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–∞, 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 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. Wolffiioideae*) the *inflorescence* is borne in a median or lateral dorsal flowering cavity (an exception is extra-Mal. *Wolffioopsis* 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 μφ, 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. 4 l), 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. *Wolffia* occurs in the subtropical and tropical parts of America and in South Africa, *Pseudowolffia* is restricted to tropical Africa, and *Wolffioopsis* has been found in the tropics of Africa and America. See *Den Hartog & Van der Plas* (Blumea 18, 1970, 355–368).
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* (Heller 1895, Le Roy Topping and Decener 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 (Maldive, 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 Lemma 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 Lemma, 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 Wolfiposis 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.

Monoeocious plants are most common; plants carrying flowers of one sex only have rarely been found in Lemma 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; protandry or proterogyny are more or less a rule. In Lemma 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 (TRELFAE, 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 Lemma 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 & Schrötter, Lebensgesch. Blütenpfl. Mittel-europas 1, 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 plume (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; ENGEL in E. & P. Nat. Pl. Fam. 2, 3, 1889, 156).

Dispersal. Dispersal of the whole plant as well as the seeds over short distances may be effected by birds; Wolffia brasiliensis was found by WEDDELL on the feathers of a shot bird (Ann. Sci. 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 restricted 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 (Lemma 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.
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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 Lemnoidae and the Wolffioideae. The Lemnoidae 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, Lemnoidae 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 root 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 LAWALKÉ (Bull. Soc. R. Bot. Belg. 77, 2, 1945, 27–38) homologize the spathe of Lemnoidae 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 LAWALKÉ, 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. Ady. 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-axes, producing at the end a new rosette. In Lemnoidae 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* Roxb., which also produces runners with apical plantlets, the latter are surrounded by a membranous spathe. The morphologic interpretation of the spathe eq. scales is unclear.

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

**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 myrothyllin cells (see *sub Halorugaceae*) occur in species of Spirodela, Wolffia and Wolfiella. The flavonoid constituents were investigated thoroughly. Four main
The flavonoid pathways leading to flavones and flavonols involve the reactions of both the pentose and hexose portions of the carbohydrate side chain with the 'B-ring' of phenylpropanoid precursors. The flavonoid pathways leading to anthocyanins, however, utilize carbohydrates of C6-C3 structure, and it is not known how these are coupled with the reaction of the 'B-ring'.

The flavonoid pathways leading to flavonols and flavones are both reductive in nature and do not make use of enzymes of the aromatic shikimate pathway. They are, however, different in that the flavonol pathway utilizes a series of enzymes with high specificity for flavonol biosynthesis, while the flavone pathway is more generalized. The flavonoid pathways leading to anthocyanins, on the other hand, are more complex and involve the formation of both flavonols and flavones as intermediates.

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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 ♀ and 2 ♂ flowers, enclosed by a membranous spathe. Anther bilocular, transversely dehiscent. ♀ Flower superior and lateral to the 2 ♂ flowers, consisting of a globular ovary with a short, partly persistent style and 1 amphitropous or 2–4 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

   1. S. polyrhiza
   2. S. punctata


Frons 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
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. Kakarêwoan, S, mata délê, 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.


— **Lemma melanorrhiza** F. v. M. ex Kurz, J. Bot. 5 (1867) 115. — **Lemma pleiorrhiza** F. v. M. ex Kurz, l.c. — **S. oligorrhiza** Hegelm. Lemnac. (1868) 147–150, incl. var. **S. melanorrhiza** (F. v. M. ex Kurz) Hegelm., var. **g. pusilla** Hegelm., var. **S. pleiorrhiza** (F. v. M. ex Kurz) Hegelm., var. **S. javanica** Hegelm.; Engl. Fl. Jahrb. 7 (1868) 448; Hegelm. Bot. Jahrb. 21 (1895) 287; F. M. Bailey, Queensl. Fl. 5 (1902) 1700; MIKI, Bot. Mag. Tokyo 48 (1934) 333; McCANN, J. Nat. Hist. Soc. 43 (1942) 157; Black, Fl. S. Austr. ed. 2 (1948) 172; Daubs, Monogr. Lemnac. (1965) 14–15; Ohwi, Fl. Japan (1965) 264; McComb & McComb, J. R. Soc. W. Aust. 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** Hegelm. l.c. 288. — **S. javanica** Hegelm. l.c. — Fig. 3. **Frods** 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 evervet 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 121), 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 **Lemma 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. paucistostata** (= **L. perpusilla**).

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2. LEMLA


Fig. 3. **Spirodela punctata** (G. F. W. Meyer) THOMPSON. a. Habit, mother frond with fruit and daughter frond, ×12, b. ditto, ×12, c. ventral view roots piercing ventral scale, ×12, d. detail of c, ×24, e. ventral view, 1-rooted frond, ×12, f. ditto, detail from e, ×24, g. habit, dorsal view, ×12, h. lateral view, ×12. i. ventral view of a plant from Java with many roots, ×12, j. ventral view of a frond with 2 roots, ×12, k. detail of the inflorescence, ×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

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 ♀ and 2 ♂ flowers enclosed by a membranous spathe. *Anther* bilocular, transversely dehiscent. ♀ *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. Leuca**. 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. Leuca**.

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.

