescences examined. Seeds showed normal germination and developed successfully into new plants. These observations on sexual reproduction suggest that the species face some inexplicable reproductive barrier. Studies on embryology of the species showed normal microsporogenesis, megasporogenesis and development of embryo-sac up to 8 nucleate stage. After 8 nucleate stage, the embryo-sac degenerate for unknown reason (Gaikwad, 2000). Thus, abortion of embryo-sac seems to be responsible for sterility.

This reproductive barrier has forced this species to adopt vegetative propagation for its survival. In natural habitat, tuber of each plant produce more than one shoot per year and consequently each shoot develops a tuber of its own, thus leading to formation of a bunch of tubers. The number of tubers in a bunch varies from 2-10 depending on the age of the plant. These tubers get separated and dispersed during ploughing and preparation of fields for the next paddy crop. The species has restricted distribution probably due to sexual sterility and absence of an effective mechanism of dispersal of its tubers.

Chr. No.: $2n = 56$ (Yadav, 1995b).

Specimens examined : Maharashtra: Nerurpar, about 9 km west to Kudal in Sindhudurg dist., 10.09.1992, *Yadav* 1 (CAL); Nerurpar 15.07.1998, *Gaikwad* 5127 (SUK).

- 4. *Aponogeton crispus*** Thunb., Nov. Gen. 4: 73. 1781 ('*crispum*'); Hook. f., Fl. Brit. Ind. 6: 564. 1893, p. p.; Trimen, Handb. Fl. Ceylon 4: 372. 1898, p. p.; Engl. & Krause in Engl. Pflanzenr. 24 (4, 13): 12. 1906 (excl. descr.); Gamble, Fl. Madras 3: 1597. 1931 (Repr. ed. 1115. 1957.) p. p.; Bruggen in Blumea 18: 481, f. 1, 6. 1970 & Biblio. Bot. 47. 1985 & Aqua Planta. 2: 31. 1990; S. Karthikeyan & al. Fl. Ind. Enum. Monocot. sr. 4. 4. 1989; Sundararagh. in Hajra & Sanjappa, Fasc. Fl. India. 22: 128. 1996; C. D. K. Cook, Aquat. Wetl. Pl. India. 48. 1996. Type : Ceylon, Thunberg *s. n.* (UPS, *n. v.*). *Aponogeton echinatus* Roxb., Fl. India 2: 210. 1832 ('*echinatum*'); Hook. f., Fl. Brit. India. 6: 564. 1893; Subr. Aquat. Angiosp. 92. 1962; Bruggen in Blumea 18: 483, f. 1, 8. 7, M. 2. 1970; C. J. Saldanha & Nicolson, Fl. Hassan: 635, f. 106. 1976; K. M. Matthew, Fl. Tamilnadu Carnatic 3: 1713. 1983; Lakshmin. in B. D. Sharma & al. Fl. Maharashtra 1: 238. 1996.

(Plate - I & Fig. 5)

Monoecious, tuberiferous, perennial, aquatic herbs, c. 75 cm high. Tubers globose-obovoid, c. 3 cm in diam.; roots slender, fibrous, from top of tubers. Leaves both submerged and floating. Submerged leaves petiolate; petioles c. 13 cm long, bluntly triangular, slender, brittle, sheathing at base; lamina c. 13 × 3.5 cm, oblong-lanceolate to elliptic, rounded or subcordate at base, obtuse at apex, flat or undulate or crisped at margin, main nerve prominent with 4-6 nerves on either side. Floating leaves petiolate; petioles c. 65 cm long, slender, terete, brittle, sheathing at base; lamina very variable, c. 18 × 4.5 cm, ovate-lanceolate, tapering above, rounded or blunt at apex, rounded or subcordate at base, main nerve prominent with 5-6 parallel nerves on either side. Spathe c. 2.5 cm, acuminate, membranous, caducous. Peduncles up to 65 cm long, cylindric, widened above. Spike simple, c. 13.5 cm long, dense or lax flowered with flowers in all directions. Tepals 2, 2-2.3 × 0.8-1.2 mm, obovate-spathulate, rounded at apex, 1-nerved, white-lilac. Stamens 6, exserted; filaments c. 2.1 mm long, widened below; anthers 2-celled, dark violet, dehiscing longitudinally; pollen yellow. Carpels 3; stigma decurrent; ovary c. 0.5 × 0.6 mm; ovules 2 per carpel. Follicles c. 1.3 × 0.4 mm, beaked, smooth or echinate, 2-seeded; seeds c. 7 mm long, with single testa; plumule attached at base, lying in a groove.

