9. DESCRIPTION OF FAMILY, GENERA, AND SPECIES OF LEMNACEAE WITH KEY FOR DETERMINATION

9.1. DESCRIPTION OF THE FAMILY OF LEMNACEAE WITH KEY TO THE SUBFAMILIES

Morphology

The plants of Lemnaceae consist basically of small leaf-like, poorly differentiated fronds of which two or more coher together and float on or below the surface of the water. Propagation is mostly vegetative through the budding of daughter fronds out of reproductive pouches or cavities. Under normal growth conditions, the fronds live for no more than a few weeks. Flowering and fruiting are rare in most species.

Fronds. Fronds are thin or thick, 0.4-15 mm long (without stalk), intensively or transparently green, sometimes reddish, surrounded at the base by a bifid scale-like leaflet (Spirodela) or without the leaflet, consisting of a lower and an upper epidermis and several cell layers between, with aerenchymatic tissue (Lemnoideae, Wolffiella) or without (Wolffia), with 1-16(21) nerves (Lemnoideae) or without nerves (Wolffioideae); at the base with two flat lateral pouches (Lemnoideae) or with one terminal pouch or cavity (Wolffioideae); roots absent (Wolffioideae) or 1-21 (Lemnoideae), surrounded at the base by a tubular sheath and enclosed at the tip by a cap; no root hairs present.

Flowers and fruits. One to two flowers per frond, bisexual (rarely unisexual), either surrounded by an utricular, scale-like leaflet and emerging from the lateral pouches (Lemnoideae) or originating in an open cavity on the upper surface (Wolffioideae); stamens 1 (Wolffioideae) or 2 (Lemnoideae) per flower, with 2 (Wolffioideae) or 4 (Lemnoideae) locules; pollen grains globular, 11-52 (mostly 15-26) µm in diameter with one pore, covered with small spiny protuberances; 1 ovary per flower, bottle-shaped, tapering into the short style with the stigma, with one ovule (1-7 ovules in Spirodela and in the group of L. minor); stigma funnel-shaped, tapering at the base in a style duct, with a spherical secretion droplet at time of pollination; ovules anatropous, amphitropous or orthotropous, with two integuments, with cellular endosperm;

flowers are mostly proterogynous; fruits with dry pericarp and usually with 1 seed (1-5 seeds in Spirodela and in the group of L. minor), 0.35-2,75 mm long. Seeds ovoid, staying within the pericarp or dropping out, longitudinally ribbed (Lemnoideae) or nearly smooth (Wolffioideae).

Size and distribution of the family

The family consists of two subfamilies with 4 genera and 34 species. The center of distribution is South America, with secondary centers in southern North America, southern Africa and Australia. Species of the family occur all over the world except in arctic, very humid and very dry regions.

Key to the subfamilies

- 1-21 roots present; fronds with 1-16(21) nerves, daughter fronds and flowers originating from two lateral pouches at the base of the frond; flowers surrounded by an utricular, scale-like membraneous leaflet, with two 4-locular stamens; crystal cells present; seeds longitudinally ribbed. Lemnoideae
- No roots present; fronds without nerves; daughter fronds originating from a single terminal pouch or cavity at the base of the frond; flowers without any leaflets, originating in a cavity on the upper surface of the frond, with one 2-locular stamen; no crystal cells present; seeds nearly smooth. Wolffioideae

9.2. SUBFAMILY OF LEMNOIDEAE

9.2.1. Description of the subfamily of Lemnoideae with key to the genera

Morphology

Fronds. Fronds orbicular to narrow elliptic, somewhat asymmetric (the side where the first daughter frond is formed is more convex), flat or sometimes gibbous; with aerenchymatic tissue (air spaces) throughout the whole frond or only around the node; 1-16(21) nerves, with tracheids at least near the node (except in sect. Biformes and Uninerves of Lemna); two triangular lateral reproductive pouches at the base from which the daughter fronds originate; with numerous stomata on the upper surface of the fronds (no stomata on the submerged vegetative fronds of L. trisulca and L. tenera); lateral walls of the epidermis cells nearly straight or undulated; crystal cells present; stipe connecting daughter with mother frond elongated, green and persevering (L. trisulca) or small and white, stays with the daughter frond after separation, then decays; roots 1-21 (rarely undeveloped in resting fronds or broken off), surrounded at the base by a tubular sheath, enclosed at the tip by a cap; no root hairs present.

Flowers and fruits. Mostly 1 flower per frond (sometimes 2 in S. polyrrhiza, L. perpusilla, L. aequinoctialis, L. trisulca and possibly other species), surrounded at the base by an utricular membraneous leaflet, originating in the lateral pouches; 2 stamens per flower with 4 locules, elongating and ripening one after the other; filaments with tracheids (except in section Biformes and Uninerves of Lemna); pollen grains with 1.0-1.8 µm long tuberances; 1 ovary, with 1-7 anatropous, amphitropous or orthotropous ovules; fruits with winged borders laterally towards the top or not winged, often reddish or without anthocyanin; seeds 0.4-2.0 mm long, with 8-70 longitudinal ribs; outer seed coat with 2-11 subepidermal cell layers; embryo sac monosporic (Spirodela) or bisporic (Lemna); endosperm with 1-5 cell layers.

Size and distribution

The subfamily of Lemnoideae consists of two genera (Spirodela and Lemna) and 16 species. The subfamily has the same distribution as the family with a center in America (13 species).

Key to the genera of Lemnoideae

- Roots 2-21 per frond (rarely only one root in S. punctata growing under poor conditions or no roots in turions of S. polyrrhiza); nerves 5-16(21) (rarely 3 nerves in S. punctata growing under poor conditions); fronds surrounded at the base by a small, scale-like leaflet covering the root point of attachment; pigment cells present (visible in dead fronds as brown dots); crystal cells with either raphides or druses; the external locules of the stamen situated at the same level as or somewhat higher than the internal ones, but not on the top of the internal ones. Spirodela
- Roots only 1 per frond (no roots in turions or rarely in L. trisulca); nerves 1-5 (very rarely 7 in L. gibba); no leaflet at the base of the frond covering the point of attachment of the root; no pigment cells (but red pigmentation present in some species); raphides but no druses present; the external locules of the stamen situated at the top of the inner ones. Lemna

Remarks on the distinction between the two genera Spirodela and Lemna. Some authors combine the two genera under the name of Lemna, arguing that the plants of both genera look very similar and that S. punctata somehow forms a transition between the two genera. Since most authors distinguish between the two genera and many different characteristics exist, the distinction between the two genera is maintained in the present work.

9.2.2. Genus Spirodela Schleiden

9.2.2.1. Description of the genus with key to the sections

Morphology

Fronds. Fronds lanceolate, ovate or suborbicular, floating on the surface of the water (only turions sink to the bottom of the water), 1 to several coher together (often rosette-like), with 5(3)-16(21) nerves; nerves up to nearly the tip with tracheids containing ring- or spiral-shaped thickenings in the lateral walls; with anthocyanins; in addition, pigment cells in the frond tissue, in the roots, in the prophyllum (leaflet at the base), in the ovary, around the stigma and along the de-

hiscence line of the stamens (visible as brown dots in the dead frond); two different crystal cells present: those with needle-shaped, bundled crystals (raphides) and those with crystals shaped like morning stars (druses); fronds surrounded at the base by a bifid scale-like leaflet (prophyllum) covering the point of attachment of the roots; roots 2-21 per frond (rarely 1 in S. punctata or not developed in turions), with tracheids at least at the base.

Flowers and fruits. Flowering fronds similar to vegetative ones; external locules of the stamens situated at the same level as or only slightly higher than the internal ones; ovary with 1 amphitropous or 2-5 anatropous ovules; embryo sac monosporic; endosperm with 3 to 5 cell layers.

Size and distribution

The genus Spirodela comprises three species of which two belong to a group of related and not much differentiated species. The genus is distributed all over the world with a center in South America, where all three species occur.

