LEMNACEAE (F. van der Plas, Leyden)

Monoecious, very rarely dioecious, small to minute aquatic annuals, floating at the surface of the water, or floating just below the surface whereby only a very small part of the frond is exposed to the air, or completely submerged and then rising to the surface in the flowering period. Fronds either solitary or connected in small groups by short to very short hyaline or rarely elongate green stipes (fig. 1 Aa, 1 Ba), symmetric or asymmetric, with reniform, round, linear-lanceolate or angular dorsal outline, green, with or without red or brown pigment cells, sometimes with both types of pigment; base symmetric or asymmetric, obtuse, emarginate or narrowing into the stipe; apex symmetric or asymmetric, round, obtuse or acute; margin entire or slightly dentate; dorsal side flat to slightly convex, smooth or with one or more small papillae; ventral side flat to strongly inflated; somewhere in the median provided with a 'node' (fig. 1 Ac). There the roots, nerves, new fronds, and flowers emerge. Nerves $0-1-\infty$, running towards the apex. New fronds attached to the node of the mother frond by means of a 'stipe' which is sometimes hardly visible and is connate with their ventral side. Daughter frond sometimes (in Spirodela) provided with 2 basally connate, roundish scales inserted at the base of the stipe (fig. 1 Ad, 2 e), unequal, one connate with the ventral side as far as its node. Roots several, one or none, unbranched, growing downward from the node; in root-producing species the root(s) closely enveloped by a sheath, which during growth is circumscissile-dehiscing, leaving a basal sheath (in some species soon hardly visible) and a 'calyptra' on top, Budding pouches 2 (fig. 1 Ab) or 1 (fig. 1 Cb); if there is one budding pouch this is basal, median, dorso-ventrally flattened or funnel-shaped and it produces only new fronds; when there are 2 budding pouches these are lateral, one on either side of the axis, dorso-ventrally flattened and produce new fronds, one pouch may give rise to an inflorescence. In taxa with only 1 budding pouch (fig. 1 Cj; subfam. Wolffioideae) the inflorescence is borne in a median or lateral dorsal flowering cavity (an exception is extra-Mal. Wolffiopsis which has 2 dorsal flowering cavities), without a spathe and consisting of 1 female and 1 male flower. In taxa with 2 budding pouches (fig. 3 k, 6 e-f) the *inflorescence* is surrounded by a spathe and consists of 1 female and 2 male flowers (female flower rarely absent). Perianth none. — Male flower consisting of 1 stamen, anther uni- (fig. 8 d) or bilocular (fig. 2 f), apically or transversely dehiscent; filament short or long and slender; pollen grains 17-21 $\mu \varnothing$, spinose. — Female flower consisting of 1 globular ovary with a short persistent style (fig. 3 k, 6 f), and containing 1-4 ovules. Ovules orthotropous, amphitropous or anatropous. Fruit symmetric (fig. 5 d-e) or asymmetric, 1-4-seeded, globose or laterally compressed, winged or without wings. Seeds smooth or ribbed (fig. 41), with little or no endosperm; operculum and chalaza prominent.

Distribution. There are 6 genera with c. 30 spp. all over the world, obviously introduced in oceanic islands (see under dispersal). The genera Spirodela, Lemna, and Wolffia are widely distributed in the temperate and tropical zones; the other genera have a more restricted range. Wolffiella occurs in the subtropical and tropical parts of America and in South Africa, Pseudowolffia is restricted to tropical Africa, and Wolffiopsis has been found in the tropics of Africa and America. See Den Hartog & Van Der Plas (Blumea 18, 1970, 355–368).

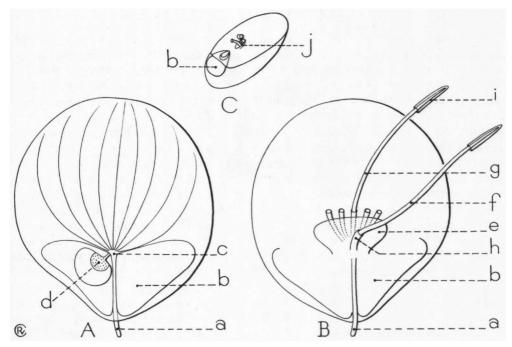


Fig. 1. Diagrams showing the external morphology of Lemnaceae.

A-B. Spirodela polyrhiza (L.) Schleid. A. Dorsal side of the frond, B. ventral side of the frond. —

C. Wolffia sp.

In all figures: a = stipe, b = budding pouch, c = node, d = young frond showing the dorsal scale, e = ventral scale, f = primary root, g = secondary root, h = root sheath, i = root cap, $j = \text{flowering cavity with } \beta$ and \emptyset flower.

In Malesia the first three mentioned genera occur with together 6 spp. As Lemnaceous plants are distinctly under-collected, their precise distribution is very incompletely known, and consequently range extensions may be expected. For this reason 3 spp. are added here which have not yet been found in Malesia, but which may be found in future.

In oceanic islands Lemnaceae are very scarce and possibly all introduced according to GUPPY. From the Pacific islands the following are known to me from collections: Hawaiian Is. Spirodela polyrhiza and Lemna perpusilla (Heller 1895, Le Roy Topping and Degener 1927). L. perpusilla is, besides in Hawaii, also collected in Polynesia already during the Wilkes' Exploring Exp. from Fiji (non vidi), and further known from New Caledonia (last century), Samoa (1893) and Tonga (1926). Spirodela punctata is also known from Fiji and New Caledonia. This is also recently collected on Mahé Atoll (Maldives, Indian Ocean).

Ecology. Lemnaceae are found in fresh water, or sometimes in brackish water or on wet mud; in stagnant waters of canals, ditches and small ponds, sometimes also in small, sluggish streams. They usually indicate eutrophic conditions, and are generally favoured by organic pollution. In Malesia they occur up to 2100 m, outside Malesia they have been found much higher, e.g. Lemna trisulca up to 3000 m. They occur in monospecific growths as well as mixed with other Lemnaceous species; they associate also with other small aquatics, e.g. with water ferns of the genera Salvinia and Azolla or with the liverwort Ricciocarpus natans. Submerged Lemnaceae sometimes associate with liverworts of the Riccia fluitans complex. They mostly form a thick layer at the surface of the water or just below it, and form a nuisance when they choke drainage ditches or cover fish ponds.

The most common species in Malesia are Spirodela polyrhiza, S. punctata (Java!), Lemna perpusilla, and Wolffia globosa (Malay Peninsula).

The ecological demands of the various species are generally similar, although not exactly the same, and the tolerance to various environmental conditions differs from species to species. In India MAHESHWARI & KAPIL (Amer. J. Bot. 50, 1963, 679) only found Wolffia microscopica in association with Lemna perpusilla, while Wolffia arrhiza (no doubt W. globosa was meant) was only found together with Spirodela polyrhiza. In the tropics of East Asia and Australia, however, mixed populations of Wolffia globosa and Lemna

perpusilla, with or without Spirodela polyrhiza, are not rare. Thus the combinations of these species appear to be of local interest.

Between the roots and in the root sheaths of the Lemnaceae blue-green Algae of the genera Nostoc and Anabaena have often been found.

Lemnaceae are attacked especially by non-aquatic insects; McCann (J. Bomb. Nat. Hist. Soc. 43, 1942, 152) found beetles (Curculionidae) and the larvae of a moth (Nymphula responsalis Walker) feeding on the upper parts of the fronds of Lemna and Spirodela. Eggs, larvae and cocoons were found within the fronds. Many small aquatic animals choose the fronds as a substratum but generally do not feed on them.

Vegetative and sexual reproduction. Multiplication takes place mainly by budding. Some species, e.g. Spirodela polyrhiza, produce specialized resting buds, i.e. modified fronds consisting of compact tissue filled with reserve food, for surviving less favourable periods (drought, low temperatures). In Spirodela and Lemna, the most primitive members of Lemnaceae, the budding pouches serve for sexual as well as for vegetative reproduction. In the more evolved genera, Wolffia, Wolffiella, Pseudowolffia and Wolffiopsis the budding pouch serves only for vegetative reproduction, while the inflorescence is borne in 1 or 2 special dorsal flowering cavities, which are only formed when the frond starts flowering.

For a number of species flowering is a rare feature, and of a few species the flowers are still unknown. However, as the flowers are small, inconspicuous and ephemeral, it is possible that flowering has often remained unobserved; only when a whole population is flowering this phenomenon is easily detected. Gregarious flowering is possibly restricted to very specific ecological conditions. In herbarium material one single flowering or fruiting plant is often to be found among many sterile ones.

Monoecious plants are most common; plants carrying flowers of one sex only have rarely been found in *Lemna gibba* (DEN HARTOG, Gorteria 4, 1968, 90–92). In *Spirodela polyrhiza* SCHLEIDEN (Beitr. Bot. 1844, 230) found "male" inflorescences, in which the male flowers were normally developed but the female flower was abortive.

The male and female flowers of one inflorescence are usually not mature at the same time; proterandry or proterogyny are more or less a rule. In *Lemna* species even the two male flowers do not grow out of the spathe at the same time (fig. 3 k, 4 i). The various types of flowering sequence may be exhibited in a single species, although the various populations are always uniform in this respect. As a consequence of this, self-pollination is excluded. Cross-pollination is possible by contact between the stamens of one plant with the stigma of another one. This contact pollination can easily be brought about by water movements (Trelease, Proc. Boston Soc. Nat. Hist. 21, 1882, 410-415; McCann, J. Bomb. Nat. Hist. Soc. 43, 1943, 151; Den Hartog, Gorteria 2, 1964, 68-72). McCann *l.c.* reports pollination by small insects. How pollination takes place in the species with a dorsal flowering cavity is not known.

In Lemna the seed is usually liberated from the fruit by decay or, more seldom, by splitting of the pericarp. Sometimes the fruit becomes detached from the frond and the seed remains enclosed by the pericarp. In autumn the fruits often remain attached to the dying fronds and sink with them to the bottom. When the seed germinates the pericarp is often still present (De Sloover, Naturalistes Belges 47, 1966, 449). Germination (fig. 4 n) can take place immediately and sometimes starts while the fruit is still attached to the frond (Ludwig in Kirchner, Loew & Schröter, Lebensgesch. Blütenpfl. Mitteleuropas I, 3, 1934, 59). In general the seeds germinate in the next favourable period, i.e. after the winter or after a period of drought. After having lain at the bottom during the resting period, the seed rises to the surface when germination starts. First the operculum is pushed off by the expanding plumule (fig. 4 n); the latter is green, rootless and does not resemble the normal frond. It gives rise to a new root-bearing frond, which in its turn gives off new fronds, and decays after some time. The first frond is slightly curved, the side that is more developed has vascular tissue and a budding pouch, both lacking on the other side. The second frond is normal, but is curved in the same way as the first frond.