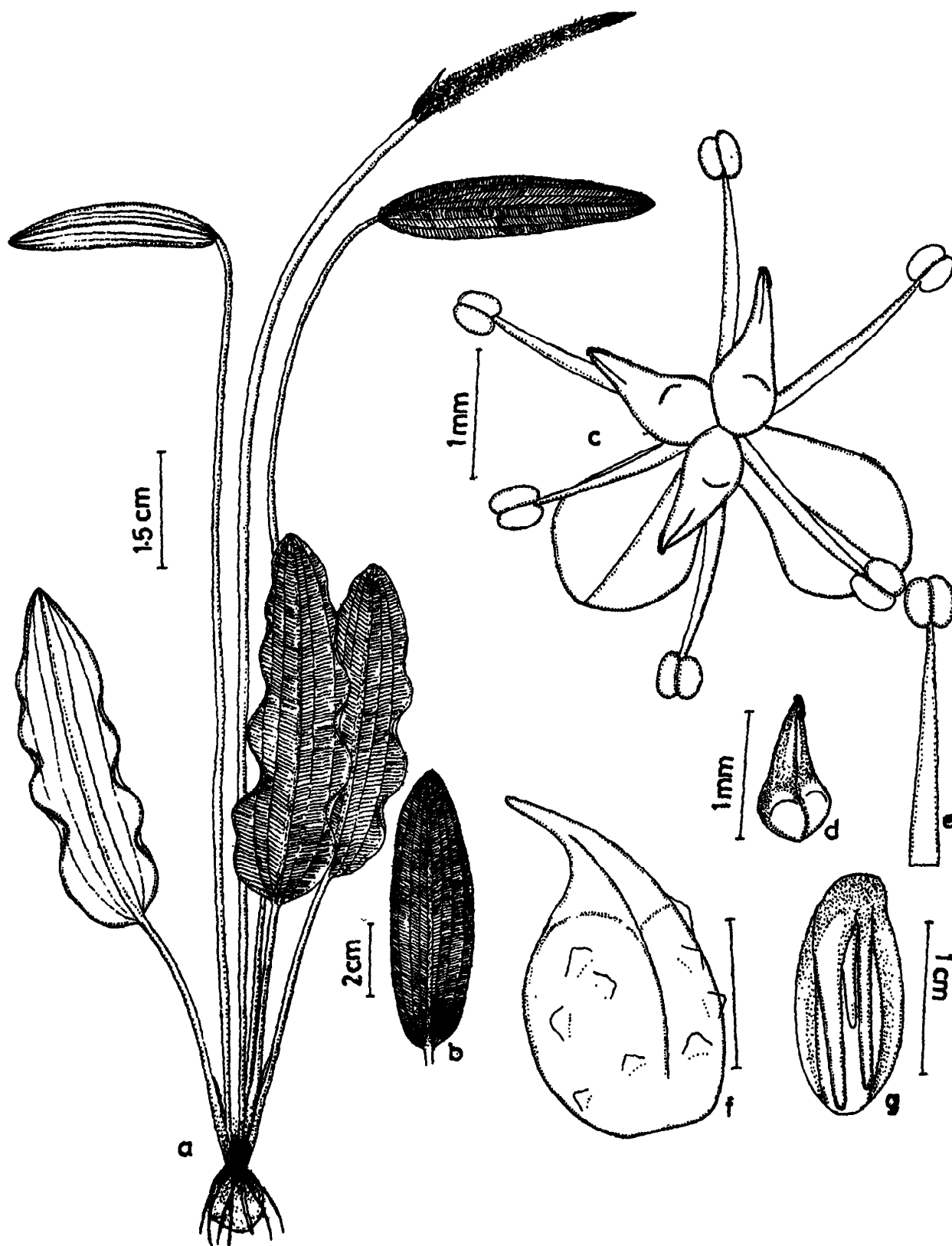


Fig.5. *Aponogeton crispus* Thunb.

a. Plant, b. Floating leaf, c. Flower, d. Carpel, e. Stamen, f. Fruit, g. Seed.

Fl. & Fr.: Throughout the year with a peak from August to November.

Distrib.: INDIA : Andhra Pradesh, Karnataka, Kerala, Maharashtra, Tamil Nadu and West Bengal; SRI LANKA.

Ecology : Permanent fresh water lakes, ponds and pools.

Note : This species produces both smooth as well echinate follicles. *Aponogeton echinatus* Roxb. with echinate follicles is a variant of *A. crispus*. Therefore, it has been merged in to *A. crispus* (Bruggen, 1985).

Aponogeton crispus may be confused with *A. natans* due to superficial similarities in vegetative morphology and overlapping range of their distribution. *Aponogeton crispus* can easily be distinguished by 2 ovuled carpel as against 4-8 ovuled in *A. natans*.

Chr. No.: $2n = 32$ (Gaikwad & al., 1998).

Specimens examined : Karnataka : Biligirirangan hills Mysore dist., 06.09.1961, A. S. Rao 73715 (BSI); Karnataka: on the road from Bangalore to Mysore 10.08.96, Gaikwad - 5133 (SUK).