Key to the sections of the genus Spirodela

- Fronds 1-1 1/2 (rarely 1 2/3) times as long as wide, with 7-16(21) nerves; roots 7-21 of which 1-5 but never all perforate the scale-like leaflet. sect. Spirodela
- Fronds 1 1/2-2 times as long as wide, with 5-7 (rarely 3) nerves; roots 2-7 (rarely 1 or 8-12), all of which perforate the scale-like leaflet. sect. Oligorrhizae

Remarks on the taxonomy of the genus Spirodela

KOCH (1933, 1934) distinguished three sections within Spirodela: 1. Polyrrhizae with S. polyrrhiza, 2. Intermediae with S. intermedia and "S. biperforata" (identical with S. intermedia), 3. Oligorrhizae with S. punctata (= S. oligorrhiza). Whereas S. punctata is well distinguished from the other species, S. polyrrhiza and S. intermedia (incl. S. biperforata) form a natural group of species sometimes difficult to distinguish from each other due to overlapping characteristics.

9.2.2.2. Section Spirodela

Morphology

Fronds. Upper surface of the frond shiny, without distinct papules; lower surface and margins of the upper surface often red coloured; 7-16(21) nerves present (the outermost ones sometimes originating from the next inner ones); the upper wall of the pouch in which the first daughter frond is formed originates by overgrowth of marginal tissue at the base of the frond; the lower wall of this pouch is formed by the ventral part of the prophyllum; both walls of the second pouch originate by overgrowth of marginal tissue at the base of the frond; roots 7-21 (not developed in turions; sometimes fewer roots in poorly developed fronds), of which 1-5 perforate the covering lobe of the prophyllum, up to 4 cm long, furnished with a tract of tracheids nearly down to the tip.

Flowers and fruits. The utricular leaflet with narrow opening at the top; external locules of the anther not situated higher than the internal ones; fruits laterally winged towards the top.

Size and distribution

The group consists of two closely related species that are difficult to distinguish from each other. One species is restricted mainly to South America, the other one has a worldwide distribution.

Key to the species of the section Spirodela

- 2-5 roots perforating the lobe of the prophyllum which covers the point of attachment of the roots; no turions present; no red spot on the upper surface of the frond above the node. S. intermedia
- Usually 1 root (rarely 2 roots) perforating the lobe of the prophyllum which covers the point of attachment of the roots; sometimes turions present (small, orbicular to reniform, brownish to olive fronds without roots which sink to the bottom of the water; they are formed under unfavourable conditions), often with a red spot on the upper surface of the frond above the node. S. polyrrhiza

Remarks on the taxonomy of the section Spirodela

KOCH (1933, 1934) was the first to distinguish 3 species within S. polyrrhiza based on the number of perforating roots and on gibbosity. Both characteristics are not very distinct. S. intermedia, as well as "S. biperforata", in the sense of KOCH, may have 3 perforating roots and

"S. biperforata" and S. polyrrhiza may have 2 perforating roots (see 2.4.10). Also, gibbosity is not restricted to S. intermedia (it occurs rarely in S. polyrrhiza), and more than half of the specimens of S. intermedia found in nature are not gibbous. DAUBS (1965) described a variety Masonii of S. polyrrhiza from the Netherlands with gibbous fronds. I have seen many samples of S. polyrrhiza from India and other countries with gibbous fronds resembling those of S. intermedia, but able to form turions and usually having only one perforating root. DE LANGE and REVIER (1982) cultivated several clones of S. polyrrhiza from the Netherlands under different conditions. Under the same conditions, the different clones showed characteristic frond thickness between 0.4 and 2.2 mm. The same clones varied from a thickness of 0.3 to 2.2 mm, depending upon growth conditions. The thickest fronds were observed under crowded conditions.

As in most critical groups, it is necessary to combine different characteristics in order to distinguish between the species. The best characteristic for determining S. polyrrhiza is its ability to form turions. In the course of our investigations of populations from Argentina, it became clear that the combination of characteristics of "S. biperforata" is within the morphological variation of S. intermedia (see also LANDOLT and ZARZYCKI in prep.). BEYER (1983) observed no significant physiological differentiation between strains of S. intermedia and S. biperforata at varying Ca and Mg content. Consequently, the distinction between S. intermedia and S. biperforata (fig. 9.1a) had to be dropped and the latter "species" included in S. intermedia.

Some differences between plants of S. polyrrhiza from various regions of the world, as mentioned in LANDOLT (1957), are not consistent enough to use for taxonomical evaluation. The fronds of North American clones are, on the average, thinner than the ones from Europe or Africa and form a red spot above the node on the upper frond surface more often. Nevertheless, as far as has been tested in our laboratory, every clone of S. polyrrhiza is able to form this red spot under certain conditions. For differing physiological characteristics of S. polyrrhiza clones from different geographical regions see chapter 7.4.

The 2 species of the group of S. polyrrhiza have different distributions and somewhat varying ecological demands. S. intermedia grows in South and Central America in tropical, subtropical, and warm temperate climates; S. polyrrhiza is practically ubiquitous, missing only in the dis-

tribution areas of S. intermedia as well as in regions with cool summers.

1. **Spirodela intermedia** W. **Koch** (fig. 9.1a,b; plate I a,b)

Morphology

Fronds. Fronds mostly rounded at the tip, 3-12 mm long, 2-9 mm wide, 1-1 1/2 times as long as wide, often gibbous, without a red spot above the node; air spaces in 3-4 layers, reaching almost to the edge; roots 6-21, 2-5 of which perforate the prophyllum; rootcap sharply pointed on living and on dry specimens; no turions present.

Flowers and fruits. Plants occasionally flowering and fruiting. Ovary with 2-5 ovules; style 0.3-0.5 mm long; fruit 1.5-2.75 mm long, 1.2-2.1 mm wide; winged edges of the fruit near the top about 0.15-0.30 mm wide; seeds 1-5, 1.0-2.0 mm long, 0.8-1.2 mm thick, with 15-22 distinct ribs.

Distribution

Warm, temperate, subtropical and tropical regions of South and Central America (fig. 6.4).

2. **Spirodela polyrrhiza (L.) Schleiden** (fig. 9.2c; plate I c,d)

Morphology

Fronds. Fronds rounded or pointed at the tip, 1.5-10 mm long, 1.5-8.0 mm wide, 1-1 1/2 times as long as wide, thin or (rarely) gibbous, sometimes with a red spot above the node; nerves 40-70 µm wide; air spaces in 2-4 layers, nearly reaching the margin; roots 7-21, 1 or (rarely) 2 of which perforate the prophyllum; rootcap rounded or pointed on living specimens, always pointed on dried specimens; small, orbicular to reniform shaped, brownish to olive turions without roots present which form under unfavourable conditions and sink to the bottom of the water.

Flowers and fruits. Plants very rarely flowering and fruiting. Ovary with 1-2 ovules (MAHESHWARI and MAHESHWARI 1963 rarely counted up to 4 ovules; but the material of these authors originated from a botanical garden and may have consisted of S. intermedia). Style about 0.3 mm long; fruit 1.0-1.5 mm long and 1.0-1.5 mm wide; winged edges of the fruit near the top about 0.15 mm wide; seeds 1 (rarely 2), 0.7-1.0 mm long, about 0.7 mm thick, with 12-20 distinct ribs; external seed coat with 8-11 subepidermal cell layers.

Distribution

All over the world except arctic, subarctic, very humid and very dry regions or regions with cool summers; rare in mediterranean climates; lacking in South America (except the northwest), in New Zealand and on some other oceanic islands (fig. 6.5).

9.2.2.3. **Section Oligorrhizae** W. Koch

Morphology

Fronds. Upper surface of the frond shiny, with a row of small but distinct papules along the median line; lower surface and margins of the upper surface often red coloured; 3-7 nerves present; both walls of the 2 pouches originate from overgrowth of marginal tissue at the base of the frond; roots 2-7 (rarely only 1 or up to 12), all of which perforate the covering lobe of the prophyllum, up to 7 cm long, furnished with a tract of tracheids only in the basal part of the root.

Flowers and fruits. The utricular leaflet surrounding the flower is open on one side; external locules of the anthers situated distinctly higher than the internal ones; fruits laterally winged towards the top.