All fronds arising from one seed are homodromous, *i.e.* all daughter fronds are similar to the mother frond. It appears namely that the 2 budding pouches of a frond are not exactly identical; one of them is somewhat larger and gives off more daughter fronds than the other. This better developed budding pouch may be the left one in the one population and the right in another one (De Sloover, Naturalistes Belges 47, 1966, 443–456; Engler in E. & P. Nat. Pfl. Fam. 2, 3, 1889, 156).

Dispersal. Dispersal of the whole plant as well as the seeds over short distances may be effectuated by birds; Wolffia brasiliensis was found by Weddell on the feathers of a shot bird (Ann. Sc. Nat. 3, Bot. 1849, 155). Over very short distances transport by amphibians is possible (Ridley, Disp. of Pl. 1930, 542-543). Water currents transport the plants and seeds as well. Transport over long distances is estricted by the fact that desiccation of the plants is a distinctly limiting factor. Seeds sink after coming free. Several islands or groups of islands have populations which are characterized by a particular pattern of pigmentation (Spirodela punctata in Fiji), a large number of roots (S. punctata of Java), or a particular shape (Lemna perpusilla of New Guinea). This 'raciation' implies that there is no regular exchange between the various populations, and that the island populations have obviously largely developed from isolated clones. This, and the fact of an endemic species in India (Wolffia microscopica), pleads against long-distance dispersal. In the oceanic islands of the Pacific (New Caledonia and Fiji) and the Indian Ocean (Maldives) Spirodela punctata occurs, but this species is notorious for being dispersed by man, e.g. in the rice fields of northern Italy and is said by Daubs to be introduced in America. Guppy concluded (Nat.

Pac. 2, 1906, 407-408) to its introduction into the Pacific islands and excluded dispersal of *Lemnaceae* over wide seas.

Taxonomy. Two subfamilies can be recognized within the Lemnaceae, the Lemnoideae and the Wolffioideae. The Lemnoideae are characterized by the presence of roots, 2 budding pouches, an inflorescence with 2 male flowers and a membranous spathe. The Wolffioideae have only 1 budding pouch and an inflorescence with 1 male flower; roots and spathe are absent. See for our new system of Lemnaceae C. DEN HARTOG & F. VAN DER PLAS (Blumea 18, 1970, 355-368).

Affinity within Lemnaceae. In comparing the genera, it is clear that there is an increase in reduction from Spirodela, via Lemna, to the Wolffioideae, Lemnoideae having 2 male flowers with bilocular stamens, roots, and a spathe, against Wolffioideae with 1 male flower with unilocular stamens but with neither roots nor spathe. The latter appear further derived because of the differentiation of the reproductive structures, viz the (vegetative) budding pouch and dorsal flowering cavity.

Compared with *Spirodela*, *Lemna* seems the more reduced or specialized genus, each frond producing only one root, or none at all; the scales are connate with the root sheath (only visible as two lateral wings on the root sheath in *L. perpusilla*), the stipe is entirely merged with the daughter frond, while the budding pouches are more marginal.

As to the position of the flowers, the gynoecium is placed at the dorsal side of the pouch, the 2 anthers at the ventral side, their insertions forming a sort of triangle.

Affinity of Lemnaceae with other families. The interpretation of the flower structure has been various. Eichler (Blüthendiagramme 1, 1875, 73-80), and recently Lawalree (Bull. Soc. R. Bot. Belg. 77, 2, 1945, 27-38) homologize the spathe of Lemnoideae with the membranous floral envelope in Najadaceae and accept the floral structure of each frond to represent a single bisexual flower.

Most authors, however, homologize the floral envelope as a true spathe comparable with that found in Araceae (in the aquatic Pistia it is also membranous) and the gynoecium and stamens as representing each a reduced unisexual flower. Furthermore, the seed structure of Lemnaceae closely resembles that of Araceae according to S. C. Maheswari & R. N. Kapil (J. Ind. Bot. Soc. 43, 1964, 270-277); in both groups there are 2 integuments. The same authors (Am. J. Bot. 50, 1963, 907-914) could show earlier that the endosperm in Lemnaceae is cellular, and not helobial as stated by Lawalrée, which is also in favour of affinity with Araceae and not with Helobiae. Furthermore, seeds of Lemnaceae have an operculum as in Araceae according to Johri (Rec. Adv. Embr. Angiosp. 1963, 398) which does not occur in Helobiae.

Among Araceae, the aquatic genus Pistia is possibly most related to Lemnaceae, in having in each spathe a single female flower and a clump-like whorl of 2-8 stamens separate from it. Furthermore, ENGLER showed (in E. & P. Nat. Pfl. Fam. 2, 3, 1889, 154-164) that the germination of the seeds in Pistia and Lemna proceeds in a rather similar way. Besides, both Pistia and Lemna have in common the occurrence of a similar vegetative reproduction. In Pistia stolons are developing from leaf-axils, producing at the end a new rosette. In Lemnoideae new fronds are produced on a stipe emitted from the budding pouch of the mother frond at the node and partly connate with it. In Pistia the young plant is originally surrounded by a membranous early disrupted sheath. A very comparable structure is found in Spirodela, where the daughter frond is basally enveloped by the partially connate dorsal and ventral scale. It seems almost impossible to escape from the impression that these scales are homologous with the envelope in Pistia. In passing, it may be remarked that in Aponogeton undulatus Roxe, which also produces runners with apical plantlets, the latter are surrounded by a membranous spathe. The morphologic interpretation of the spathe cq. scales is unclear.

Whereas these arguments indubitably show the affinity of Lemnaceae with Araceae, the homology of the 'frond' of Lemnaceae is less evident. Velenovski (Vergl. Morph. Pfl. 2, 1907, 339–345) mentioned the occasional reduction of the leaves in Pistia to a few or even one. In both the frond of Lemnaceae and Pistia veins are curvinerved. I envisage to elaborate the idea of the homology of the Lemnaceous frond and the leaf rosette of Pistia in another paper.

Palynology. The palynological data give no indication about the systematic relationship of the Lemnaceae with other families. Erdtman (Pollen Morph. Pl. Tax. Angiosp. 1952, 232) found that the pollen of some Lemnaceae have some characters in common with the pollen of some Araceae, while the pollen of the Najadaceae seems to be less similar. Thankaimoni (Trav. Sect. Sc. & Tech. 5, 5, 1969, 19-26) found no affinity between Pistia and the Lemnaceae. The pollen type of the Lemnaceae has not been found in the genera of the Araceae so far studied by Thankaimoni.

Palaeobotany. Fossil Lemnaceae are very scarce; most fossils described as Lemna are not Lemnaceae at all. Henslow (J. Linn. Soc. Bot. 29, 1893, 486-487) reported a Protolemna described by SAPORTA from strata above the Later Jura. This plant resembles the present Lemnaceae in some respects, but it possesses an axis bearing leaves with a dicotyledon-like venation. Beatson (New Phytol. 54, 1955, 208) reported subfossil Lemna-like pollen in Quarternary deposits. DARRAH (Textbook of Paleobotany, 1939, 300-302) reported a Spirodela from the Miocene and questioned the identity of some species reported from the Cretaceous and the Tertiary.

Phytochemistry. Oxalate of lime (raphides; clustered crystals) is present in many, but by no means in all, members of the family. So-called myriophyllin cells (see sub Haloragaceae) occur in species of Spirodela, Wolffia and Wolffiella. The flavonoid constituents were investigated thoroughly. Four main

types of flavonoid compounds occur in the family and each species and genus is said to be characterized by a distinct pattern of flavonoids. According to J. W. McClure & R. E. Alston (Am. J. Bot. 53, 1966, 849–860) and B. L. Turner (Chemistry Nat. Prod., 4th Int. Symp. Stockh. 1966, 1967, 201–205) Spirodela shows the most complex pattern of flavonoid compounds; anthocyanins, flavonols, flavones and C-glycoflavones are present. In Lemna the property to produce flavonols is lost. The only flavonoid compounds observed in Wolffiela are flavonols. Three species of Wolffia were found to contain only flavonols and two species to produce only flavones and glycoflavones. Two lines of reductive biochemical evolution, both starting with Spirodela are evident: Spirodela \rightarrow Lemna \rightarrow Wolffia p.p. and Spirodela \rightarrow Wolffiella \rightarrow Wolffia p.p. The American authors assume that the evolution of taxa most probably followed the same pathway and that Wolffia, as defined by morphology, represents a biphyletic group. Regrettably, members of the genera Pseudowolffia and Wolffiopsis were not included in these studies. The pectic substances of cell walls of Lemnaceae contain galacturonic acid, apiose and xylose (E. Beck, Z. Pflanzenphys. 57, 1967, 444–461). Such apiose-containing pectines occur in all members of the family investigated hitherto. This striking chemical feature, however, seems to be linked with ecology rather than with systematics (C. F. Van Beusekom, Phytochemistry 6, 1967, 573–576).

Most authors assume intimate relationships between Araceae and Lemnaceae. The chemical characters so far known from both families (Hegnauer, Chemotax. d. Pfl. 2, 1963, 73-99, 267-269, 483) are in perfect agreement with such a hypothesis. The fact, however, that chemical information about these families is still scanty implies that such a statement indicates lack of negative evidence, rather, than strong positive evidence. — R. Hegnauer.

Uses. Because of their high rate of vegetative reproduction and the ease with which they can be cultured, *Lemnaceae* are often used in plant physiological experiments (HILLMAN, Bot. Rev. 27, 1961, 221-287).