5. ***Aponogeton lakhonensis*** A. Camus, Nat. Syst. 1: 273, f. 18. 1909 & in Lecomte, Fl. Gen. Indo Chine 6: 1226. 1942; Bruggen in Blumea 18: 479, f. 2, 12, 3a. 1970; Biblioth. Bot. 51. 1985; Aqua Planta. 2: 51.1990; Steenis, Fl. Males. 1, 7: 216, f. 1 & 3. 1971; S. Karthikeyan & al. Fl. Ind. Enum. Monocot. Sr. 4. 4. 1989; C. D. K. Cook, Aquat. Wetl. Pl. India 48. 1996; Sundararagh. in Hajra & Sanjappa, Fasc. Fl. India 22: 129. 1998. Type : Loas, river Attpeu-Lakhon mountains, Harmand *s.n.* (P !). *Aponogeton pygmaeus* K. Krause in Bot. Jahrb. Syst. 44, Beibl. 101: 8. 1910; A. Camus, Fl. Gen. Indo Chine 6: 1227. 1942. Type: Harmand *s.n.* (P). *A. luteus* A. Camus, Notul Syst. 2: 204. 191 & in Fl. Gen. Indo Chine 6: 1227. 1942. Type: Robinson 1177 (P). *A. monostachyus* sensu A. Camus in Fl. Gen. Indo Chine 6: 1225. 1942; Larsen in Dansk Bot. Ark. 20: 134. 1962, *non* L. f. 1782.

Monoecious, tuberiferous, perennial, aquatic herbs. Tuber globose-obovoid, c. 2 cm in diam.; roots slender, fibrous, from top of tubers. Leaves both submerged & floating. Submerged leaves petiolate; petioles 7 - 35 cm long, slender, cylindric; lamina very variable, narrowly linear, c. 25×6 cm; narrow at base, narrowly tapering with blunt or rounded tip at apex; main nerve with 7 - 9 parallel nerves. Floating leaves petiolate; petioles 10 - 40 cm long, slender, brittle, thickened above; lamina c. 17×4 cm; cordate or rounded at base, tapering with blunt or rounded tip at apex, main nerve with 7 - 9 parallel nerves. Spathe c. 1.7 mm long, caducous or rarely persistent. Peduncles cylindrical, 15 - 40 cm long; spike simple, yellow, c. 8 cm long, laxly or densely flowered with flowers in all directions. Tepals 2, obovate, yellow, $1-2 \times 0.75-1.5$ mm, 1-nerved. Stamens 6, exserted; filaments 1.5-3 mm long, widened below; anthers 2-celled. Carpels 3 or 4 (5), $1-1.75 \times 0.75-1$ mm; ovules 4-8. Follicles 3-5 mm long, with a terminal or lateral beak; seeds c. $2-3 \times 1$ mm, testa double; outer one loose, membranous & reticulately veined, inner one brown, closely fitting; embryo $1.25-2.5 \times 0.5$ mm; plumule absent.

Fl. & Fr.: October - March.

Distrib.: INDIA : Assam, Meghalaya, Nagaland; BANGLADESH, CAMBODIA, CHINA, LAOS, MALESIA, THAILAND and VIETNAM.

Ecology : Running streams, flooded paddy fields and ponds, not frequent but locally abundant.

Note : This species is most common in SE Asia but infrequent in India, confined to hilly tracts of NE India. It is readily distinguished from other Indian species by its yellow tepals.

Specimen examined : Hock 170 and Assam-1836, 647 (CAL).

6. **Aponogeton natans** (L.) Engl. & Krause in Engl., Pflanzenr. 24 (4, 13): 11. 1906; Fisch. Fl. Madras 9: 1598. 1918; Fyson, Fl. S. India Hill Stat. 684, t. 563. 1931 (Repr. ed. 3: 1115. 1957); Subr., Aquat. Angsp. 92, t. 5. f. 54. 1962; Nair in Rec. Bot. Surv. Ind. 21(1): 256. 1978; Bruggen in Blumea 18: 477, f. 2. 1970; Biblioth.

Bot. 50. 1985; Aqua Planta. 2: 60. 1990; Manilal & Sivar. Fl. Calicut 306. 1982; K. M. Matthew, Fl. Tamil Nadu Carnatic 3: 1714. 1983; S. Karthikeyan & al. Fl. Ind. Enum. Monocot. Sr. 4. 5. 1989; Sundararagh. in P. K. Hajra & M. Sanjappa, Fasc. Fl. Ind. 22: 130. 1996; C. D. K. Cook, Aquat. Wetl. Pl. India 48. 1996; Lakshmin. in B. D. Sharma & al. Fl. Maharashtra 1: 238. 1996. Type : India, Koenig s. n. LINN - 479.1. *A. monostachyon* L. f., Suppl. Pl. 214. 1782: Roxb., Pl. Coromandel 1: 58, t. 81. 1795 & Fl. India 2: 210. 1832; Edgew., London J. Bot. Kew 3: 404, f. 17. 1844; Hook. f. Fl. Brit. India 6: 564. 1893; Trimen, Handb. Fl. Ceylon 4: 372. 1898; T. Cooke, Fl. Bombay 3: 348. 1958 (Repr. ed.). *Spathium monostachyum* Edgew. in Calcutta J. Nat. Hist. 3: 533, f. 16. 1843. *Parua kelanga* Rheede, Hort. Malab. 11: 34, t. 15. 1642. *Potamogeton indicus sensu* Roth ex Roem. & Schult. Syst. Veg. 3: 516. 1818 (*non* Roxb. 1832).