Size and distribution

S. punctata is the only species of this section and has a very wide distribution today.

Remarks on the taxonomy of the section Oligorrhizae

The only species of this section (S. punctata) is very polymorphic in relation to size, gibbosity, pigmentation and number of roots. Under controlled, identical conditions (1/5 Hutner, 30000 lux, 25°C), the differences between about one hundred clones tested at our laboratory were rather small: variations in length were between 2.5 and 4.0 mm; 2-4 to 2-5 roots; similar length to width ratio; similar weak pigmentation; similar lack of gibbosity. In nature, there are many more different types to be found, which is apparently due more to varying environmental conditions rather than to genetical differences. The major differences between plants from different origins led HEGELMAIER (1895) to distinguish 5 species: S. oligorrhiza (Kurz) Hegelmaier (fronds thin, elongated, with 2-3 roots, strongly pigmentated); S. pusilla (Hegelm.) Hegelm. (fronds rather thick, short and small, with 2, rarely 3 roots, with medium pigmentation); S. melanorrhiza (F. Müller ex Kurz) Hegelm. (fronds rather thick, elongated, large, with 2, rarely 3 roots, strongly pigmen-

tated); S. pleiorrhiza (F. Müller ex Kurz) Hegelm. (fronds thin, elongated with 4-8 roots, with medium pigmentation); S. javanica (Bauer) Hegelm. (fronds rather thick, short, rather large, with 4-5 roots, with medium pigmentation). EVANS (1970) distinguished plants of Australia which are very small (up to 3.0 mm long and 1.75 mm wide) and with 1-5 roots as S. pusilla while he identified S. oligorrhiza as having a length of up to 5 mm and a width of up to 4 mm and with 2-8 (11) roots. In his fig. 1, which shows a two-year-old culture, 2 different sizes of the fronds are clearly visible, but this might be due to different genetical and/or developmental characteristics of the fronds. When plants called S. pusilla are cultivated under identical conditions together with plants called S. oligorrhiza, there is no distinct difference visible any more (own observations). In an aquarium I could get the same size differences in S. punctata fronds with a single clone, as shown by the figure of EVANS (1970).

HEGELMAIER (1868, 1895) never saw plants from South America; therefore he could not comment on the relationship between his S. oligorrhiza and the S. punctata described from South America. It was THOMPSON (1898) who first described the plants collected from the southern point of South America; he referred to them as S. punctata, described earlier from Guayana by MEYER (1818). In culture, there is no consistent difference between the plants from different parts of the world. The distribution of characteristics within the area of the whole group does not even suggest a division in different varieties. Therefore, there is no reason to have more than one species within this section as has already been proposed by MASON (1957), DAUBS (1965), DEN HARTOG and VAN DER PLAS (1970, 1972) and VAN DER PLAS (1971).

3. **Spirodela punctata (G.F.W. Meyer) Thompson** (fig. 9.1d; plate IIa,b)

Morphology

Fronds. Fronds ovate to lanceolate, often somewhat pointed, 1.5-8.0 mm long, 1-5 mm wide, 1 1/2-2 times as long as wide; no distinct turions present but sometimes small single fronds formed with only one fragmentary root.

Flowers and fruits. Plants occasionally flowering and fruiting. Ovary with 1-2 ovules; style 0.15-0.20 mm long; fruit 0.8-1.0 mm long and 1.0-1.2 mm wide; winge of the fruit about 0.1 mm wide; seeds 1 (rarely 2), 0.8-1.0 mm long, 0.5-0.6 mm thick, with 10-15 distinct ribs.

Distribution

S. punctata grows in all climates with mild winters; originally it occurred only in the southern hemisphere and East Asia; today it has been introduced to all continents (fig. 6.6).

9.2.3. Genus Lemna L.

9.2.3.1. Description of the genus Lemna with key to the sections

Morphology

Fronds. Fronds lanceolate to ovate, floating on or below the surface of the water, 1 or more coher together (sometimes form chains or balls), with 1-5 (rarely 7) nerves; nerves with or without tracheids (containing ring- or spiral-shaped thickenings along the lateral walls); no pigment cells present; crystal cells with raphides but not with druses present; fronds not surrounded by a leaflet at the base which covers the root; 1 root per frond, without tracheids; rarely no roots in L. trisulca or in turions.

Flowers and fruits. Some flowering fronds similar to the vegetative ones, while others differ (L. trisulca, L. tenera); outer locules of the stamens situated at the top of the inner locules; ovary with 1 orthotropous or amphitropous ovule or 2-7 anatropous ovules; embryo sac bisporic; endosperm with 1 to 3 cell layers.

Size and distribution

The genus Lemna comprises 13 species; 5 sections may be distinguished: 3 sections with closely related species difficult to distinguish among and two isolated sections consisting of one well distinct species. This genus is distributed all over the world with centers in North America (9 species), Asia (7 species), and South America (5 species).

Key to the sections of the genus Lemna

- Margin of fronds in the distal part denticulate; fronds narrowed to a green stalk at the base, 3-50 coher together, submerged (except when flowering) and often form long and branched chains.

  sect. Hydrophylla

- Margin of fronds is whole; fronds rounded at the base, with a very small white stipe often decaying (no green stalk present).
  - Fronds with 3-5 (rarely 7) nerves.

- Fronds floating on the surface of the water, more or less rounded at apex, 1-2 times as long as wide.
  - Root sheath not winged; root tip mostly rounded; roots often longer than 3 cm; fronds often with reddish tinge or spots of anthocyanins. sect. Lemna
  - Root sheath winged at the base; root tip usually sharply pointed; roots no longer than 3 cm; fronds without reddish colour. sect. Alatae
- Fronds submerged (except when flowering or fruiting), 2 1/2-4 times as long as wide, tapering in a long point. sect. Biformes
- Fronds with 1 nerve. sect. Uninerves

Remarks on the taxonomy of the genus Lemna

The genus Lemna was divided by HEGELMAIER (1868) into 2 subgenera Hydrophace and Telmatophace, the latter containing only L. gibba. The subgenus Hydrophace consisted of 2 sections: Eulemna and Staurogeton (only species L. trisulca). Within section Eulemna, he distinguished 3 groups: L. minor - L. perpusilla, L. paucicostata, L. angolensis - L. valdiviana. HEGELMAIER changed his classification in 1895. He no longer distinguished subgenera but proposed 5 sections: Telmatophace (L. gibba), Eulemna (L. disperma, L. minor), Staurogeton (L. trisulca, L. tenera), Alatae (L. perpusilla, L. paucicostata, L. angolensis) and Uninerves (L. valdiviana, L. minima). DEN HARTOG and VAN DER PLAS (1970) grouped the species of the genus into 2 subgenera: Staurogeton (L. trisulca, L. tenera) and Lemna (all other species). In the present work, the genus is divided into 5 sections. The divison into subgenera is probably not justified. If a grouping of subgenera should be made, the dividing line is more reasonable with the sections Hydrophylla (Staurogeton) and Lemna on one side and the other 3 sections on the other side. L. trisulca has the same ovule positions, similar seeds and the ability to form anthocyanin, characteristics in common with species of the section Lemna. The submerged trait of L. trisulca is very characteristic but not such a great difference that it justifies its own subgenus. It is possible to change the growth form within a section (e. g. L. minuscula can live only when floating on the surface of the water; L. valdiviana, which is very similar to L. minuscula, is able to live submerged).

From our experience with Lemnaceae, the separation of L. gibba from L. disperma and other species of the L. minor group at the subgeneric or

sectional level is not justified since there are no distinct, qualitative characteristic differences between the two. On the other hand, the relation between L. trisulca and L. tenera is rather superficial: both species live submerged; since L. tenera does not have the same flower and fruit characteristics as L. trisulca and does not form anthocyanins, a separation and a classification in a section of its own is advisable; the relationship of L. tenera is probably closer to the groups of L. perpusilla or L. valdiviana.

9.2.3.2. Section Lemna

Morphology

Fronds. Fronds floating on the surface of the water, ovate and lanceolate with whole margins, rounded at the base, with a very small white stipe often decaying; numerous stomata and small, often indistinct papules on the upper surface; 3-5 (rarely 7) nerves; middle nerve with tracheids from the node up to near the tip; anthocyanins present; the frond therefore sometimes reddish or with red spots; air spaces in 2-3 layers spreading through nearly the whole frond; root length up to 15 cm (rarely not developed in turions); root sheath not winged; rootcap rounded, rarely pointed (often pointed in dried material).

Flowers and fruits. Flowering fronds similar to vegetative ones; the utricular leaflet with a narrow opening at the top; ovary with 1 amphitropous ovule or 2-7 anatropous ovules; fruit symmetrical, in some species laterally winged towards the top; outer seed coat with 7-9 subepidermal cell layers.