Collecting & preservation. For the identification of Wolffia species it is necessary to know the exact shape of the fronds. Unfortunately the usual procedure of boiling dried specimens for a while is inadequate as the pressed fronds generally remain flat. Those which do not are mostly resting buds which usually have a somewhat aberrant shape. Therefore, it is recommended that when collecting the plants should be put in fluid at once. Formalin is not advisable since the plants become very fragile in it, although they keep their original form. They remain more plastic and cannot be damaged in any way when collected in FAPA (ingredients for 1 liter: 50 cc formalin 40 %, 25 cc acetic acid, 25 cc propionic acid and 900 cc spirit 50-70 %).

KEY TO THE GENERA

- 1. Roots present. Budding pouches 2, basal, lateral, one on either side of the axis. Inflorescence developing from one of the budding pouches, consisting of 1 \(\varphi\$ and 2 \(\precedit{\pi}\$ flowers enclosed by a membranous spathe. Anther bilocular, transversely dehiscent. Stipe present. Raphides present.
- Fronds with a dorsal and a ventral scale, one to many roots and 3-15 nerves. Stipe ventrally attached. Brown pigment cells and druses in the parenchyma.
 1. Spirodela
- Fronds without dorsal and ventral scales, with one root (rarely none) and 1-3, often indistinct nerves. Stipe marginally attached. Brown pigment cells and druses absent.
 2. Lemna

1. SPIRODELA

Schleid. Linnaea 13 (1839) 391, nom. gen. cons. prop.; Hegelm. Lemnac. (1868) 147; Bot. Jahrb. 21 (1895) 283; Daubs, Monogr. Lemnac. (1965) 8; Hartog, Taxon 19 (1970) 647–648; Hartog & Plas, Blumea 18 (1970) 358. — Lenticularia Séguier, Pl. Veron. 3 (1754) 129, nom. gen. rejic. prop. — Lemna sect. Spirodela Coss. & Germ. Fl. Env. Paris 2 (1845) 577. — Lemna subg. Spirodela Peterm. Deutschl. Fl. (1849) 540; Rouy, Fl. Fr. 13 (1912) 285. — Fig. 1 A-B, 2-3.

Small water plants, floating at the surface. Fronds either solitary or connected in groups of 2-5 (sometimes even more), symmetric or asymmetric, reniform to obovate, flat or distinctly inflated; dorsal side flat or slightly convex, smooth or with some small median papillae; underside often red due to pigment cells in the epidermis; brown pigment cells, raphides and druses in the parenchyma; stomata on the dorsal side; margin entire; nerves 3-15. Stipe hyaline, fugacious,

short or relatively long, attached to the underside of the frond. Dorsal scale present, fugacious in older plants. Ventral scale broad, often pigmented. Roots 1-18, more or less vascularized; root sheaths short, clustered together and covered by the ventral scale with which some of them are adnate; one or more roots perforating this scale (primary roots); root cap straight or slightly curved, acute or rarely obtuse. Budding pouches 2, basal, lateral, one on either side of the axis, dorso-ventrally flattened, more or less triangular in outline, opening by a transverse slit, which is ventral to the margin of the frond. Inflorescence 1, lateral, developing from one of the budding pouches, consisting of $1 \circ 2$ and $2 \circ 3$ flowers, enclosed by a membranous spathe. Anther bilocular, transversely dehiscent. $9 \circ 3$ Flower superior and lateral to the $3 \circ 3$ flowers, consisting of a globular ovary with a short, partly persistent style and 1 amphitropous or $3 \circ 3$ anatropous ovula. Fruit asymmetric, slightly or distinctly winged. Seed smooth or longitudinally ribbed.

Distr. Worldwide, the Arctic regions excepted, consisting of 4 spp.

KEY TO THE SPECIES

- Fronds 5-12 mm long. Roots 7-16, one perforating the ventral scale. Nerves 7-12. Seeds smooth.
 S. polyrhiza
- Fronds 2-5 mm long. Roots 1-9(-12), all perforating the ventral scale. Nerves 3-5. Seeds ribbed.
 S. punctata

1. Spirodela polyrhiza (L.) Schleid. Linnaea 13 (1839) 392; ZOLL. Nat. Geneesk. Arch. N. I. 2 (1845) 212; HASSK. Flora 30 (1847) 469; Miq. Fl. Ind. Bat. 3 (1855) 222; Kurz, Nat. Tijd. N. I. 27 (1864) 220; HEGELM. Lemnac. (1868) 151-152; Bot. Zeit. 29 (1871) 621, 645; FRANCH. & SAV. En. Pl. Jap. 2 (1879) 13; HEGELM. Bot. Jahrb. 21 (1895) 284; THOMPSON, Rep. Mo. Bot. Gard. 9 (1897) 27; USTERI, Vierteljahrschr. Naturf. Ges. Zürich 50 (1905) 453; MERR. Fl. Manila (1912) 134; En. Philip. 1 (1923) 190; BACK. Handb. Fl. Java 3 (1924) 1; Onkruidfl. Jav. Suikerr. 1 (1928) 175; Steen. Arch. f. Hydrobiol. Suppl. 11 (1932) 292; HAND.-MAZZ. Symb. Sin. 7 (1936) 1368; JUMELLE in Humbert, Fl. Madag. fam. 32 (1937) 3-4; McCann, J. Bomb. Nat. Hist. Soc. 43 (1942) 156-157; MASAMUNE, Fl. Kainantensis (1943) 394; Sc. Rep. Kanazawa Univ. 5 (1957) 92-93; DAUBS, Monogr. Lemnac. (1965) 10-13, incl. var. masonii Daubs; Hess, Landolt & Hirzel, Fl. Schweiz 1 (1967) 497; BACK. & BAKH. f. Fl. Java 3 (1968) 127; CLARK & THIERET, Mich. Botanist 7, 2 (1968) 69; HARTOG & PLAS, Blumea 18 (1970) 360. — Lemna polyrhiza Linné, Sp. Pl. (1753) 970; Kurz, J. Linn. Soc. Lond. 9 (1866) 267-268; BENTH. Fl. Austr. 7 (1878) 164; Naves, Novis. App. (1882) 296; Hook. f. Fl. Br. Ind. 6 (1893) 557; TRIM. Handb. Fl. Ceyl. 4 (1898) 367; RIDL. J. Str. Br. R. As. Soc. n. 33 (1900) 179; BROWN, Fl. Trop. Afr. 8, 2 (1901) 201; COLLETT, Fl. Simlensis (1902) 545; WRIGHT, J. Linn. Soc. Bot. 36 (1903) 188; PRAIN, Bengal Pl. 2 (1903) 841; Ridl. Mat. Fl. Mal. Pen. 3 (1907) 53; F. M. Bailey, Queensl. Agric. J. 2, 1 (1914) 78; RIDL. J. Mal. Br. R. As. Soc. 1 (1923) 106; Fl. Mal. Pen. 5 (1925) 132; HEND. Gard. Bull. S. S. 4 (1928) 352; FISCHER in Gamble, Fl. Madras 3, 9 (1931) 1593; GAGNEP. Fl. Gén. I.-C. 6 (1942) 1198; MITRA, Fl. Pl. E. India 1 (1958) 86; HUNDLEY & U CHIT Ko Ko, List trees etc. Burma ed. 3 (1961) 292; LARSEN, Dansk Bot. Ark. 20 (1962) 136; OHWI, Fl. Japan (1965) 264. — Lenticula polyrhiza (L.) LAMK, Fl. Fr. 2 (1778) 189. — Lemna orbicularis KIT. ex SCHULTES, Oesterr. Fl. ed. 2, 1 (1814) 64, nomen seminudum. — Lemna thermalis BEAUV. J. Phys. Chim. Hist. Nat. 82 (1816) 102, 113, f. 23; NUTTALL, Gen. Amer. 1 (1818) 19. — Lemna orbiculata ROXB. [Hort. Beng. (1814) 66, nomen] Fl. Ind. ed. Carey 3 (1832) 565. — Telmatophace polyrhiza (L.) Goden Fl. Lorr. ed. 1, 3 (1843) 18. — Lemna major [C. A. MEYER, Ind. Cauc. (1831) 11, nomen] GRIFF. Not. 3 (1851) 216; Ic. Pl. As. 3 (1851) t. 264. — Telmatophace orbicularis Schur, En. Pl. Transs. (1866) 635. — S. atropurpurea Montand. Guide Bot. (1868) 309. — Lemna maxima Blatter & Hallb. J. Ind. Bot. Soc. 2 (1921) 49. — S. maxima (BLAT-TER & HALLB.) MCCANN, J. Bomb. Nat. Hist. Soc. 43 (1942) 158. — Fig. 1 A-B, 2.

Fronds solitary or cohering in groups of 2-5, symmetric or asymmetric, reniform to round or obovate, 3-12 by 2½-8 mm; base obtuse; apex obtuse or round; dorsal side flat, smooth; ventral side flat to strongly inflated; green, ventral side and margin often red-purple; nerves 7-12; stipe hyaline, often long, prominent; dorsal scale membranous, orbicular to reniform, attached to the base, disappearing in older plants; ventral scale membranous, broad, with much brown pigment, almost centrally attached near the node, covering

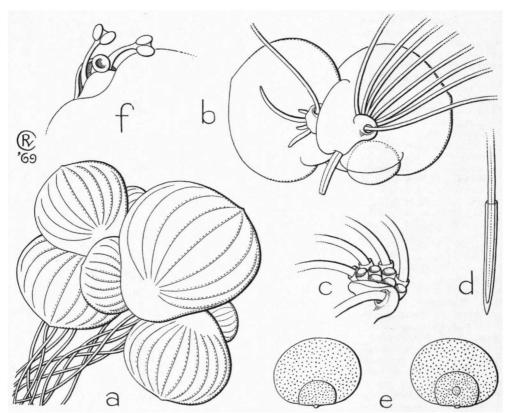


Fig. 2. Spirodela polyrhiza (L.) SCHLEID. a. Habit, mother frond with adhering offspring, dorsal view, $\times 6$, b. habit, ventral view, the sheaths of the secundary roots covered by the ventral scale, $\times 6$, c. detail from ventral side, the primary root piercing the ventral scale, $\times 12$, d. root cap, $\times 12$, e. turion, dorsal view (left) showing dorsal scale and ventral view (right) showing ventral scale, primordium of primary root sipe a minute protuberance, $\times 18$, f. detail of flowering frond, with style and 2 stamens enveloped by the spathe, $\times 18$ (a-d Van der Plas 23-9-69, e Hall Sept. 1867, f Stalin 451).

the bases of the roots. Roots 7-16, one (very rarely 2) perforating the ventral scale (primary roots), the others passing between the scale and the frond (secondary roots); primary roots appearing earlier than the secondary ones. Root cap acute. Ovary with 1 amphitropous ovule or 2 anatropous ones. Fruit a 1-2 seeded utricle, slightly winged. Seed smooth.