(Plate - I & Fig. 6)

Monoecious, tuberiferous, perennial, aquatic herbs, c. 75 cm tall. Tubers globose or elongate, 1.5-2 cm across; roots fibrous, slender, from top of tubers. Leaves both submerged and floating. Submerged leaves petiolate; petioles c. 13 cm long, sheathing at base, bluntly triangular, brittle; lamina c. 10 × 4.5 cm, oblong-lanceolate, elliptic, rounded at base, rounded or obtuse at apex; main nerve prominent with 6-8 parallel nerves on either side. Floating leaves petiolate; petioles c. 63 cm long, slender, terete, sheathing at base; lamina c. 14.5 × 4.6 cm, oblong, narrow at apex, entire, blunt or rounded at tip, cordate at base, main vein prominent with 5-8 parallel nerves. Spathe c. 2 cm long, membranous, acute, caducous. Penduncles c. 85 cm long, cylindric, thickened above; spike simple, 5 -10 cm long, elongate with maturity, dense flowered with flowers in all directions. Tepals 2, persistent, oblong-spathulate, 1.5-2 mm long, rounded at tip, 1-nerved, pink. Stamens 6, exserted; filaments c. 2.5 mm long, widened at base; anther 2-celled, dark blue, globose, dehiscing longitudinally; pollens yellow, c. 18.03 × 13.81 µm. Carpels 3; stigma decurrent; ovules 4-8 per carpel. Follicles c. 4 × 2 mm, beaked; seeds 4-8 with double testa, outer testa transparent, inner testa thin, brown, reticulate.

Fl. & Fr.: Almost throughout the year with a peak from Sept. to Nov.