Size and distribution

The section consists of seven closely related species with mostly extratropical worldwide distribution.

Key to the species of the section Lemna (see also tables 9.1 and 9.2)

- Fronds without distinct papules or with papules near the tip distinctly larger than the proximal ones; no turions present (rarely in L. japonica); seed with 10-16 ribs.
  - Largest air spaces normally more than 0.3 mm in diameter; red colouring of the lower surface beginning from the margin (not from the node); very often 4-5 (rarely 7) nerves originating from the node; ovary with 1-7 ovules.

- Fronds mostly without a distinct papule near the tip; margin of the fruit 0.1-0.2 mm wide; found in all continents except Australia. L. gibba
- Fronds with distinct papules near the tip; winged margin of the fruit 0.05-0.1 mm wide; found only in Australia and New Zealand. L. disperma

- Largest air spaces normally less than 0.3 mm in diameter; red colouring of the lower surface beginning from the node if present; mostly 3 nerves, if 4-5 nerves present the outer lateral originate from the lower part of the inner lateral nerves; ovary with 1 ovule.
  - Fronds very rarely gibbous; papule near the tip not very distinct (but larger than the other papules); greatest distance between the inner lateral nerves mostly in or below the middle.
    - Fronds not coloured on the lower surface or if slightly reddish, the upper surface is more intensely coloured; does not occur in East Asia. L. minor
    - Fronds often coloured on the lower surface (always more intensely than on the upper side); found only in East Asia. L. japonica
  - Fronds often gibbous; with a very distinct papule near the tip; greatest distance between the lateral inner nerves mostly above the middle.
    - Fronds 1 1/2-2 times as long as wide; with pronounced papules along the midnerve; found only in Ecuador. L. ecuadoriensis
    - Fronds 1 1/5-1 2/3 times as long as wide; without pronounced papules along the midnerve; found only in North America, Hawaii. L. obscura

- Fronds with distinct papules along the median line of the upper surface, the papule at the tip not distinctly larger than the proximal papules; under unfavourable conditions plants form small olive to brown coloured, rootless turions that sink to the bottom of the water; seed with 30-60 ribs. L. turionifera

Remarks on the taxonomy of the section Lemna

The section Lemna is one of the most difficult groups to distinguish within the family. Many authors (including HEGELMAIER 1868, 1895) distinguished L. gibba as a subgenus or a section of its own due to its number of ovules (2-7 instead of 1). Recent publications show the diffi-

culty of separating L. gibba from L. minor and other species of the group (DE LANGE 1975, PIETERSE 1975, KANDELER 1975, VEEN 1975, LANDOLT 1975, DE LANGE and WESTINGA 1979, STARFINGER 1983). There are some species not known to HEGELMAIER which mediate between L. gibba and L. minor. There is also a possibility that hybrids or hybridogenous offsprings do occur. KANDELER (1975) mentions a possible hybrid between L. gibba and L. minor occurring in Campania (Italy) with 1-2 ovules and sterile flowers. The putative hybrid was first found and named (but not validly published) by GIUGA (1973), as L. symmeter. On the locality where it grows, it is only slightly gibbous, whereas L. gibba in the same place is very gibbous. The present author has observed several times in nature flowering L. gibba which shows no stamens. Also, several times in California and Argentina he found clones of small, flat L. gibba growing side by side with large and gibbous L. gibba. In culture, the clone showed mostly certain genetical differences; however, small, flat fronds could also become gibbous under different conditions (cf. LANDOLT and DANN 1983).

The genetical variability within L. gibba can be extremely great in some regions. Through vegetative propagation, the single plants form large patches of genetically identical fronds which can simulate clearly distinct species. GIARDELLI (1937) described a species similar to L. gibba from Argentina (L. Parodiana) with smaller size, red spots near the tip of the upper surface and only 1-2 seeds per fruit. The author saw many living clones from Argentina and made some observations in the field, but he found every transition from very typical "L. Parodiana" to L. gibba with large gibbous fronds; also, fronds with other combinations of characteristics occur frequently. The typical red spots near the tip have been recognized in many other regions of the world. Out of eight tested fruiting clones of typical L. gibba, three showed under the laboratory conditions 1-2 seeds per fruit and five 2-4 seeds per fruit. Also, a small form of L. gibba has been reported as a spontaneous somatic mutation by BOWEN (1958a).

LANGE (1975), PIETERSE (1975) and VEEN (1975) suggest that there are transition forms between L. gibba and L. minor in the Netherlands. But nevertheless there is some hiatus between the 2 species with regard to gibbosity (DE LANGE 1975, fig. 4) and to the flavonoid content (VEEN 1975). LANGE et al. (1981) showed that EDDHA added to the culture solution caused gibbosity in flat fronds of L. gibba, but not in L. minor:

the thickness of L. gibba becomes 1.8-3.6 mm, 3 1/2-10 times thicker than without EDDHA; the thickness of L. minor reaches scarcely more than 1 mm, at most 2 times thicker than without EDDHA. The difficulty in distinguishing between the 2 species is due to the modifiability of the taxonomically important characteristics of the species. Under some conditions, it is impossible to recognize the differentiating characteristics. The form of the rootcap is not a distinguishing characteristic between L. gibba and L. minor (KANDELER 1975, LANDOLT 1975). In living samples of both species rootcaps are predominantly rounded. Other characteristics are not reliable either (e.g. length/width ratio or length of the rootcap). Also, the fruit characteristics are not so different between the 2 species as suggested by KANDELER (1975). KANDELER based his statements on a figure of a fruit of L. minor in MASON (1957) which shows no winged margin, whereas L. gibba is distinctly winged. In my opinion, MASON reproduced a fruit of L. turionifera which is widespread in California and was not distinguished from L. minor by MASON. My observations, as well as figure 33 of ROSTOWZEW (1905) and figure IX,8 of HEGELMAIER 1868, reveal a winged margin of the fruit, though not so wide as that in L. gibba. According to HEGELMAIER (1868) and KANDELER (1975) L. gibba contains only one endosperm cell layer whereas the endosperm of L. minor is laterally 2-4 layered. The pericarp disintegrates rather quickly in L. gibba and with delay in L. minor, according to KANDELER (1975).

L. disperma also shows a combination of the characteristics of L. gibba and L. minor, the pigmentation and gibbosity similar to L. gibba, but only 1, rarely 2 seeds per fruit. The ecology is similar to that of L. gibba. A pronounced papule on the upper surface near the tip is typical but may occasionally be seen also with L. gibba. L. disperma is restricted to Australia and New Zealand (L. gibba is not native there; L. minor is introduced in New Zealand and Southern Australia). GIARDELLI (1941) mentions L. disperma as also from Argentina and (in a footnote) from Berlin. The plants probably belong to L. gibba but look very similar to L. disperma. Similar plants are also known from California. The characteristics of both species overlap. L. disperma probably originated from L. gibba. The isolated populations in Australia deviated somewhat from the rest of L. gibba.

In a similar way, L. japonica restricted to Eastern Asia and isolated from the area of L. minor probably originated from L. minor. The main

distinction is the red pigmentation of the lower surface of L. japonica, which only shows up under certain conditions. Sometimes L. japonica shows some gibbosity. Also, a few of the clones cultivated in our laboratory were able to form some turion-like fronds. Therefore, L. turionifera which occurs in northern Asia might have contributed to the origin of L. japonica. L. japonica is able to grow in warmer regions than L. minor (similar to L. obscura in North America).

Two further species of the group are sometimes difficult to distinguish from L. minor and L. gibba, too. L. turionifera forms turions similar to those of S. polyrrhiza, and L. obscura has a very distinct papule on the upper surface near the tip and is able to become gibbous under certain conditions. The fruit and the seed are good, distinct characteristics. Both species develop fruits without winged margins; furthermore, L. turionifera forms seeds with 30-60 indistinct ribs (all other species of the section have no more than 16 ribs). The turions enable L. turionifera to grow in regions with cold winters. Therefore, it is distributed in northern and continental North America and Asia. L. obscura, on the other hand, is restricted to the central and southeastern states of the U.S.A. and the highlands of Mexico (introduced to Hawaii). L. obscura, which was distinguished by DAUBS (1965), was previously regarded as L. minor (HEGELMAIER 1868) or as L. gibba (many American authors). HEGELMAIER (1868) identified L. turionifera as L. minor; DAUBS (1965) and many American authors considered L. turionifera as L. gibba, L. minor or L. obscura. In the field the fronds of L. minor have mostly a higher length/width ratio than the fronds of L. turionifera (higher and lower than 1 1/2, respectively. As DOCAUER (1984) demonstrated this characteristic is dependent on a low phosphorus content of the medium. At a higher phosphorus concentration the ratio for both species is around 1.5.