Distr. Almost cosmopolitan, common in the northern hemisphere, rather rare in Africa and Australia, in South America replaced by two closely related species; in *Malesia* common: Sumatra, Malay Peninsula, W.-E. Java, Flores Sea (Tanah Djampea, S of Celebes, N. Celebes, Philippines (Luzon to Mindanao), New Guinea. Also in the Hawaiian Is. (1895 Heller; 1927 LE ROY TOPPING), together with *Lemna perpusilla*.

Ecol. Stagnant fresh water habitats such as sawahs, ponds and ditches, rarely in slightly brackish water, from the lowland to c. 2100 m. Vern. Kakarèwoan, S, mata lèlè, J.

Notes. Like many other Lemnaceae this species often forms resting-buds to survive less favourable times. In S. polyrhiza these resting-buds are easier to distinguish from the normal fronds than in the other Lemnaceous species and are often called 'turions'. They are produced in the normal way in the budding pouch. The turion is reniform, dorso-ventrally flattened, variable in size, consisting of dense tissue. Its roots are still present but when dormant only the primary roots are visible. On both sides it bears a membranous scale as does a normal young frond.

2. Spirodela punctata (G. F. W. MEYER) THOMP-SON, Rep. Mo. Bot. Gard. 9 (1897) 28; DAUBS, Monogr. Lemnac. (1965) 15; CLARK & THIERET, Mich. Bot. 7, 2 (1968) 69; HARTOG & PLAS, Blumea 18 (1970) 360. — Lemna punctata G. F. W. MEYER, Prim. Fl. Esseq. (1818) 262. — Lemna gibba (non L.) BLANCO, Fl. Filip. ed. 1 (1837) 672; ed. 2 (1845) 468; ed. 3, 3 (1879) 78; NAVES, Novis. App. (1882) 296. — Lemna oligorrhiza Kurz, J. Linn. Soc. Lond. 9 (1866) 267, t. 5, f. 1-6; BENTH. Fl. Austr. 7 (1878) 163; NAVES, Novis. App. (1882) 296; Hook. f. Fl. Br. Ind. 6 (1893) 557; Prain, Bengal Pl. 2 (1903) 841; Guppy, Observ. Nat. Pac. 2 (1906) 407-408; SCHWARZ in Fedde, Rep. 24 (1928) 80; GREENWOOD Proc. Linn. Soc. 154, 2 (1943) 104; Guillaumin, Fl. Nouv.-Caléd. (1948) 48; MITRA, Fl. Pl. E. India 1 (1958) 86; Guillaumin, Mém. Mus. Hist. Nat. Paris n.s. sér. B, Bot. 8 (1959) 189; ibid. (1962) 213; PARHAM, Pl. Fiji Is. (1964) 268. – Lemna melanorrhiza F. v. M. ex Kurz, J. Bot. 5 (1867) 115. — Lemna pleiorrhiza F. v. M. ex Kurz, I.c. — S. oligorrhiza Hegelm. Lemnac. (1868) 147–150, incl. var. β melanorrhiza (F. v. M. ex Kurz) Hegelm., var. γ pusilla Hegelm., var. δ pleiorrhiza (F. v. M. ex Kurz) Hegelm., var. ε javanica HEGELM.; ENGL. Bot. Jahrb. 7 (1886) 448; HEGELM. Bot. Jahrb. 21 (1895) 287; F. M. BAILEY, Queensl. Fl. 5 (1902) 1700; MIKI, Bot. Mag. Tokyo 48 (1934) 333; McCann, J. Bomb. Nat. Hist. Soc. 43 (1942) 157; Black, Fl. S. Austr. ed. 2 (1948) 172; DAUBS, Monogr. Lemnac. (1965) 14-15; Oнwi, Fl. Japan (1965) 264; МсСомв & McComb, J. R. Soc. W. Austr. 50, 4 (1967) 107; BACK. & BAKH. f. Fl. Java 3 (1968) 127. — S. melanorrhiza HEGELM. Bot. Jahrb. 21 (1895) 287. - S. pusilla Hegelm. l.c. — S. pleiorrhiza He-GELM. I.c. 288. — S. javanica HEGELM. I.c. — Fig 3.

Fronds solitary or cohering in groups of 2-6, asymmetric, elliptic to obovate, 2.8-4.5 by 1.4-2.6 mm, base and apex asymmetric, obtuse; mostly thick, dorsal side flat to slightly convex, smooth or with a median row of small papillae; ventral side flat to convex, sometimes slightly inflated and with relatively few large air spaces; green, sometimes red; nerves 3-5; stipe hyaline, often long and distinct; dorsal scale strongly reduced, fugacious; ventral scale membranous, often pigmented, perforated by the short sheaths of all (1-9, sometimes 12) roots; root cap straight or slightly curved, acute, with or without pigment. Ovary with 1 amphitropous ovule. Fruit asymmetric, winged. Seed longitudinally ribbed.

Distr. Apparently rare in Africa and South

America, common in Asia and Australia, in the Indian Ocean in the Maldives (Mahé Atoll), in the Pacific Ocean in New Caledonia and Fiji; in *Malesia*: Malay Peninsula (Pahang) and Java (west to east).

According to DAUBS (1965) introduced in America, but this must then have been before 1814 when G. W. F. MEYER recorded it from there already. According to GUPPY (1906) introduced in the Pacific islands. Dispersal by man has certainly given this species a wider distribution in recent time; it is e.g. not rare in the rice-fields in Italy. Also its obviously local occurrence in Malesia might point to introduction.

Ecol. From sea-level to c. 2100 m, both in everwet areas and areas subject to a severe dry season.

Notes. S. punctata is a very variable species; several of its characters show considerable variations in different localities. As a result of this there are some populations which are characterized by a certain peculiarity not occurring in other populations. In some collections from Java the number of roots is extremely large (up to 12!), in other areas the number of roots rarely exceeds 5. The plants from New Caledonia and Fiji are characterized by a much heavier pigmentation than in other areas. These characters vary independently of each other, and do not seem to be constant even within one collection.

It is thus understandable that F. VON MÜLLER (ex Kurz, 1867) on the grounds of a small number of collections came to recognize 3 species in this complex, and that HEGELMAIER (1868) distinguished 5 varieties within S. oligorrhiza (raised to the rank of species in his paper of 1895). My investigation of much more material than these authors had at their disposal leads, however, to the conclusion that these taxa all belong to a single species, S. punctata, in which they are linked by all possible transitions.

From Blanco's description of Lemna gibba it is obvious that the plant in question was in fact S. punctata. Merrill (Sp. Blanc. 1918, 93) erroneously interpreted L. gibba 'Blanco' as L. paucicostata (= L. perpusilla).

2. LEMNA

LINNÉ, Gen. Pl. ed. 5 (1754) 417; Sp. Pl. (1753) 970; HEGELM. Lemnac. (1868) 134; Bot. Jahrb. 21 (1895) 288; DAUBS, Monogr. Lemnac. (1965) 16; HARTOG & PLAS, Blumea 18 (1970) 360. — Lenticula [HILL. Brit. Herb. (1757) 530] BOEHMER in Ludwig, Def. Gen. Pl. (1760) 499. — Hydrophace HALL. Hist. Stirp. Indig. Helv.

Fig. 3. Spirodela punctata (G. F. W. MEYER) THOMPSON. a. Habit, mother frond with fruit and daughter frond, $\times 12$, b. ditto, $\times 12$, c. ventral view roots piercing ventral scale, $\times 12$, d. detail of c, $\times 24$, e. ventral view, 1-rooted frond, $\times 12$, f. ditto, detail from e, $\times 24$, g. habit, dorsal view, $\times 12$, h. lateral view, $\times 12$, i. ventral view of a plant from Java with many roots, $\times 12$, j. ventral view of a frond with 2 roots, $\times 12$, k, detail of the inflorescence, $\times 24$ (a Den Hartog 779, b-d Den Hartog s.n., e-f, j-k Den Hartog 1161, g-h Den Hartog 190, i Koorders 21531).

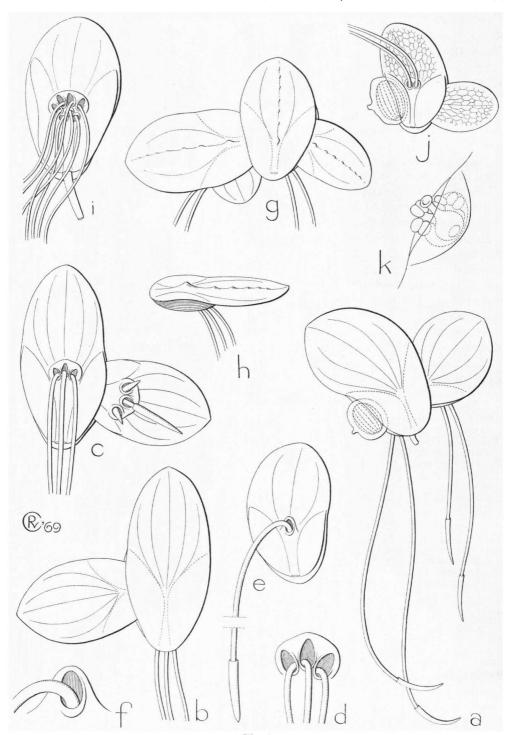


Fig. 3

3 (1768) 68. — Telmatophace Schleid. Linnaea 13 (1839) 391. — Staurogeton Rchb. [Consp. (1828) 288, nomen] Nom. (1841) 33. — Lenticularia Montandon, Guide Bot. (1868) 308, non Séguier, Pl. Veron. 3 (1754) 129. — Fig. 4–7.