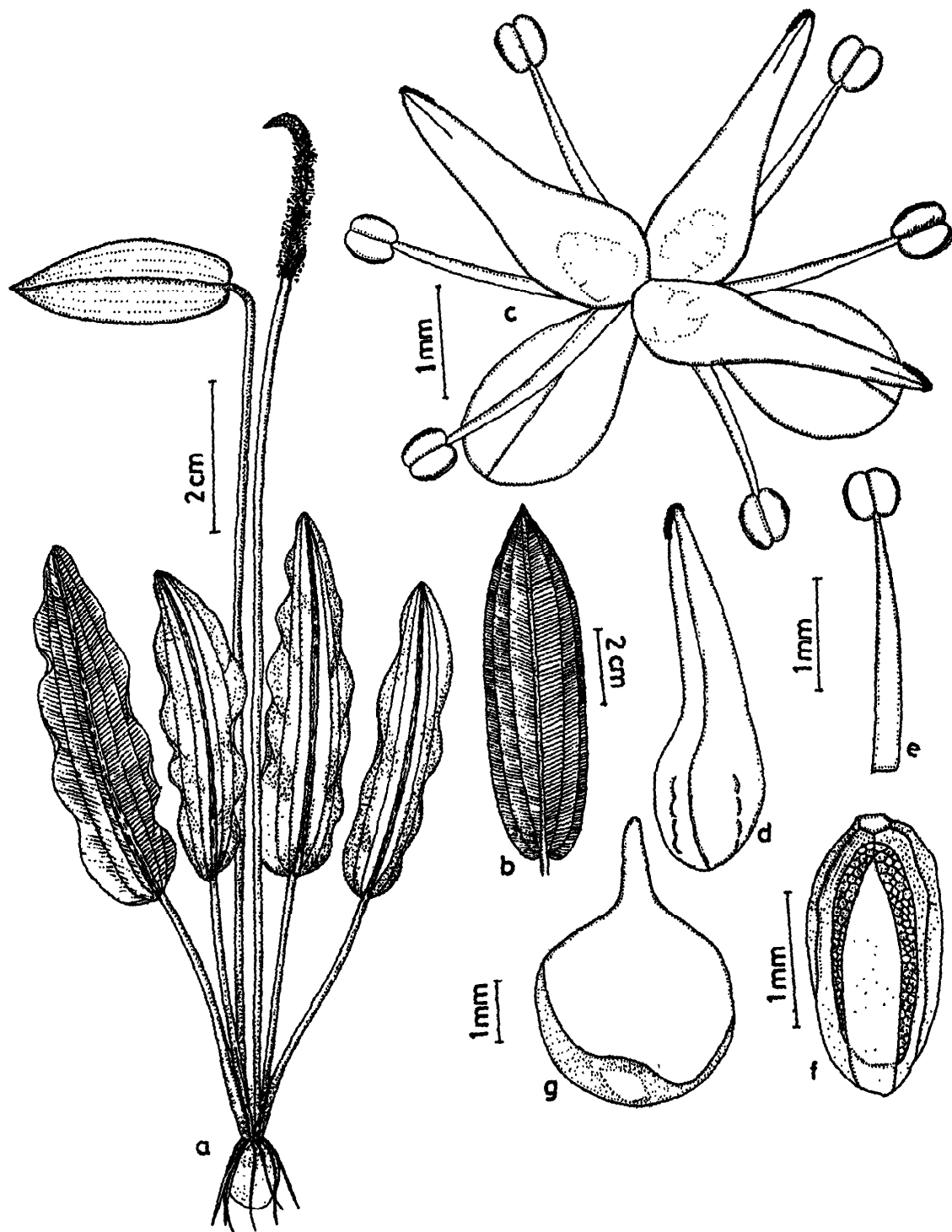


Fig.6. *Aponogeton natans* (L.) Engl. and Prantl.
a. Plant, b. Floating leaf, c. Flower, d. Carpel, e. Stamen, f. Fruit, g. Seed.

Distrib.: INDIA : Almost throughout the country and probably the most common species; SRI LANKA.

Ecology : Freshwater shallow ponds and lakes.

Note : All carpels of all flowers of an inflorescence develop into follicles and all seeds are viable. It indicates that there is a possibility of development of at least some seeds through apomixis (Bruggen, 1985).

In addition to difference in number of ovules per carpel, *A. natans* can be distinguished from *A. crispus* by its cordate base of floating leaves as against rounded base in *A. crispus*.

Chr. No.: $2n = 80$ (Gaikwad, 2000).

Specimens examined : Karnataka: Someshwar tank, Bilirirangan hills, 24.04.1962, A. S. Rao 79784 (BSI); Maharashtra: Amgoan in Bhandara dist., 10. 10. 96, Gaikwad 5128 (SUK).

7. **Aponogeton satarensis** Sundararagh., Kulkarni & Yadav in Kew Bull. 36: 687, f. I. 1982; Bruggen in Biblioth. Bot. 57. 1985 & Aqua Planta. 2: 1990; Karthik. & al. in Fl. India Enum. Monocot. Sr. 4. 5. 1989; Sundararagh. in Hajra & Sanjappa, Fasc. Fl. India. 50. f. 32. 1996; C. D. K. Cook, Aquat. Wetl. Pl. India 50, f. 32. 1996; Lakshmin. in B. D. Sharma & al. Fl. Maharashtra 1: 239. 1996. Type : Mavashi plateau, Satara dist. Maharashtra Yadav-15 (holotype CAL !, iso K! BSI and Ram Narain Ruia College, Bombay). (Plate - I & Fig.-7)

Dioecious, tuberiferous, perennial, aquatic or semiaquatic herbs, up to 30 cm high. Tubers $1-2 \times 2.5$ cm across, globose-ellipsoid; roots slender, fibrous, from top of tuber. Leaves floating or emergent, petiolate; petiole up to 18 cm long, cylindric, sheathing at base; lamina c. 11.5×1.75 cm, lanceolate-elliptic, entire, glabrous, shiny, acute or obtuse, main nerve prominent with 2-4 parallel nerves on either side. Spathe 1-2 cm long, membranous, conical, acute or acuminate, caducous, enclosing inflorescence

when young. Peduncle slender, terete, c. 25 cm long, thickened above; spike biforked, 4-7 cm long, female spike elongated with maturity, up to 13 cm. Tepals in male flower 2, oblong, orbicular to suborbicular, $1.6-2 \times 1.1-1.2$ mm, lilac-pink. Stamens 6, in two whorls, exserted; filaments purple, 1.4-2 mm long; anthers 2-celled, dark brown, dehiscing longitudinally; pollens small, elliptic, $18-26 \mu\text{m}$ in diam., monosulcate, reticulate; pistilode 3, small, conical. Carpels 3, free; stigma decurrent. Follicles $4-7 \times 4$ mm, oblong, beaked, pericarp membranous; seeds 1-2, elliptic, c. 5×3 mm, testa simple, plumule in a groove.

Fl. & Fr.: June - September.

Distrib.: Endemic to the State of Maharashtra, so far known only from its type locality *i.e.* plateaus of higher altitude (1200-1300 m above mean sea level) in Satara district.

Ecology : It grows in temporary ponds and puddles as well as on marshy ground of plateaus. The plateaus enjoy misty climate throughout rainy season (June-October). The common associates are *Habenaria panchganensis* Sant. & Kapad., *Dipcadi montanum* Baker, *D. ursulae* Blatter, *Scilla hyacinthina* (Roth) Macbr., *Pancratium triflorum* Roxb., *Iphigenia stellata* Blatt. and number of *Impatiens*, *Eriocaulon*, *Murdania*, *Rotala* and *Utricularia* species.