L. ecuadoriensis is only known from the two collections of Ecuador, where it grows in a rather dry and hot region. It looks like a narrow L. obscura. The different climatic conditions of the habitat and the long distance to the next station of L. obscura in Mexico (more than 3,000 km) suggest a distinct taxon. More material on this species has to be compiled.

DE SLOOVER (1973) published a new Lemna species from central Africa under the name L. rwandensis. The described species is characterized by its large size and its lack of papules. The fronds are rather thin and flat. I saw similar fronds of L. minor from the mediterranean regions

Tab. 9.1. Characteristics of the species of section Lemna

1 L. gibba, 2 L. disperma, 3 L. minor, 4 L. japonica, 5 L. ecuadoriensis, 6 L. obscura, 7 L. turionifera

+ rarely occurring and not very distinct
++ occasionally occurring and rather distinct
+++ often occurring and distinct
++++ nearly always occurring and very distinct
- never occurring
? not known

Characteristics	Species of section Lemna						
	1	2	3	4	5	6	7
Lower surface of the frond gibbous	+++	++	-	+	++	++	+
Length-width ratio more than 1.6	+	++	+++	++	++	++	-
Fronds wider than 3.5 mm	+++	-	++	++	++	-	+
Lower surface of the frond red	++	++	-	++	+++	+++	++
Red spot around the point of attachment of the root present	-	-	-	++	++	++	++
Red spots near the tip of the upper surface present	++	++	-	-	-	+	+
4-5 nerves present	++++	++	++	++	-	-	-
4th and 5th nerve originating from the node	++++	++++	-	-	-	-	-
4th and 5th nerve originating from the lower part of the inner nerves	-	-	++++	++++	-	-	-
The biggest distance of inner lateral nerves within the distal half of the frond	+++	+++	+	+	++	++	++
The biggest distance of inner lateral nerves within the proximal half of the frond	+	+	+++	+++	-	+	+
Pronounced papules along the mid-nerve present	-	-	+	+	+++	+	+++
The papule near the tip larger than the proximal ones	++	++++	+++	+++	++++	++++	+
Air spaces larger than 0.3 mm in diameter	+++	+++	-	-	+	++	+
Small rootless turions present which sink to the bottom	-	-	-	+	-	-	+++
More than one seed per fruit	+++	+	-	-	?	-	-
Margin of the fruit winged	++++	+++	+++	?	?	-	-

which had reached 8 mm in length and showed no papules. Under culture conditions, these fronds never grew longer than 5 mm and they developed papules like any other L. minor. The localities in Ruanda where L. rwandensis was found is situated within the area of L. minor. It is very probable that the samples of L. rwandensis (fig. 9.2d) of which I did not see living specimens, consist of very large fronds of L. minor formed under very special conditions. Similar, unusually large fronds are known for other Lemnaceae (S. polyrrhiza, S. punctata, L. gibba, W. neotropica, W. arrhiza).

To identify specimens of the section Lemna, it is best to use a combination of characteristics and to take geographical distribution into consideration. As DE LANGE and WESTINGA (1979) pointed out, many characteristics overlap and the plants are only recognizable if they show traits which lie outside of this overlapping area. Tables 9.1 and 9.2 summarize relevant characteristics for recognition of the species within the section Lemna.

Two varieties (var. oxymitra, var. colorata) of L. minor described by HEGELMAIER (1868) have no taxonomical value. They contain plants with acute rootcaps and red coloured surfaces, respectively. HEGELMAIER (1868) included in both varieties plants from L. minor, as well as from L. turionifera and L. obscura.

Tab. 9.2. Occurrence of the species of section Lemna

1 L. gibba 2 L. disperma 3 L. minor 4 L. japonica
5 L. ecuadoriensis 6 L. obscura 7 L. turionifera

v occurring
- not occurring

Regions	Species of section Lemna						
	1	2	3	4	5	6	7
North America	v	-	v	-	-	v	v
South and Central America	v	-	-	-	v	-	-
Africa, Europe, southern and western Asia	v	-	v	-	-	-	(v)
Northern and eastern Asia	-	-	-	v	-	-	v
Australia, New Zealand	-	v	v	-	-	-	-

4. Lemna gibba L. (fig. 9.2a; plate IIIa,b)

Morphology

Fronds. Fronds 1-8 mm long, 0.8-6 mm wide, 1-1 1/2 times as long as wide; somewhat shiny on the upper surface, usually without distinct papules (sometime smaller fronds with well visible papules near the tip), usually with 4-5 nerves (rarely up to 7 nerves; small fronds sometimes only with 3 nerves); the lateral nerves originate independently from the node; very often gibbous (up to 4 mm thick); on the upper surface occasionally with distinct red spots, especially near the tip; on the lower surface sometimes red coloured, especially near the margins, on the nerves or on the cells between the air spaces, the pigmentation rarely beginning from the node; greatest distance between the inner lateral nerves in or somewhat above the middle of the nerves; largest air spaces wider than 0.3 mm; rootcap mostly rounded (living material) or often pointed (dried material), 0.6-1.8 mm long (the other species of the group up to 1.2 mm long); no rootless turions which sink to the bottom of the water present.

Flowers and fruits. Plants often flowering and fruiting. Ovary with 1-7 ovules; style 0.05-0.1 mm long; fruit 0.6-1.0 mm long, 0.8-1.2 mm wide, with winged margin; wing 0.1-0.2 mm wide; seeds 1-5 per fruit, 0.7-0.9 mm long, 0.4-0.6 mm thick, whitish, with 8-16 distinct ribs, fall out of the fruit wall after ripening.

Distribution

Areas of temperate climate with a dry season and mild winters (especially in mediterranean climates; America, Europe, Africa, Southwest Asia); not found in Australia (fig. 6.7.).

5. Lemna disperma Hegelmaier (fig. 9.2b; plate IIIc,d)

Morphology

Fronds. Fronds 0.8-4.0 mm long, 0.6-3.0 mm wide, 1-2 times as long as wide; somewhat shiny on the upper surface, with a distinct papule near the tip and above the node; with 3-5 nerves, the lateral nerves originate from the node; often gibbous (up to 2.5 mm thick); on the upper surface, occasionally with distinct red spots, especially near the tip; on the lower surface sometimes red coloured, especially near the margins, the pigmentation rarely beginning from the node; greatest distance

between the inner lateral nerves in or somewhat above the middle of the nerves; largest air spaces mostly wider than 0.3 mm; rootcap rounded or pointed (living material) or usually pointed (dried material); no rootless turions which sink to the bottom of the water present.

Flowers and fruits. Plants often flowering and fruiting. Ovary with 1-2 (very rarely 3) ovules; style 0.05-0.10 mm long; fruit 0.7-0.8 mm long, 0.6-0.7 mm wide, with winged margin; wing 0.05-0.10 mm wide; seed 1 (rarely 2), 0.7-0.9 mm long, 0.4-0.6 mm thick, whitish, with 10-16 distinct ribs, fall out of the fruit wall after ripening.

Distribution

Warm temperate regions of Australia and New Zealand (fig. 6.7.).

6. Lemna minor L. (fig. 9.2c,d; plate IVa,b)

Morphology

Fronds. Fronds 1-8 (very rarely up to 10) mm long, 0.6-5.0 (very rarely up to 7.0) mm wide, 1 1/3-2 times as long as wide; shiny on the upper surface; with some indistinct papules along the median line (papules near the tip and above the node somewhat larger than the ones between), with 3 (rarely up to 4-5) nerves; if 4-5 nerves present the outer lateral nerves originate from the lower part of the inner lateral nerves; never gibbous (not thicker than about 1 mm), on the upper surface occasionally diffusely reddish (especially during the cold season), on the lower surface very rarely slightly reddish (but much less intensely than on the upper surface); greatest distance between the inner lateral nerves in or somewhat below the middle of the nerves; largest air spaces rarely wider than 0.3 mm; rootcap usually rounded (living and dried material); no rootless turions which sink to the bottom of the water present.