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**Fig. 4.** *Leuca perpusilla* Torrey. a. Habit, mother frond with adhering offspring, dorsal view, × 18, b. root cap, × 36, c. lateral view, frond with apical and nodal papillae, × 18, d. *ditto*, only with apical papilla, × 18, e. *ditto*, without papillae, × 18, f. habit, plant from New Guinea, dorsal view, elongated fronds, × 18, g. ventral view, showing root emitted, × 18, h. detail of root sheath provided with 2 lateral wings, × 36, i. mother frond and daughter frond, both with inflorescence, × 18, j. detail of a flowering frond in which inflorescence and daughter frond develop simultaneously in the same reproductive pouch, × 36, k. frond with fruit and daughter frond, dorsal view, × 18, l. seed, × 40, m. *ditto*, longitudinal section, × 80, n. germinating seed, showing plumule and first frond, dorsal (left) and ventral view (right), × 18 (a–c, i–n DEN HARTOG 632, d BACKER 19104, e BACKER 25650, f BRASS 8112, g LÜTJEHARMS 5387, h DEN HARTOG 188).
Fig. 4
3. Fron diversely symmetrical, 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 frown. — L. minor

3. Fron diversely asymmetrical, ventral side flat to strongly inflated. Cells on ventral side clearly visible to the naked eye. Fruit with lateral wings. Ovules 1, amphitropous or ovules 2-4, anatropous. Slit budwing pouch ventral to the margin of the frown. — L. gibba

1. Submerged water plants, only floating at the surface when flowering. Frons oblong to linear-lanceolate, often without a root. Silt of budwing pouch just dorsal to the margin of the frown. Subg. Staurogeton.

4. Margin denticate towards the apex. Stipe usually strongly elongate, green, persistent.

2. L. trisulca

3. L. tenera


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 papilae, 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. Silt of budwing pouch coinciding with the margin of the frownd. 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 sub-tropics. 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.

Ecological. The 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. Klambang, M. (Sum.), ganggêng, S; Philippines: inalâ, 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. aequinocialis 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. Bl. 1918, 93) referred L. gibba (non L.) BLACO to L. paucicostata (= L. perpusilla). As BLACO 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.


Small floating aquatic. Fronds solitary or cohereing 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 ± 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. Silt 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.


Small floating aquatic. Fronds solitary or cohereing 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. Silt 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; Mq. Fl. Ind. Bat. 3 (1855) 222; GRIEBE. 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, ×8, b. ventral view showing subepidermal air cavities, ×8, c. lateral view, ×8, d. winged fruit with 2 seeds, ×18, e. ditto, with 1 seed, ×18. — *L. minor* L. f. Habit dorsal view, ×8, g. ditto ventral view, ×8, h. lateral view, ×8 (a–e Heller 5571, f–h Van der Plas 294-69).

Fig. 6. *Lemna trisulca* L. a. Habit, submerged plant, × 6, b. floating plant with inflorescence, dorsal view, × 6, c. frond with fruit, ventral view, × 6, d. *ditto*, × 6, e. part of a flowering frond, dorsal view, × 12, f. detail of inflorescence surrounded by spathe, × 24, g. stamen, × 24 (*a* Den Hartog 1162, *b–g* Holmberg 433).

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 ls.: 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, ×12, b. ventral view of floating frond with inflorescence, ×12, c. ventral view, of submerged frond, ×12, d. habit, dorsal view of submerged plant, ×12 (a, c–d Ridley 10778, b Möller 30).

Submerged aquatic, only floating at the surface when flowering. *Frons* 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. *Silt 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


Minute aquatics, floating at the surface. *Frons* either solitary or connected in groups of 2, symmetric, thick, more or less globular, ellipsoid or ovoid, sometimes dorsally flattened, with fleshy parenchyma without air spaces, green with or without brown pigment cells in the epidermis; raphides none; stomata at the dorsal part of the frond; margin entire or with a few more or less prominent papillae; nerves and roots absent. *Vascular tissue* absent, except for an occasional trace in the stamen. *Budding pouch* basal, median, funnel-shaped with circular opening and with a rudimentary *stipe* (not visible to the naked eye). *Inflorescence* 1, dorsal, consisting of a cavity containing 1 ♂ and 1 ♀ flower, without a spathe, protogynic. *Anther* unilocular, dehiscent along an apical, pigmented line. ♀ *Flower* situated nearer to the budding pouch than the ♂ flower, consisting of a globular ovary with a short persistent style. *Ovule* 1, orthotropous. *Fruit* globular. *Seed* globose or slightly compressed, smooth.

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.

1. Dorsal outline of the frond angular. Ventral side with a central conical protuberance. *W. microscopica*
1. Wolffia globosa (ROXB.) HARTOG & PLAS.


Fronds with elliptic to oblong dorsal outline, c. 1½ 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 elongate 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 Red jasa 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, ×18, a¹. ditto, ×18, a². dorsal view, ×18. — W. arrhiza var. australiana BENTH. b. Habit, lateral view, ×18, b¹. ditto, ×18, b². ditto, dorsal view, ×18. — W. arrhiza (L.) HORKEL ex WIMMER. c. Habit with a daughter frond, ×18, c¹. ditto, dorsal view, ×18. — W. microcephala (GRIFF.) KURZ. d. Habit of a flowering plant with a daughter frond, showing elongated ventral side, and dorsal inflorescence, ×18, d¹. ditto, frond without protuberance, ×18, d². dorsal view, ×18, d³. ditto, more angular outline, ×18, d⁴. detail of the inflorescence (1 pistil, 1 stamen), ×36 (a–a) JAA 1956, b–b⁴) DEN HARTOOG 1186, c–c⁵) VAN DER PLAS 28–9–67, d–d⁵) DESHPANDE 1727)
LEMNACEAE (van der Plas) 237

BACKE & 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, 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., *lid*, Tag.

*Notes.* The specimens of *W. globosa* of Malesia are c. 1½ 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).


*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 ±; 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 *Lemma perpusilla*. According to MAHESWARI and KAPIL (Am. J. Bot. 50, 1963, 679) it never co-exists with *Spirodea 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, 2–2½ mm long; epidermis cells gyrose.'

I have not seen this material.

**Dubious**