Note : *Aponogeton satarensis* is the only Asiatic species with dioecious habit and forked inflorescence. In natural population, male plants are more abundant than females (70-80 %). It's close affinities with Madagascan species *A. decaryi* has been confirmed by hybridization experiments (Yadav, 1995). *Aponogeton satarensis* with low ploidy level ($2n = 26$) propagates only through sexual means, while *A. decaryi* with high ploidy level ($2n = 56$) behaves as an apomicts (Yadav, 1995) and propagates through seeds in absence of male plants. Observations on morphology, cytology and hybridization suggest their common ancestry. *Aponogeton satarensis* seems to be a relict palaeoendemic in Indian subcontinent.

Chr. No.: $2n = 26$ (Yadav & al., 1989).

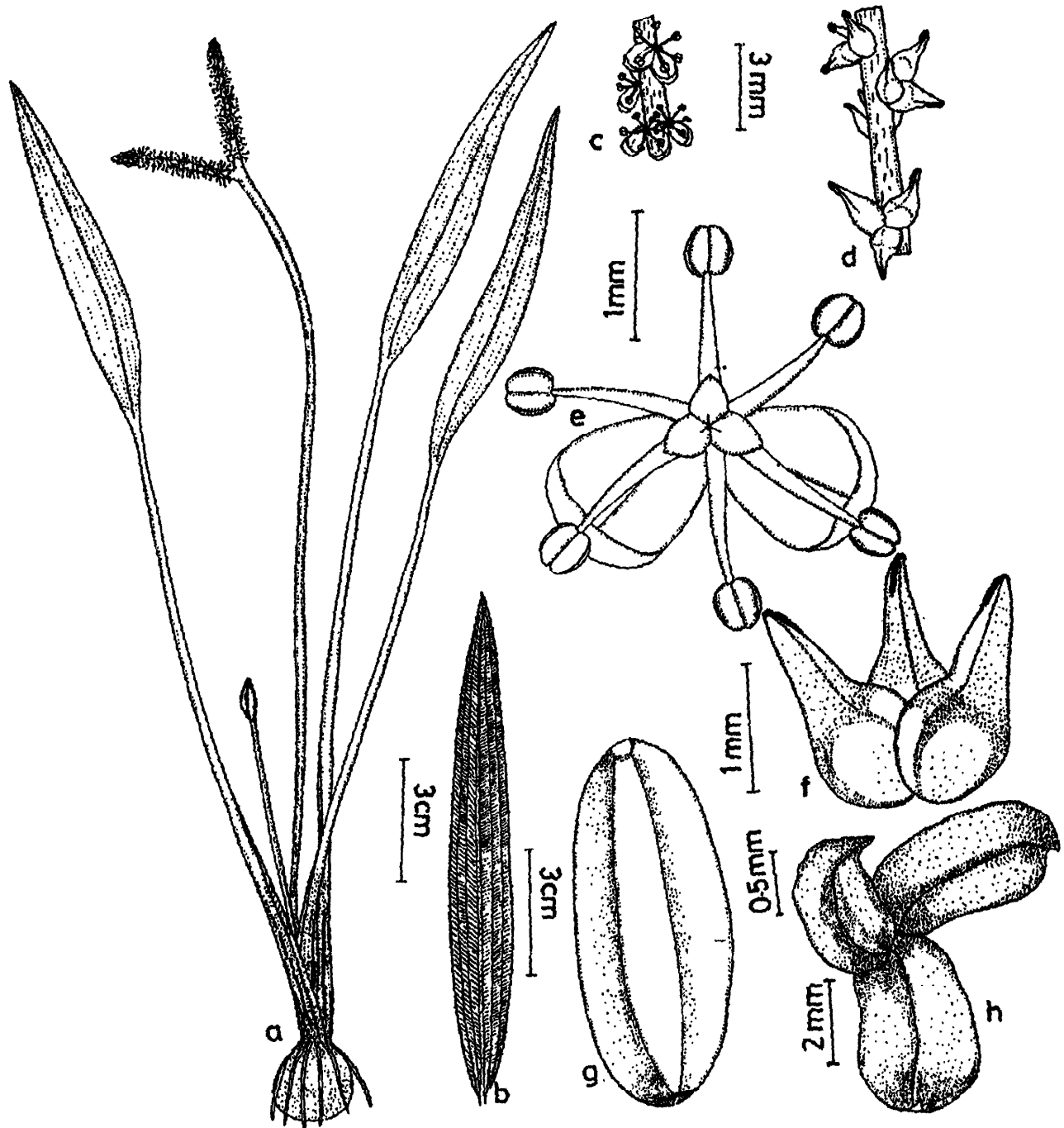


Fig.7. *Aponogeton satarensis* Sundararagh., Kulkarni and Yadav
 a. Plant, b. Leaf, c. Portion of male inflorescence, d. Portion of female inflorescence,
 e. Male flower, f. Female flower, g. Seed, h. Fruitlet.

Specimens examined : Type as above; *Sundara Raghavan* 161738 (BSI); Maharashtra : Kas plateau 25 km west to Satara, 05.07.1998, *Gaikwad* 5129, (SUK).