Flowers and fruits. Plants occasionally flowering and very rarely fruiting. Ovary with 1 ovule; style 0.10-0.15 mm long; fruit 0.8-1.0 mm long, 0.8-1.1 mm wide, with winged margin; wing 0.05-0.10 mm wide; seed 0.7-1.0 mm long, 0.4-0.6 mm thick, whitish, with 10-16 distinct ribs, stays within the fruit wall after ripening.

Distribution

Temperate regions of the whole world except East Asia and Australia (introduced around Melbourne), with relatively mild winters (fig. 6.8).

7. Lemna japonica Landolt (fig. 9.2e; plate IVc,d)

Morphology

Fronds. Fronds 1-6 mm long, 0.6-4.0 mm wide, 1 1/3-1 4/5 times as long as wide; shiny on the upper surface; with some indistinct papules along the median line (papules near the tip and above the node larger than the ones between), with 3 (rarely 4-5) nerves; the outer lateral nerves originate from the lower part of the inner lateral nerves; rarely gibbous (up to 2 mm thick); on the upper surface very rarely reddish, on the lower surface sometimes reddish coloured (always more intensely than on the upper surface), the pigmentation beginning around the node; greatest distance between the inner lateral nerves in or somewhat below the middle of the nerves; largest air spaces rarely wider than 0.3 mm; rootcap usually rounded (living and dried material); nearly rootless turions which sometimes sink to the bottom of the water rarely present.

Flowers and fruits. Plants occasionally flowering, fruits not known.

Distribution

Warm temperate regions of East Asia with relatively mild winters (fig. 6.8).

8. Lemna ecuadoriensis Landolt (fig. 9.2f; plate Vc,b)

Morphology

Fronds. Fronds 1-3 mm long, 0.7-2.0 mm wide, 1 1/2-2 times as long as wide; shiny on the upper surface; with distinct papules along the middle nerve and a very distinct papule near the tip; 3 nerves; occasionally gibbous, red pigmentation on the lower surface, the pigmentation beginning around the node; greatest distance between the lateral nerves in or slightly below the middle of the nerves; largest air spaces rarely wider than 0.3 mm; rootcap rounded (living material); no rootless turions which sink to the bottom of the water present; other characteristics and the range of variations not known.

Flowers and fruits. Not known.

Distribution

Only known from Ecuador (rather dry and warm tropical climate) (fig. 6.9).

9. Lemna obscura (Austin) Daubs (fig. 9.2g; plate Vc,d)

Morphology

Fronds. Fronds 1.0-3.5 mm long, 0.8-3.0 mm wide, 1 1/5-1 2/3 times as large as wide; shiny on the upper surface; very distinct papule near the tip and several indistinct smaller papules along the middle nerve; 3 nerves; occasionally gibbous (up to 2.5 mm thick); sometimes with red spots on the upper surface (especially near the tip); red pigmentation often on the lower surface (always more intensely red than on the upper side), the pigmentation beginning around the node; greatest distance between the lateral nerves usually near the middle of the nerves; largest air spaces rarely wider than 0.3 mm; rootcap rounded (living material) or pointed (dried material); no rootless turions which sink to the bottom of the water present.

Flowers and fruits. Plants occasionally flowering and fruiting. Ovary with 1 ovule; style 0.15-0.20 mm long; fruit 0.5-0.7 mm long, about 0.8 mm wide, without winged margin; seed 0.7-0.8 mm long, 0.4-0.6 mm thick, whitish, with 10-16 distinct ribs, stays within the fruit wall after ripening.

Distribution

Warm temperate regions of North America with relatively mild winters and wet summers; introduced in Hawaii (fig. 6.9).

10. Lemna turionifera Landolt (fig. 9.2h; plate VIa,b)

Morphology

Fronds. Fronds 1-4 mm long, 0.8-3.5 mm wide, mostly 1-1 1/2 times as long as wide (the relatively roundish shape is restricted to certain environmental conditions especially under limiting phosphate concentrations, a situation which is very often found in nature cf. DOCAUER 1984); somewhat shiny on the upper surface; rather distinct papules along the nerves (the papule near the tip usually not larger than the other papules); 3 nerves; rarely gibbous (up to 2 mm thick); sometimes with red spots on the upper surface (especially near the tip); often red pigmentation on the lower surface (always more intensely red than on the upper surface), the pigmentation beginning around the node; greatest distance between the lateral nerves in or slightly above the middle of the nerves; largest air spaces rarely wider than 0.3 mm; rootcap mostly

rounded, sometimes pointed (living material), rounded or pointed (dried material); occasionally (especially at the end of the vegetation period) rootless, small, olive to brown coloured turions present, which sink to the bottom of the water and stay there for the cold season.

Flowers and fruits. Plants occasionally flowering and rarely fruiting. Ovary with 1 ovule; style 0.15-0.20 mm long; fruit 0.5-0.6 mm long; 0.6-0.8 mm wide, without winged margin; seed 0.5-0.8 mm long, about 0.5 mm thick, whitish, with 30-60 indistinct ribs, stays within the fruit wall after ripening.

Distribution

Found in temperate regions of North America and Asia with continental climates (fig. 6.10).

9.2.3.3. Section Hydrophylla Dumortier

Morphology

Fronds. Vegetative fronds submerged, narrowly ovate, with denticulate margins in the distal part, narrowed at the base to a green stalk, without stomata and papules on the upper surface, with 3 (rarely 1) nerves; middle nerve with tracheids near the node; anthocyanins present, the frond therefore sometimes reddish coloured; air spaces in 1-2 layers, only in the distal part of the frond (in all other sections, and in flowering fronds air spaces also in the basal part), filling out 1/3-2/3 of the distal part; root up to 2.5 cm long, sometimes not developed; root sheath not winged; rootcap pointed.

Flowers and fruits. Flowering fronds float on the surface of the water, ovate, with numerous stomata; the utricular leaflet with narrow opening at the top (according to MASON 1957 open on one side); ovary with 1 amphitropous ovule; fruits laterally winged towards the top; outer seed coat with 7-9 subepidermal cell layers.

Size and distribution

L. trisulca is the only species of the section and has a holarctic distribution with limited occurrence in Africa, Southern Asia and Australia.

Remarks on the taxonomy of the section Hydrophylla

The section consists of only one polymorphic species. A var. pygmaea Hennings with small fronds can be observed within the whole distribution area of the species. It consists of genetically small-fronded plants, as

well as of plants poorly developed due to unfavourable growth conditions. This "variety" and other named forms are of no taxonomic significance. The Australian populations have somewhat different characteristics. Under the culture conditions in our laboratory (Hutner solution 1/5, 25°C, different light intensities), all five investigated strains from Australia did not develop any roots, and the fronds showed consistently one nerve; most of the other strains from other continents have one root and 3 nerves. However, there are herbarium samples of L. trisulca from Australia with one root and 3 nerves; on the other hand, there are many specimens of L. trisulca known from outside of Australia that have no root and only one nerve. Furthermore these two characteristics are not always connected. Therefore, it is not advisable to separate the Australian plants from the other ones. I did not see fruits of the Australian specimens of L. trisulca.

11. Lemna trisulca L. (fig. 9.2i,k; plate VIc,d)

Morphology

Fronds. Fronds 3-50 coher together and very often form branched chains, 3-15 mm long (without stalk), 1-5 mm wide, 2-3 1/2 times as long as wide; stalk 2-20 mm long; no distinct turions which sink individually to the bottom of the water present.

Flowers and fruits. Plants occasionally flowering and rarely fruiting. Fruit symmetrical, 0.6-0.9 mm long, 0.7-1.2 mm wide; winged margin about 0.15 mm wide; style about 0.15 mm long; seed 0.6-1.1 mm long, 0.5-0.8 mm thick, with 12-18 distinct ribs.

Distribution

Areas with temperate climates in the whole world except very dry, very humid regions and South America; also not found in most of the oceanic islands (fig. 6.11).