Small aquatics, floating at the surface or sometimes completely submerged in which case they come to the surface only in the flowering period. Fronds either solitary or connected in groups of 2-10 (sometimes even more), symmetric to slightly asymmetric, round, elliptic, oblong, obovate or lanceolate, flat or slightly swollen, sometimes considerably inflated at the ventral side, often with a median row of papillae on the flat or slightly convex dorsal side; with or without red pigment cells in the epidermis; raphides in the parenchyma; no brown pigment cells; druses none; stomata on the dorsal side of floating plants, but absent in the submerged plants; margin entire, rarely denticulate; nerves 1-3(-5). Stipe hyaline and fugacious or green and persistent, attached to the margin. Dorsal as well as ventral scale absent. Root 1 (rarely absent), slightly vascularized, with or without a distinct root sheath; root cap straight or curved, obtuse, mucronate or acute. Budding pouches 2, basal, lateral, one on either side of the axis, dorso-ventrally flattened, more or less triangular in outline, opening by a transverse slit; slit coinciding with the margin of the frond, rarely ventral or dorsal to the margin. Inflorescence 1, lateral, developing from one of the budding pouches, consisting of 1 \Q and 2 \d flowers enclosed by a membranous spathe. Anther bilocular, transversely dehiscent. Q Flower superior and lateral to the 2 & flowers, consisting of a globular ovary with a short, persistent style. Ovary with 1 orthotropous or amphitropous ovule or with 2-4 anatropous ovules. Fruit symmetric or asymmetric, more or less compressed, with or without wings. Seeds longitudinally ribbed, rarely smooth.

Distr. 9 spp., worldwide with the exception of the Arctic regions.

Taxon. The genus can be subdivided into 2 subgenera:

1. Subg. Lemna. Floating water plants with round, elliptic, oblong or obovate fronds. Root 1, with a distinct root sheath. Slit of budding pouch coinciding with the margin of the frond, rarely ventral to the margin. Ovary with 1-4 ovules.

2. Subg. Staurogeton RCHB. Fl. Germ. 1 (1830) 10. Submerged water plants, only rising to the surface in the flowering period. Fronds oblong to linear-lanceolate, with or without a root. Root sheath indistinct. Slit of budding pouch just dorsal to the margin of the frond.

KEY TO THE SPECIES

- 1. Floating water plants. Fronds round to oblong or obovate, with 1 root. Slit of budding pouch coinciding with the margin of the frond, rarely ventral to the margin. Subg. Lemna.
- 2. Root sheath with lateral wings. Fruit asymmetric; ovule 1, orthotropous. 1. L. perpusilla
- 2. Root sheath without wings. Fruit symmetric; ovules amphitropous or anatropous.

Fig. 4. Lemna perpusilla Torrey. a. Habit, mother frond with adhering offspring, dorsal view, $\times 18$, b. root cap, $\times 36$, c. lateral view, frond with apical and nodal papillae, $\times 18$, d. ditto, only with apical papilla, $\times 18$, e. ditto, without papillae, $\times 18$, f. habit, plant from New Guinea, dorsal view, elongated fronds, $\times 18$, g. ventral view, showing root emitted, $\times 18$, h. detail of root sheath provided with 2 lateral wings, $\times 36$, t. mother frond and daughter frond, both with inflorescence, $\times 18$, j. detail of a flowering frond in which inflorescence and daughter frond develop simultaneously in the same reproductive pouch, $\times 36$, k. frond with fruit and daughter frond, dorsal view, $\times 18$, l. seed, $\times 40$, m. ditto, longitudinal section, $\times 80$, n. germinating seed, showing plumule and first frond, dorsal (left) and ventral view (right), $\times 18$ (a-c, i-n Den Hartog 632, d Backer 19104, e Backer 25650, f Brass 8112, g Lutieharms 5387, h Den Hartog 188).

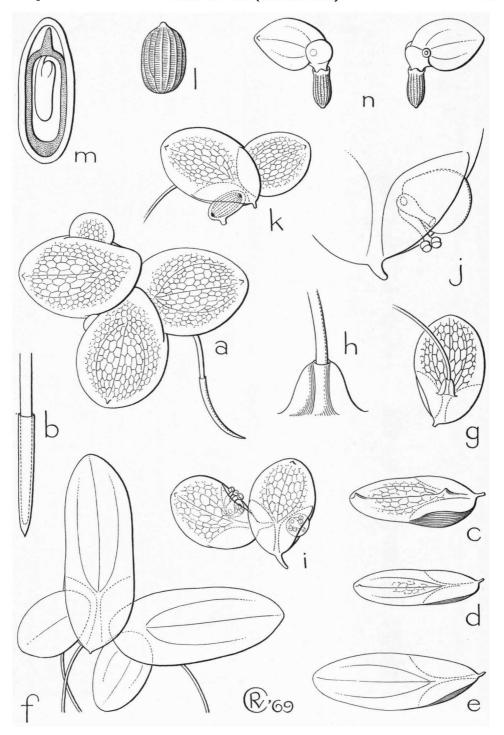


Fig. 4

- 3. Frond mostly symmetric, ventral side flat to slightly convex, never inflated. Cells on ventral side not visible to the naked eye. Fruit without wings. Ovule 1, amphitropous. Slit of budding pouch coinciding with the margin of the frond
- 1. Submerged water plants, only floating at the surface when flowering. Fronds oblong to linear-lanceolate, often without a root. Slit of budding pouch just dorsal to the margin of the frond. Subg. Staurogeton.
- 4. Margin denticulate towards the apex. Stipe usually strongly elongate, green, persistent.

1. Lemna perpusilla Torrey, Fl. N. Y. 2 (1843) 245; Austin in A. Gray, Man. Bot. ed. 5 (1867) 479, incl. var. trinervis Austin; Hegelm. Lemnac. (1868) 139; Bot. Jahrb. 21 (1895) 294; THOMPSON, Rep. Mo. Bot. Gard. 9 (1897) 33; DAUBS, Monogr. Lemnac. (1965) 25-27; BACK. & BAKH. f. Fl. Java 3 (1968) 127. — L. minor (non L.) Lour. Fl. Cochinch. 2 (1790) 550; HASSK. Cat. Hort. Bog. (1844) 53, 302; Jungh. Reisen (1845) 42; GRIFF. Not. 3 (1851) 216; MIQ. Pl. Jungh. (1852) 169; JUNGH. Java ed. 2, 1 (1853) 285-287; Miq. Fl. Ind. Bat. 3 (1855) 221; Kurz, Nat. Tijd. N. I. 27 (1864) 220; J. Linn. Soc. Lond. 9 (1866) 266; J. Bot. 5 (1867) 115; BENTH. Fl. Austr. 7 (1878) 163, p.p.; NAVES, Novis. App. (1882) 296; Hook. f. Fl. Br. Ind. 6 (1893) 556, p.p.; MASSART, Bull. Soc. R. Bot. Belg. 34 (1895) 184; KOORD. Med. Lands Plantentuin 19 (1898) 305; F. M. BAILEY, Queensl. Fl. 5 (1902) 1700, p.p.; GUPPY, Observ. Nat. Pac. 2 (1906) 407-408; Koord. Exk. Fl. Java 1 (1911) 268; BOLD. Zakfl. Landbouwstr. Java (1916) 125; BURK. Dict. (1935) 1328; GAGNEP. Fl. Gén. I.-C. 6 (1942) 1197; GUILLAUMIN, Fl. Nouv.-Caléd. (1948) 48; Larsen, Dansk Bot. Ark. 20 (1962) 136; GUILLAUMIN, Mém. Mus. Hist. Nat. Paris n.s. sér. B, Bot. 8 (1962) 213; PARHAM, Pl. Fiji Is. (1964) 268. — L. aequinoctialis Welw. Apontam. Phytogeogr. Fl. Prov. Angola, Ann. Conselho Ultram. Dec. 1858, n. 55. (1859) 578; Brown, Fl. Trop. Afr. 8, 2 (1901) 203; GIARDELLI, Darwinia 11 (1959) 584-590. - L. angolensis Welw. ex Hegelm. J. Bot. 3 (1865) 112; HEGELM. Lemnac. (1868) 141-142; Bot. Jahrb. 21 (1895) 296. — L. paucicostata HEGELM. Lemnac. (1868) 139, incl. var. membranacea HEGELM. I.c. 141; KURZ, J. As. Soc. Beng. 45, ii (1876) 153; Franch. & Sav. En. Pl. Jap. 2 (1879) 12; HOOK. f. Fl. Br. Ind. 6 (1893) 556; HEGELM. Bot. Jahrb. 21 (1895) 294-296; TRIM. Handb. Fl. Ceyl. 4 (1898) 366; RIDL. J. Str. Br. R. As. Soc. n. 33 (1900) 179; Brown, Fl. Trop. Afr. 8, 2 (1901) 202-203; PRAIN, Bengal Pl. 2 (1903) 841; Wright, J. Linn. Soc. Bot. 36 (1903) 188; Usteri, Vierteljahrschr. Naturf. Ges. Zürich 50 (1905) 453; Guppy, Observ. Nat. Pac. 2 (1906) 407-408; RIDL. Mat. Fl. Mal. Pen. 3 (1907) 52; Merr. Fl. Manila (1912) 134; RIDL. J. Mal. Br. R. As. Soc. 87 (1923) 106; Merr. En. Philip. 1 (1923) 190; BACK. Handb. Fl. Java 3 (1924) 2; RIDL. Fl. Mal. Pen. 5 (1925) 132; HEND. Gard.

Bull. S. S. 4 (1928) 352; BACK. Onkruidfl. Jav. Suikerr. 1 (1928) 175; Fischer in Gamble, Fl. Madras 3 (1931) 1593; Steen. Arch. f. Hydrobiol. Suppl. 11 (1932) 291; MERR. Trans. Am. Phil. Soc. 24, 2 (1935) 100; CHRISTOPH. B. P. Bish. Mus. Bull. 128 (1935) 44; JUMELLE in Humbert, Fl. Madag. fam. 32 (1937) 2; McCann, J. Bomb. Nat. Hist. Soc. 43 (1942) 153; MASAMUNE, Fl. Kainantensis (1943) 394; BACK. Bekn. Fl. Java (em. ed.) 10 (1949) fam. 226, p. 2; HEND. Mal. Wild Fl. Monocot. (1959) 210; MASAMUNE, Sc. Rep. Kanazawa Univ. 5 (1957) 94; MITRA, Fl. Pl. E. India 1 (1958) 86; HUNDLEY & U CHIT Ko Ko, List trees etc. Burma ed. 3 (1961) 292; LARSEN, Dansk Bot. Ark. 20 (1962) 135; OHWI, Fl. Japan (1965) 265. — L. trinervis (AUSTIN) SMALL, Fl. SE. U.S. (1903) 230; DAUBS, Monogr. Lemnac. (1965) 27. — Hydrophace perpusilla (TORREY) LUNELL, Am. Midl. Nat. 4 (1915) 237. — L. minima BLATT. & HALLB. J. Ind. Bot. Soc. 2 (1921) 50. — L. blatteri McCANN J. Bomb. Nat. Hist. Soc. 43 (1942) 153. — L. eleanorae McCann, l. c. 154. — Fig. 4.