- 8. *Aponogeton undulatus* Roxb.** [Hort. Beng.: 26, 1814, *nom. nud.*] Fl. India 2: 211. 1832 ('*undulatum*'); Engl. & Krause in Pflanzenr. 24 (4, 13): 11. 1906, excl. descr.; Bruggen in Blumea 18 : 465, f. 2. 1970 & in Steenis Fl. Males. 1, 7: 213, f. 1: 1, 2. 1971; Biblioth. Bot. 41. 1985 & Aqua Planta 2: 77. 1990; S. Karthikeyan & al. Fl. Ind. Enum. Monocot. Sr. 4. 5. 1989; Sundararagh. in Hajra & Sanjappa, Fasc. Fl. India 22: 136. 1996; Lakshminarasimhan in B. D. Sharma & al. Fl. Maharashtra 1: 239. 1996; C. D. K. Cook, Aquat. Wetl. Pl. India 49. 1996. Type : Roxb. Icon. No.936 (CAL), Ined (K). *Aponogeton microphyllum* Roxb., Fl. Ind. 2: 210. 1832; Hook. f., Fl. Brit. Ind. 6: 564. 1893. Type: Roxburgh Drawing 1232 (K). *Spathium undulatum* (Roxb.) Edgew. in Calcutta J. Nat. Hist 3: 534, f. 15. 1843. *Ouvirandra undulata* (Roxb.) Edgew. in Hook., London J. Bot. 3: 405, f. 15. 1844. *Aponogeton stachyosporus* de Wit, in Med. Bot. Tuinen Belm. Arb. Wagen. 2: 96. f. 1 - 3. 1958. Type : *Zewald s.n.*(Cult.) 20.09.1958 (WAG). *A. crispum* sensu Hook. f., Fl. Brit. India 6: 564. 1894, *p. p. non* Thunb. 1781. *Spathium microphyllum* (Roxb.) Voigt, Hort. Suburb. Calcutt.. 694. 1845. *Aponogeton monostachyon* sensu Andrews, Bot. Repos 6: t. 406. 1797 *non* L. f. 1782. (Plate - I & Fig. 8)

Monoecious, tuberiferous, perennial, aquatic herbs. Tubers globose-obovoid, 1-2.5 cm across; root slender, fibrous, from top of tuber. Leaves both submerged & floating. Submerged leaves petiolate; petioles c. 14 cm long, brittle, bluntly triangular; lamina c. 12 × 3.7 cm, elliptic lanceolate, narrow at apex, obtuse or rounded at base sometimes cordate with opaque areas between veins, undulate at margin, midrib with 5-6 parallel nerves. Floating leaves petiolate; petioles cylindric, up to 40 cm long; lamina c. 8 × 2.5 cm, oblong, lanceolate, entire, narrow at apex, obtuse at tip, rounded or rarely cordate at base, main nerves with 5-6 parallel nerves. Propagules (young plantlets) developed on inflorescence-like axis. Spathe semipersistent, 1-2 cm long, membranous, acuminate. Peduncle develop on same axis on which propagules develop, c. 20 cm long, cylindric; spike simple, 2-10 cm long, lax flowered, flowers in all directions. Tepals 2, 3-6 × 1.6-2 mm, spathulate, clawed, caducous, 1-nerved, oblong-obovate, obtuse, pinkish-white.