9.2.3.4. Section Alatae Hegelmaier

Morphology

Fronds. Fronds floating on the surface of the water, ovate to lanceolate, with whole margins, rounded at the base, a very small white stipe often decays; numerous stomata and one distinct papule near the tip on the upper surface and one to several papules above the node; 3 nerves,

middle nerve with tracheids only near the node; no reddish colour (anthocyanins) present; air spaces in 1-3 layers spreading through nearly the whole frond; root length up to 3.5 cm (BEPPU et al. 1985 report of a root length of 6-7 cm; this value probably has to be devided by 2; cf. the relation of frond size and root length of their fig. 5); root sheath laterally winged; rootcap sharply pointed (living and dried material).

Flowers and fruits. Flowering fronds similar to the vegetative ones; the utricular leaflet open on one side; ovary with 1 nearly orthotropous ovule, directed slightly towards the tip; fruit asymmetrical (style inserted on the side in direction towards the frond base), with a very small or no wing at the margin; outer seed coat with 2-7 subepidermal cell layers.

Size and distribution

The section comprises two species of which one is restriced to North America and the other has a worldwide tropical and subtropical distribution.

Key to the species of the section Alatae.

- Seeds with 35-70 indistinct ribs, stay within the fruit wall after ripening; wing of the root sheath 2-3 times as long as wide; very often 2-3 papules above the node which are bigger than the papule near the tip. Found in North America. L. perpusilla

- Seeds with 8-26 distinct ribs, fall out of the fruit wall after ripening; wing of the root sheath 1-2 1/2 times as long as wide; mostly one papule above the node which is smaller than the one near the tip. Found in warmer regions of the whole world. L. aequinoctialis

Remarks on the taxonomy of the section Alatae

HEGELMAIER (1868, 1895) distinguished three species within the group: L. perpusilla, L. paucicostata and L. angolensis. L. perpusilla shows seeds with 35-70 not very distinct ribs; 8-26 distinct ribs are characteristic for the other two "species". L. angolensis attracts attention with its very pronounced papule near the tip which is higher than the distance from the papule to the tip of the frond. At first HEGELMAIER was of the opinion that this characteristic was restricted to Central Africa. But GIARDELLI (1959) observed similar plants in samples from North and South America and the Philippines. McCANN (1942) described a new species with

the same characteristics as L. Eleonorae from India. There are three clones in our living collection which could be attributed to L. angolensis (one from Botswana, fig. 9.2n, and two from India). But there are many clones that form a transition between the type with very pronounced papules and the types with indistinct papules, the latter of which were called L. Blatteri by McCANN. Furthermore, the height of the papules can vary according to the external conditions (KANDELER 1975 and own observations). Therefore, the characteristic of papule height is not taxonomically relevant. L. paucicostata and L. angolensis belong to the same species, which has to be referred to according to the earliest name L. aequinoctialis.

THOMPSON (1898) and most American authors did not distinguish between L. aequinoctialis and L. perpusilla. THOMPSON investigated mixed populations of L. aequinoctialis and L. perpusilla around St.Louis, Missouri, where the two species occur together. He was of the opinion that the two fruit types belong to the same population due to the fact that both species have nearly identical vegetative fronds. It was KANDELER and HUEGEL (1974a) who showed that HEGELMAIER was right in distinguishing between the two species by noting some additional fruit and seed characteristics. There is a statistical difference with the width of the wing of the root sheath being a little smaller in L. perpusilla than in L. aequinoctialis. Furthermore, the living fronds of our clones of L. perpusilla show 2-3 distinct papules above the node whereas there is normally only one in L. aequinoctialis. But, this characteristic is not very easy to see in dried material and it is probably not valid for all clones of the two species. There is an ecological difference between the two species. The seeds of L. aequinoctialis fall out of the fruit wall after ripening and germinate relatively quickly at warm temperatures; seeds of L. perpusilla stay within the fruit wall after ripening (KANDELER and HUEGEL 1974a); they sink with the dead fronds to the bottom and do not germinate until after extended exposure to cold temperatures. Since the fronds of both species are not very frost tolerant, they have to pass the winter with fruits or seeds in cooler regions. As already mentioned, the seeds of L. aequinoctialis germinate at once in warmer waters; under cooler conditions, they do not form flowers and fruits. Therefore L. aequinoctialis is not able to pass the winter in regions with cold winters except in cases where the seeds are not able to germinate during the warm season because the locality has dried out and

remained dry throughout the winter. However, special ecotypes are occurring in Japan (see below). The distribution of L. aequinoctialis is as a consequence mostly subtropical and tropical; L. perpusilla, on the other hand, is restricted to the middle and eastern states of the U.S.A.

Recently, BEPPU et al. (1985) distinguished in Japan a new species (L. aoukikusa Beppu and Murata) with two subspecies (ssp. aoukikusa and ssp. hokurikuensis) from L. aequinoctialis. The main differences (beside chromosome numbers and physiological properties) to L. aequinoctialis are given in Table 9.3. The characteristics of L. aoukikusa are reliable to distinguish the taxon in Japan. But, compared with strains of L. aequinoctialis of other parts of the world, they are within the variation of L. aequinoctialis. Especially the higher number of lateral ribs is not restricted to L. aoukikusa. From 10 studied seeds of L. aequinoctialis, 5 (2 from Oklahoma and 1 each from California, Colombia and France) have more than 50 lateral ribs (LANDOLT unpubl.). The authors of L. aoukikusa found also some smaller differences in the Bam Hl restriction pattern of chloroplast DNAs (see LANDOLT and KANDELER 1987). The best characteristics for the new described taxa are the special physiological and ecological features (see chapter 7.4.3). L. aoukikusa ssp. aoukikusa has 2n=66-84 and occurs throughout Japan (except the South). L. aoukikusa ssp. hokurikuensis has 2n=40 and is restricted to Niigata, Yamagata and Gifu Prefectures of Honshu, Japan. It is interesting to note that the new taxa apparently seem to be adapted to the cool winter climate in central and northern Japan which is beyond the normal climatic boundaries of L. aequinoctialis in other regions of the world. They overwinter as seeds (N_1-type) or as true turions (N_2-type) (BEPPU et al.

Table 9.3. Morphological characteristics of L. aoukikusa (according to BEPPU et al. 1985; * according to earlier publications of BEPPU et al.)

Species	Type*	length of seeds	width of seeds	number of lateral ribs
L. aequinoctialis	S	0.44-0.60	0.34-0.44	33-50
L. aoukikusa ssp. aoukikusa	N_1	0.58-0.74	0.37-0.52	44-82
L. aoukikusa ssp. hokurikuensis	N_2	0.60-0.76	0.35-0.68	53-80

1985). The systematic ranks of the newly described taxa have to be evaluated by studies of the whole group throughout the world-wide range.
Under certain conditions in nature (probably cool waters of poor nutrient content), the plants of both species form light green, flat and elongated fronds. These fronds show only undistinct papules and, sometimes, the nerves may be clearly visible from above. Fronds of this type were called L. trinervis by DAUBS (1965) (cf. fig. 9.2 o). They can be found within the distribution area of L. aequinoctialis and L. perpusilla and are merely modifications of these species.
Fortunately, L. perpusilla and L. aequinoctialis fruit relatively frequently.

12. Lemna perpusilla Torrey (fig. 9.2 l; plate VIIa,b)

Morphology

Fronds. Fronds 1-4 mm long, 0.8-3.0 mm wide, 1-1 2/3 times as long as wide; on the upper surface often 2-3 papules above the node which are bigger than the ones near the tip; wing of the root sheath 2-3 times as long as wide.

Flowers and fruits. Plants often flowering and fruiting. Fruit 0.7-1.0 mm long, 0.5-0.7 mm wide; laterally with a winged margin; wing about 0.05 mm wide; style 0.2-0.4 mm long; seed 0.6-0.8 mm long, 0.4-0.6 mm thick, whitish, with 35-70 indistinct ribs, stays within the fruit wall after ripening; outer seed coat with 5-7 subepidermal cell layers.

Distribution

Temperate oceanic region of central and Eastern North America (fig. 6.12).

13. Lemna aequinoctialis Welwitsch (fig. 9.2m,n,o; plate VIIc,d)

Morphology

Fronds. Fronds 1-6.5 mm long, 0.8-4.5 mm wide, 1-3 times as long as wide; usually with one papule which is located on the upper surface above the node and is smaller than the one near the tip; wing of the root sheath 1-2 1/2 times as long as wide.