Small floating aquatic. Fronds solitary or cohering in groups of 2-5, asymmetric, ovate to obovate or sometimes obovate-oblong, 1.2-4.8 by 0.7-2.8 mm, thin, membranous to thickened, green, no red pigment cells; base strongly asymmetric, obtuse or slightly acute; apex nearly symmetric or asymmetric, obtuse to slightly acute; dorsal side slightly convex, with or without a row of median papillae, but often with a distinct, hook-shaped papilla near the apex; ventral side flat to convex, not inflated; nerves 3, sometimes indistinct; margin entire. Stipe hyaline, fugacious, sometimes persistent. Root sheath cylindrical with 2 lateral wings; root cap acute. Slit of budding pouch coinciding with the margin of the frond. Ovary with 1 orthotropous ovulum, style subapical, persistent. Fruit asymmetric, ellipsoid, laterally slightly compressed. Seed with 12-18 distinct longitudinal ribs, laterally slightly compressed.

Distr. Worldwide in the tropics and subtropics. In the Pacific islands in several Hawaiian Is. (first 1895), Samoa (1893), Tonga (1926), Fiji (1842), New Caledonia; common in Malesia: Sumatra (also Enggano), Malay Peninsula, W.-E. Java (also Madura & Kangean Is.), Lesser Sunda Is. (Timor), Flores Sea (Tanah Djampea), North Borneo, Philippines (Luzon to

Mindanao), Moluccas (Ambon; Aru Is.: Maikoor), and W.-E. New Guinea.

Ecol. The most common duckweed in Malesia. It occurs mostly in fresh water, but is sometimes found in slightly brackish water. In sawahs, ditches and small streams up to 2100 m, often together with other Lemnaceae (Spirodela). Flowering and fruiting occur commonly in this species.

Vern. Kiambang, M (Sum.), ganggéng, S; Philippines: inalia, lia, liya, Tag.

Notes. BACKER (1924) was the first to point out that *L. minor* does not occur in Malesia; he referred this material to *L. paucicostata*.

L. perpusilla is an extremely variable species. HEGELMAIER (1868) distinguished in his monograph 3 species, viz L. perpusilla (seed with 30-60 ribs, restricted to the eastern part of the U.S.A.), L. paucicostata (seed with 12-20 ribs, occurring in the tropics of the Old and the New Worlds; also in the S. and SE. parts of the U.S.A.) and L. angolensis (seed with 12-15 ribs, and moreover a conspicuous apical papilla on the frond, restricted to tropical Africa). L. angolensis, already earlier described as L. aequinoctialis by Welwitsch, is with respect to the seed character within the range of variation of L. paucicostata. The development of the apical papilla on the frond is subject to so much variation, even within one sample, that it is not useful as a specific character. THOMPSON (Ann. Rep. Mo. Bot. Gard. 9, 1897, 33) who investigated L. perpusilla and L. paucicostata in the U.S.A. found the number of ribs on the seeds of these species so variable that he could not distinguish the species with certainty, and for that reason he regarded them as forms of one species.

Some flat, membranous forms with a distinct venation, but otherwise not different from L. perpusilla, have been distinguished as L. perpusilla var. trinervis, L. paucicostata var. membranacea or as L. trinervis. They have been recorded from America and India. In my opinion they represent only forms of L. perpusilla, induced by poor environmental circumstances. McClure & Alston (Am. J. Bot. 53, 1966, 849-860), however, found L. trinervis to be quite distinct from L. perpusilla with respect to the flavonoid chemistry. Therefore, membranous forms require re-investigation.

The fronds from New Guinea are often twice as long as wide, in contrast to those from the rest of Malesia.

MERRILL (Sp. Blanc. 1918, 93) referred L. gibba (non L.) BLANCO to L. paucicostata (= L. perpusilla). As BLANCO recorded the occurrence of 2 roots, his plants must have belonged to Spirodela punctata. MERRILL's representative specimen Sp. Bl. 131 belongs to L. perpusilla.

Lemna minor Linné, Sp. Pl. (1753) 970; Hegelm. Lemnac. (1868) 142-144; Hook. f. Fl. Br. Ind. 6 (1893) 556, pro parte; Hegelm. Bot. Jahrb. 21 (1895) 291-292; Daubs, Monogr. Lemnac. (1965) 21-25. — Fig. 5 f-h.

Small floating aquatic. Fronds solitary or cohering in groups of 2-5 (sometimes many more),

symmetric to slightly asymmetric, round-elliptic to elliptic or ovate; 1.5-4.6 by 1-2.9 mm; base \pm symmetric, obtuse; apex symmetric or slightly asymmetric; margin entire; dorsal side flat to slightly convex, often with a median row of papillae; ventral side flat to slightly convex; cells on ventral side not visible to the naked eye, green; nerves 3. Stipe often persistent and prominent; root sheath cylindrical, without wings, root cap obtuse. Slit of budding pouch coinciding with the margin of the frond. Ovary with 1 amphitropous ovule. Fruit ellipsoid, symmetric, laterally compressed, without wings. Seed smooth.

Distr. Widely distributed in the temperate zone of the northern hemisphere, reaching as far north as Alaska and northern Scandinavia. All records of *L. minor* from tropical Asia, Malesia and tropical Australia relate to *L. perpusilla*.

Lemna gibba Linné, Sp. Pl. (1753) 970; HEGELM. Lemnac. (1868) 145-147; HOOK. f. Fl. Br. Ind. 6 (1893) 556-557; HEGELM. Bot. Jahrb. 21 (1895) 289-290; KOORD. Exk. Fl. Java 1 (1911) 268-269; BACK. Bekn. Fl. Java (em. ed.) 10 (1949) fam. 226, p. 2; DAUBS, MONOGT. Lemnac. (1965) 17-19; BACK. & BAKH. f. Fl. Java 3 (1968) 127. — Telmatophace gibba (L.) SCHLEID. Linnaea 13 (1839) 391; MIQ. Fl. Ind. Bat. 3 (1855) 222; KURZ, J. Linn. Soc. Lond. 9 (1866) Bot. 266. — Fig. 5 a-e.

Small floating aquatic. Fronds solitary or cohering in groups of 2-4, mostly asymmetric, sometimes almost symmetric; round, ovate or obovate, 2.1-4.9 by 1.7-3.7 mm; base almost symmetric, obtuse to emarginate; apex mostly asymmetric, sometimes symmetric, obtuse to round; margin entire; dorsal side flat or convex, smooth or with a median row of papillae; ventral side flat to strongly inflated and globular, with a relatively small number of large air cavities; green or red on both sides; nerves 3-5, sometimes indistinct. Stipe often prominent and persistent. Root sheath cylindrical, short, without wings; root cap obtuse or sometimes acute. Slit of budding pouch ventral to the margin of the frond. Ovary with 1 amphitropous ovule or 2-4 anatropous ones. Fruit symmetric, ellipsoid, with lateral wings, dorso-ventrally compressed, with 1-4 seeds. Seeds longitudinally ribbed.

Distr. Reported from the temperate and tropical zones of the whole world, but doubtless many records relate to other species.

The records from Malesia are doubtful; among the material studied not one specimen of *L. gibba* was found. The record from the Philippines, listed by DAUBS, no doubt refers to MERRILL'S Sp. Bl. 131, which is *L. perpusilla*. The Australian records of *L. gibba* probably must be referred to *L. disperma* HEGELM.

2. Lemna trisulca LINNÉ, Sp. Pl. (1753) 970; SCHLEID. Linnaea 13 (1839) 391; Miq. Fl. Ind. Bat. 3 (1855) 222; GRISEB. Fl. Br. W. Ind. Is. (1864) 512; KURZ, J. Linn. Soc. Lond. 9 (1866) 268; J. Bot. 5 (1867) 166; HEGELM. Lemnac.

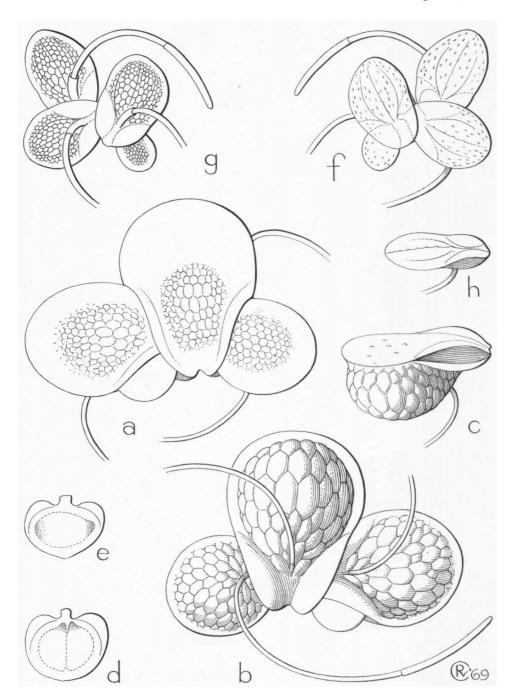


Fig. 5. Lemna gibba L. a. Habit, dorsal view, $\times 8$, b. ventral view showing subepidermal air cavities, $\times 8$, c. lateral view, $\times 8$, d. winged fruit with 2 seeds, $\times 18$, e. ditto, with 1 seed, $\times 18$. — L. minor L. f. Habit dorsal view, $\times 8$, g. ditto ventral view, $\times 8$, h. lateral view, $\times 8$ (a—e Heller 5571, f—h Van der Plas 29-4-69).