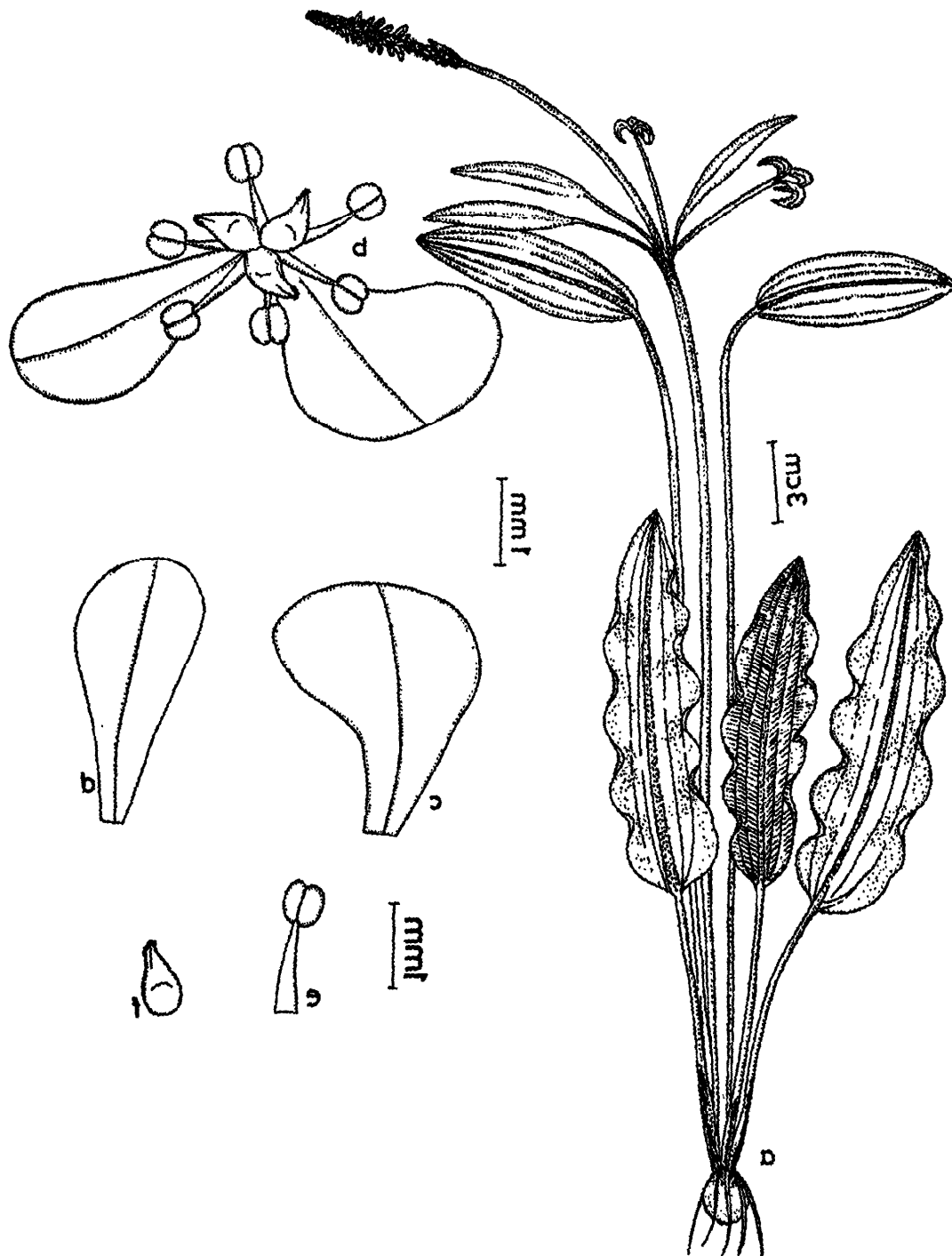


Fig.8. *Aponogeton undulatus* Roxb. ($2n = 86$)
 a. Plant, b. Flower, c. & d. Tepals, e. Stamen, f. Carpel.

Stamens 6, exserted; filaments 1.3-1.5 mm long, widened at base; anthers 2-celled, obovoid-globose, blue; pollen grains yellow, c. $20.7 \times 20 \mu\text{m}$. Carpels 3; ovules 2, basal. Follicles $5-7 \times 4 \text{ mm}$, with a short, terminal, curved beak; seeds with a simple testa, embryo up to $5 \times 2 \text{ mm}$, plumule attached near the base to the embryo and in a very wide groove.

Fl. & Fr.: December - May (very rare).

Distrib.: INDIA : Assam, Bihar, Maharashtra, Orissa, Punjab, Uttar Pradesh, West Bengal; BANGLADESH, INDONESIA, MALESIA, MYANMAR and THAILAND.

Ecology : Freshwater shallow ponds and lakes.

Note : *Aponogeton undulatus* is a very distinctive Asiatic species in its longest tepals and vegetative propagation through propagules on inflorescence like-axis. Field and laboratory observations revealed that the species seldom flower in nature as well as under cultivation and rarely reproduce sexually. The species has adopted vegetative means of propagation by developing propagules (young plantlets) on inflorescence like axis. They get detached from mother plant and establish as separate individuals. These usually non-flowering populations from various places show $2n = 70$. Regular yearly flowering of the species in nature was observed in the population at Ghadbadya Lake near Amgaon in Bhandara district of Maharashtra. Few (1-3) inflorescences develop on same axis on which propagules are developed. Though, large number of inflorescences and normal flowers are developed, the species fails to set seeds. Cytological studies revealed that somatic chromosome number in flowering population was $2n = 86$. Similarly, an interesting robust form of *A. undulatus* was observed at Kittur in Belgaum district of Karnataka, which produces healthy inflorescence, normal flower with persistent tepals (as against the caducous tepals of the species) and fails to set the seeds. The population was with $2n = 74$ and found to be sexually sterile.

Chr. No.: $2n = 70, 74, 86$. (Gaikwad, 2000).

Specimens examined : Maharashtra: Anderi, 27.04.1941, Santapau 204.1 (BLAT);

Malad, 19.10.1957, *Shah* 9322, 9324 (BLAT); Borivali, 24.07.1955, *Fernandez* 1944-1947 (BLAT), 20.10.1953, *Fernandez* 1600 (BLAT); Amgoan, Bhandara dist. Maharashtra 04.04.1998, *Gaikwad* 5130 (SUK); Kittur, Dharwar dist. Karnataka 18.10.1999 *Gaikwad* 5140 (SUK).

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