(1868) 134-136; BENTH. Fl. Austr. 7 (1878) 162; FRANCH. & SAV. En. Pl. Jap. 2 (1879) 12; HOOK. f. Fl. Br. Ind. 6 (1893) 557; HEGELM. Bot. Jahrb. 21 (1895) 293; MASSART, Bull. Soc. R. Bot. Belg. 34 (1895) 184; F. M. BAILEY, Queensl. Fl. 5 (1902) 1700; PRAIN, Bengal Pl. 2 (1903) 841; K. SCH. & LAUT. Nachtr. Fl. Schutzgeb. (1905) 62; KOORD. Exk. Fl. Java 1 (1911) 268; MERR. En. Philip. 1 (1923) 190; BACK. Handb. Fl. Java 3 (1924) 2; STEEN. Arch. f. Hydrobiol. Suppl. 11 (1932) 291; HAND.-MAZZ. Symb. Sin. 7 (1932) 1368; GAGNEP. Fl. Gén. I.—C. 6 (1942) 1198; MCCANN, J. Bomb. Nat. Hist. Soc. 43 (1942) 154; BLACK, Fl. S. Austr.

ed. 1, 2 (1948) 172; BACK. Bekn. Fl. Java (em. ed.) 10 (1949) fam. 226, p. 2; HERTER, Rev. Sudam. Bot. 9 (1954) 185; MITRA, Fl. Pl. E. India 1 (1958) 86; HUNDLEY & U CHIT KO KO, List trees etc. Burma ed. 3 (1961) 292; WILLIS, Handb. Pl. Vict. 1 (1962) 271; ZUTSHI & KAUL, Trop. Ecol. 4 (1963) 95-96; DAUBS, Monogr. Lemnac. (1965) 32-34; OHWI, Fl. Japan (1965) 265; HESS, LANDOLT & HIRZEL, Fl. Schweiz 1 (1967) 496; CLARK & THIERET, Mich. Bot. 7, 2 (1968) 73; BACK. & BAKH. f. Fl. Java 3 (1968) 127. — Lenticula trisulca Scop. Fl. Carn. ed. 2 (1772) 213; MOENCH, Meth. (1794) 319; St. HIL. Exp. fam.

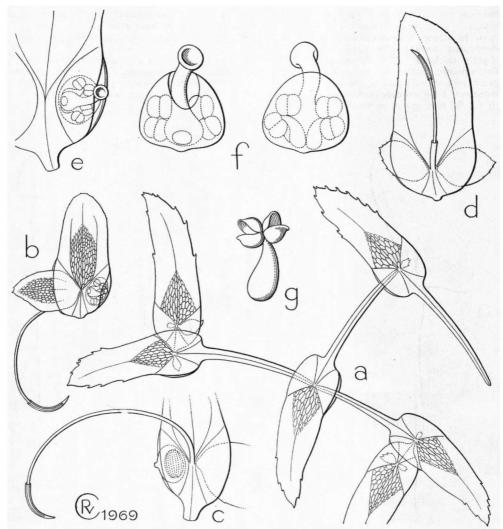


Fig. 6. Lemna trisulca L. a. Habit, submerged plant, \times 6, b. floating plant with inflorescence, dorsal view, \times 6, c. frond with fruit, ventral view, \times 6, d. ditto. \times 6, e. part of a flowering frond, dorsal view, \times 12, f. detail of inflorescence surrounded by spathe, \times 24, g. stamen, \times 24 (a Den Hartog 1162, b-g Holm-Berg 453).

nat. germ. pl. 1 (1805) 53. — Lenticula ramosa Lamk, Fl. Fr. 2 (1778) 189. — L. cruciata Roxb. [Hort. Beng. (1814) 66, nomen] Fl. Ind. ed. Carey 3 (1832) 566. — L. intermedia Ruthe, Fl. Mark Brandenb. Niederlausitz, ed. 2 (1834) 277. — L. bisulca C. A. Meyer, Beitr. Pfl. Russ. Reich 9 (1854) 104. — Staurogeton trisulcus (L.) Schur, En. Pl. Transs. (1866) 636. — Hydrophace trisulca (L.) Bubani, Fl. Pyren. 4 (1897) 23; Lunell, Am. Midl. Natur. 4 (1915) 237. — Fig. 6.

Submerged aquatic, only floating at the surface when flowering; when sterile many fronds connected in large groups, when fertile only 2 fronds cohering. Fronds symmetric, or almost so, oblong to linear-lanceolate, 2.5-6.9 by 1.1-2.9 mm; base slightly asymmetric or symmetric, narrowing into the stipe; apex symmetric or almost so, acute to obtuse; margin distinctly or indistinctly denticulate towards the apex; frond thin or slightly thickened when flowering; dorsal side flat, smooth; ventral side flat to slightly convex; green, without red pigment; nerves 1-3, sometimes indistinct. Stipe strongly prolonged, flat, up to 11 by 0.2-0.3 mm, green, persistent; when flowering

less distinct or not developed at all. Root often absent in submerged plants; root sheath very short, most indistinct; root cap acute. Slit of budding pouch just dorsal to the margin of the frond. Ovary with 1 amphitropous ovulum. Fruit broad, more or less symmetric. Seed ribbed.

Distr. Worldwide, but curiously absent from South America, extremely scarce in *Malesia*: North Sumatra (Toba Lake, not collected, cf. STEEN. 1932), Philippines (Luzon, Mindanao), S. Moluccas (Aru Is.: Maikoor I. leg. BECCARI, 26-6-73), and New Guinea.

For Java recorded from Bogor by MIQUEL (1855, l.c.) and again by MASSART (Un botaniste en Malaisie, 1895, 184) from inundated rice-fields near Bandung and Garut. No other botanists or collectors have ever found it in Java, so that we may safely assume that these two records rest on errors.

Ecol. Stagnant waters up to 1800 m, outside Malesia even recorded from 2800-3000 m. Mostly submerged, forming a dense layer below the surface of the water, sometimes together with Riccia spp.

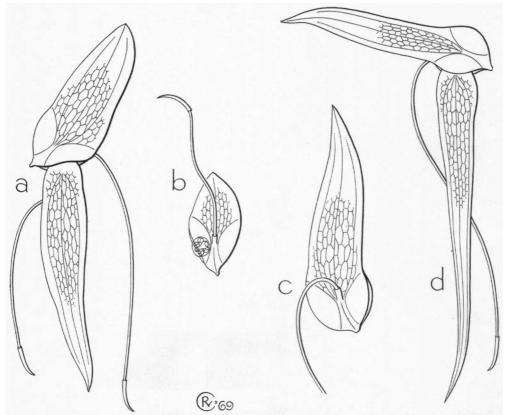


Fig. 7. Lemna tenera Kurz. a. Habit, dorsal view, $\times 12$, b. ventral view of floating frond with inflorescence, $\times 12$, c. ventral view, of submerged frond, $\times 12$, d. habit, dorsal view of submerged plant, $\times 12$ (a, c-d RIDLEY 10778, b MÖLLER 30).

3. Lemna tenera Kurz, J. As. Soc. Beng. 40, ii (1871) 78; Hegelm. Bot. Jahrb. 21 (1895) 293-294; RIDL. Mat. Fl. Mal. Pen. 3 (1907) 52; Fl. Mal. Pen. 5 (1925) 132. — Lemna sp. near L. trisulca, RIDL. J. Str. Br. R. As. Soc. n. 33 (1900) 179. — Fig. 7.

Submerged aquatic, only floating at the surface when flowering. Fronds solitary or connected in groups of 2, seldom 3, slightly or strongly asymmetric, often curved; oblong to linear-lanceolate; 3-7.8 by 1-2.3 mm; frond when floating slightly convex; base slightly to strongly asymmetric, attenuate; apex symmetric, acute; margin entire; dorsal side smooth or with an indistinct apical papilla; ventral side flat, or convex when floating; green without red pigment; nerves 3, sometimes indistinct. Stipe short, hyaline, sometimes persistent. Root 1, slender, very long; root sheath absent or most indistinct; root cap strongly curved, sometimes straight, acute. Slit of budding pouch just dorsal to the margin of the frond. Fruit unknown.

Distr. Burma (Pegu, type), in Malesia: Malay Peninsula (Singapore; Wellesley; Dindings), Galang (possibly Galang I. in Riouw Arch., RIDLEY 10374, Sept. 1899, SING).

Ecol. In ditches and ponds, in rice-lands often together with *L. perpusilla*, at low altitude, in

swamp forest (Kurz), rare.

Note. Only one collection of flowering *L. tenera* is known (Möller 30 from Singapore); although only a few plants have flowers, all the plants are thickened and it is, therefore, probable that they were floating at the surface; they have stomata at the dorsal side. Some other collections also consist of completely or partly thickened plants. They are very similar to *L. perpusilla* in their shape and in bearing an apical papilla, however, they can be recognized by their more acute apex and in the absence of a distinct root sheath. *L. tenera* can easily be distinguished from the related *L. trisulca* by its entire margin, the absence of a long stipe, and by the fact that only 2-3 fronds remain connected.

3. WOLFFIA

HORKEL ex SCHLEID. Beitr. Bot. 1 (1844) 233, nom. gen. cons. prop.; DAUBS, Monogr. Lemnac. (1965) 41, pro parte; HARTOG, Taxon 18 (1969) 591-592; HARTOG & PLAS, Blumea 18 (1970) 366. — Grantia GRIFF. ex VOIGT, HORT. Suburb. Calc. (1845) 692; Not. 3 (1851) 223. — Bruniera FRANCH. Billotia 1 (1864) 25, 30. — Wolffia sect. Uniflorae subsect. Estipitatae HEGELM. Lemnac. (1868) 122; Bot. Jahrb. 21 (1895) 301. — Fig. 1 C, 8.

Distr. At least 7 spp. in the tropical, subtropical and temperate regions of the world.

KEY TO THE SPECIES

- 1. Dorsal outline of the frond round or elliptic. Ventral side inflated, globular.
- Dorsal outline of the frond elliptic. Dorsal side flat to convex. Width greatest below the dorsal plane, at ± half the height.
 Lorsal outline of the frond round to ovate. Dorsal side flat. Width greatest in the dorsal plane.

W. arrhiza

1. Dorsal outline of the frond angular. Ventral side with a central conical protuberance.

W. microscopica

1. Wolffia globosa (ROXB.) HARTOG & PLAS, Blumea 18 (1970) 367. — Lemna globosa ROXB. [Hort. Beng. (1814) 66, nomen] Fl. Ind. ed. Carey 3 (1832) 565; GRAHAM, Cat. Bomb. Pl. (1839) 252; DALZ. & GIBS. Bomb. Fl. (1861) 281. - Grantia globosa (ROXB.) GRIFF. ex VOIGT, Hort. Suburb. Calc. (1845) 692; Not. 3 (1851) 229. - W. schleideni MIQ. Ned. Kruidk. Arch. 3 (1855) 428; Fl. Ind. Bat. 3 (1855) 221; Nat. Tijd. N. I. 10 (1856) 399-402; Kurz, ibid. 27 (1864) 220; NAVES, Novis. App. (1882) 296; BACK. Handb. Fl. Java 3 (1924) 2; ibid. 2 (1928) 290; Bekn. Fl. Java (em. ed.) 10 (1949) fam. 226, p. 3; BACK. & BAKH. f. Fl. Java 3 (1968) 128. – W. delilii var. schleideni (MIQ.) Kurz, J. Linn. Soc. Bot. 9 (1866) 265. - W. arrhiza (non WIM-MER) MARTENS, Preuss. Exp. O.-Asien, Bot. Teil, Tange (1866) 143; HEGELM. Lemnac. (1868) 124-126, p.p.; Hook. f. Fl. Br. Ind. 6 (1893) 557-558, p.p.; HEGELM. Bot. Jahrb. 21 (1895) 301-302, p.p.; TRIM. Handb. Fl. Ceyl. 4 (1898) 367; RIDL. J. Str. Br. R. As. Soc. n. 33 (1900) 79; COLLETT, Fl. Simlensis (1902) 545; PRAIN, Bengal Pl. 2 (1903) 841; RIDL. Mat. Fl. Mal. Pen. 3 (1907) 53; KOORD. Exk. Fl. Java 1 (1911) 269; MERR. Philip. J. Sc. 12 (1917) Bot. 101; En. Philip. 1 (1923) 190; BACK. Handb. Fl. Java 3 (1924) 2; RIDL. Fl. Mal. Pen. 5 (1925) 132; HEND. Gard. Bull. S. S. 4 (1928) 352; FISCHER in Gamble, Fl. Madras 9 (1931) 1593; Burk. Dict. (1935) 1328; GAGNEP. Fl. Gén. I.-C. 6 (1942) 1198; McCann, J. Bomb. Nat. Hist. Soc. 43 (1942) 159-160; BACK. Bekn. Fl. Java (em. ed.) 10 (1949) fam. 226, p. 3; HEND. Mal. Wild Fl. Monocot. (1954) 210; MASAMUNE, Sc. Rep. Kanazawa Univ. 5 (1957) 94; MITRA, Fl. Pl. E. India 1 (1958) 86; LARSEN, Dansk Bot. Ark. 20 (1962) 136; OHWI, Fl. Japan (1965) 265; SHRI & NAIK, Fl. Osmanabad (1968) 682; BACK. & BAKH. f. Fl. Java 3 (1968) 128. - W. cylindracea HEGELM. Lemnac. (1868) 123; Bot. Jahrb. 21 (1895) 302; Brown, Fl. Trop. Afr. 8, 2 (1901) 205. - W. delilii (non Schleid.) Naves, Novis. App. (1882) 296. — W. microscopica (non Kurz) MATSAMURA & HAYATA, En. Pl. Form. (1906) 463; Miki, Bot. Mag. Tokyo 48 (1934) 334. Lemna arrhiza (non L.) BACK. Bull. Jard. Bot. Btzg II, 12 (1913) 21. — Fig. 8 a-a².

Fronds with elliptic to oblong dorsal outline, c. $1\frac{1}{2}$ times as long as wide, 0.30-0.73 by 0.20-0.33 mm, 0.23-0.55 mm high; base and apex obtuse; margin with a few papillose cells; dorsal side flat near the apex and convex near the base, with a few papillose cells; ventral side strongly inflated, globular, with large cells; width greatest below the dorsal plane, at about half the height; green, without brown pigment cells in the epidermis. Budding pouch often with a distinct collar of elon-

gate cells. Fruit unknown.

Distr. E. Asia (Japan; China: Fukien; Ryukyu Is.), SE. Asia (Tonkin; India: Sibpur, Dehra Dun, Peshawar, etc.; Ceylon), also in Africa and Australia; in Malesia: Malay Peninsula (Singapore: Selangor: Kuala Lumpur: Malacca). E. Java (near Surabaja and near Redjasa E of Pasuruan), Kangean Is. (Sepandjang), Lesser Sunda Is. (Flores: Rana Mesé), Philippines (Central Luzon: Pampanga, Bulacan, Rizal).

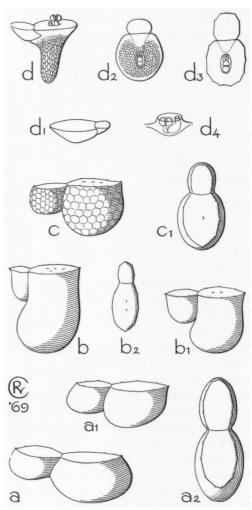


Fig. 8. Wolffia globosa (ROXB.) HARTOG & PLAS. a. Habit with a daughter frond, lateral, $\times 18$, a^1 . ditto, $\times 18$, a^8 . dorsal view, $\times 18$. — W. arrhiza var. australiana BENTH. b. Habit, lateral view, $\times 18$, b^1 . ditto, $\times 18$, b^2 . ditto, dorsal view, ×18. — W. arrhiza (L.) HORKEL ex WIMMER. c. Habit with a daughter frond, ×18, c1. ditto, dorsal view, ×18. - W. microscopica (GRIFF.) KURZ, d. Habit of a flowering plant with a daughter frond, showing elongated ventral side, and dorsal inflorescence, $\times 18$, d^1 . ditto, frond without protuberance, $\times 18$, d^3 . dorsal view, $\times 18$, d^3 . ditto, more angular outline, $\times 18$, d. detail of the inflorescence (1 pistil, 1 stamen), $\times 36$ (a-a² JAAG 1956, b-b² DEN HARTOG 1186, $c-c^{1}$ Van der plas 28-9-67, $d-d^{4}$ Deshpande 1727)

BACKER & BAKHUIZEN f. note this also from Mts Jang & Idjen in E. Java at 2200 m, but I believe this to be an error.

Ecol. Stagnant water and ditches, once in calciferous water, in Malaya in everwet climate, in E. Java under severe monsoon conditions, all localities in Malesia at low altitude. Near Redjasa under a thick cover of Azolla pinnata; at 1000 m in Rana Mesé.

Vern. Philippines: dugmán, Bis., liá, Tag.

Notes. The specimens of W. globosa of Malesia are c. $1\frac{1}{2}$ times as long as wide, while the Australian specimens are usually twice as long as wide. The size of both the Malesian and Australian plants of W. globosa is smaller than that of W. arrhiza. In Australia still another Wolffia is found with an elliptic dorsal outline and which is much higher than all other species in the genus. It is known as W. arrhiza var. australiana BENTH. but no doubt represents a good species (fig. 8 b-b2).

Wolffia arthiza (L.) Horkel ex Wimmer, Fl. Schles. ed. 3 (1857) 140; Hegelm. Lemnac. (1868) 124-126, p.p.; HOOK. f. Fl. Br. Ind. 6 (1893) 557-558, p.p.; Hegelm. Bot. Jahrb. 21 (1895) 301-302, p.p.; DAUBS, Monogr. Lemnac. (1965) 48-49. — Lemna arrhiza LINNE, Mant. (1771) 294. — W. michelii SCHLEID. Beitr. Bot. (1844) 233. — Fig. 8 c-c1.

Fronds with round to ovate dorsal outline, usually as long as wide, rarely somewhat longer, 0.8-1.3 by 0.6-0.8 mm; 0.6-0.8 mm high; base and apex obtuse; margin entire or with papillae; dorsal side flat to slightly convex; ventral side strongly inflated, globular, consisting of large cells; width greatest in the dorsal plane; green, without brown pigment cells in the epidermis.

Distr. Temperate zone of the Old World, in Africa also in the tropics, not yet found in Malesia and probably absent from the whole of East Asia and Australia. Records of W. arrhiza from these areas seem to relate to the closely allied W. globosa.

Ecol. Stagnant waters, often mixed with other floating aquatics.

Wolffia microscopica (GRIFF.) KURZ, J. Linn. Soc. Bot. 9 (1866) 265; HEGELM. Lemnac. (1868) 127-128; Hook. f. Fl. Br. Ind. 6 (1893) 558; HEGELM. Bot. Jahrb. 21 (1895) 301; PRAIN, Bengal Pl. 2 (1903) 841; MITRA, Fl. Pl. E. India 1 (1958) 86; Daubs, Monogr. Lemnac. (1965) 44. -Grantia microscopica GRIFF. ex VOIGT, Hort. Suburb. Calc. (1845) 692; Not. 3 (1851) 226. — Fig. 8 d-d4.

Fronds with pentagonal or hexagonal dorsal outline, 0.4-0.6 mm ø; margin entire except for the papillose corner cells; dorsal side flat; ventral side elongated into a central, conical, parenchymatic protuberance up to 1.8 mm long; green, without brown pigment cells in the epidermis.

Distr. So far this species is only known from India. It is probable that this minute plant has been often overlooked; therefore, it is expected to occur also elsewhere in East Asia and even in Malesia.

Ecol. Occurs usually mixed with other floating aquatics, especially with Lemna perpusilla. According to Maheswari and Kapil (Am. J. Bot. 50, 1963, 679) it never co-exists with Spirodela polyrhiza.

Note. Records of W. microscopica from Formosa and Japan relate to W. globosa.

Doubtful

MIQUEL (Ned. Kruidk. Arch. 3, 1855, 429; Fl. Ind. Bat. 3, 1855, 221) reported that a second considerably larger Wolffia species was found together with W. schleideni near Surabaia. He thought that this species was identical or related to W. delilii SCHLEID., but unfortunately he restricted the description to a few remarks, which are repeated here:

'Frond complanate, slightly lenticular, 2-21/2 mm long; epidermis cells gyrose.'

I have not seen this material.

Dubious

Lemna obcordata Winberg in Thunberg, Fl. Jav. 1 (1825) 2, nomen.