Flowers and fruits. Plants often flowering and fruiting. Fruit 0.5-0.8 mm long, 0.4-0.7 mm wide, not winged; style 0.05-0.20 mm long; seed 0.45-0.80 mm long, 0.3-0.7 mm thick, brownish, with 8-26 distinct longi-

tudinal and 30-80 lateral ribs, falls out of the fruit wall after ripening; outer seed coat with 2-4 subepidermal cell layers.

Distribution

Subtropical and tropical regions of the whole world; introduced to more northern regions by rice cultures (fig. 6.13).

9.2.3.5. Section Biformes sect. nov.

Morphology

Fronds. Vegetative fronds submerged, elongated, lanceolate, tapering into a long pointed tip, with entire margins, rounded at the base, with a very small white stipe often decaying, without stomata and papules; 3 nerves; no tracheids in the nerves present; no reddish colour (anthocyanins) present; air spaces in 1 layer, spreading through 1/3-2/3 of the distance between the node and the tip; roots up to 2.5 cm long; root sheath not winged; rootcap rounded.

Flowers and fruits. Flowering fronds floating on the surface of the water, lanceolate, pointed, with numerous stomata and one papule near the tip; the utricular leaflet open on one side; ovary with 1 nearly orthotropous ovule directed slightly towards the tip of the frond; fruits not known.

Size and distribution

L. tenera grows in southeastern Asia and is the only species of the section.

Remarks on the taxonomy of the section Biformes

L. tenera forms a kind of transition between the sections Alatae and Uninerves. But the very elongated vegetative fronds, which live submerged, and the sharply pointed tip of the frond are very characteristic. The relationship to L. trisulca as assumed by HEGELMAIER (1895), DEN HARTOG and VAN DER PLAS (1970) is very superficial (submerged trait of both species). As shown in L. valdiviana and in the genus Wolffiella, the submerged trait is not restricted to a single taxonomical group.

14. Lemna tenera (fig. 9.2p,q)

Morphology

Fronds. Vegetative fronds coher 1-3 together, often bent in a sabre-like position; 3.5-9.0 mm long, 1.2-3.0 mm wide, 2 1/2-4 times as long as wide; no turions known.

Flowers and fruits. Flowering fronds 2.0-3.5 mm long and 1.5-2.5 mm wide, 1 1/3-2 times as long as wide. Fruits not known.

Distribution

Humid, tropical region of Southeastern Asia (fig. 6.12).

9.2.3.6. Section Uninerves Hegelmaier

Morphology

Fronds. Fronds float on or below the water surface, ovate to lanceolate, with whole margins, rounded at the base, with a very small white stipe often decaying; numerous stomata and with or without indistinct papules along the median line; 1 nerve; no tracheids in the nerve; no reddish colour (anthocyanins); air spaces in 1-2 layers spread nearly through the whole frond or only near the node; root up to 1.5 cm long, the tip very often bent upwards; root sheath not winged; rootcap often rounded to somewhat pointed (living and dried material).

Flowers and fruits. Flowering fronds similar to the vegetative ones; the utricular leaflet open on one side; ovary with 1 nearly orthotropous ovule directed slightly towards the tip of the frond; fruit asymmetrical (style inserted on the side in direction towards the frond base); much longer than the seed (in all other sections the seed is nearly as long as the fruit), not winged at the margin; number of cell layers of the outer seed coat not investigated.

Size and distribution

The section is originally restricted to America. It consists of two closely related species.

Key to the species of the section Uninerves

- Nerve mostly prominent, longer than the extension of the air spaces or running through at least 3/4 of the distance between the node and the tip; only 1 layer of air spaces present; plants sometimes live submerged; fruit 1.0-1.35 mm long. L. valdiviana
- Nerve sometimes indistinct, very rarely longer than the extension of the air spaces, not longer than 2/3 of the distance between the node and the tip; 1-2 layers of air spaces; plants always float on the surface of the water; fruit 0.6-1.0 mm long. L. minuscula

Remarks on the taxonomy of section Uninerves

The two species are very difficult to separate. Under certain conditions, they are able to form nearly identical fronds. The size and the length-width ratio are dependent on external factors. Under our culture conditions (Hutner solution 1/5, 24-28°C, 25,000 lux), only very slight differences were observed; this was especially true for the length-width ratios which are the main differentiating characteristics according to HEGELMAIER, as the values were nearly identical. Contrary to the opinion of THOMPSON (1898) and BRAVO (1930), the presence of papules is not a characteristic property of L. minuscula. Papules can be observed in many clones of both species. Both species may develop under certain although, not exactly known, conditions very typical forms of fronds: L. valdiviana, especially in cooler regions, shows elongated fronds which are 2-3 times as long as wide; pronounced asymmetrical fronds having bent the tract of elongated cells at the base of the fronds away from the median line; very often, many fronds coher together. On the other hand, L. minuscula forms under crowded or otherwise unfavourable conditions small thick suborbicular fronds (often single or cohering 2-4 together) which never can be observed in L. valdiviana. The best distinguishing characteristic which can be seen only in transparent slides, is the length of the nerve in relation to the extension of the air spaces. However, flowering fronds in both species have air spaces nearly throughout the frond. There are some overlapping variations, too. Since fruiting is rare, the seed and fruit characteristics which differ slightly, are of no great value. McCLURE and ALSTON (1966) show some very pronounced differencies in the flavonoid content of the two species. Since the two authors apparently did not have the same classification of the investigated clones as the present author, the validity of this characteristic has to be checked (see also volume 2, chapter 1.2.6., LANDOLT and KANDELER 1987). There is a pronounced difference in the ecological behaviour of the two species. L. valdiviana has its center of distribution in regions with relatively high rainfall, whereas L. minuscula grows mostly in regions with drier climates. It is not found in very hot regions (lowlands in the tropics). L. minuscula is easily transplanted and has been introduced to Europe and Asia. On the other hand, L. valdiviana develops only under stabilized long-term conditions where it is even able to grow submerged, similar to L. trisulca. Indications of L. trisulca being present in Central and South America are probably due to confusion with submerged L. valdiviana.

HEGELMAIER (1895) distinguished two further species within this section of which he was not certain: L. abbreviata and L. platyclados are somewhat aberrant morphological forms without any taxonomical relevance. Under L. platyclados, he combined all plants of L. valdiviana with large wide fronds. L. abbreviata includes plants with thin fronds of a medium length-width ratio. They belong partly to L. valdiviana and more often to L. minuscula.

15. Lemna valdiviana Phil. (fig. 9.2r,s; plate VIIIa)

Morphology

Fronds. Fronds 1-5 mm long, 0.6-3.0 mm wide, 1 1/3-3 times as long as wide, occasionally somewhat pointed, 4-20 coher together, often submerged; air spaces in only 1 layer, rarely extended further to the tip than 2/3 of the distance from the node to the tip (flowering fronds with more extended aerenchymatic tissue); nerve mostly pronounced, longer than the extension of the air spaces or at least running through 3/4 of the distance between the node and the tip; forming mostly a distinct angle with the tract of elongated cells at the base (frond at the base distinctly asymmetric).

Flowers and fruits. Plants occasionally flowering and fruiting. Style about 0.2 mm long; fruit 1.0-1.35 mm long, 0.7-0.9 mm wide; seed 0.6-0.8 mm long, 0.4-0.6 mm thick, with 15-29 ribs.

Distribution

Rather humid regions of America with oceanic climate (no low winter temperatures) (fig. 6.14).

16. Lemna minuscula Herter (fig. 9.2t,u; plate VIIIb)

Morphology

Fronds. Fronds 0.8-4.0 mm long, 0.5-2.5 mm wide, 1-2 times as long as wide, never pointed, 1-4 (rarely more) coher together; air spaces in 1-2 layers, often extended to the tip of the frond; nerve often not very distinct, rarely longer than the extension of the air spaces, running no further to the tip of the frond than 2/3 of the distance between the node and the tip; usually extending straight into the tract of elongated cells at the base (no angle; frond only slightly asymmetrical at the base).

Flowers and fruits. Plants occasionally flowering and fruiting. Style 0.2-0.4 mm long; fruit 0.6-1.0 mm long, 0.4-0.7 mm wide; seed 0.4-0.55 mm long, about 0.3 mm thick, with 12-15 ribs.

Distribution. Dry to moderately humid temperate and subtropical regions of America with mild winters; introduced in Europe and Eastern Asia (fig. 6.15).

Remarks to the figures 9.1 to 9.4 (p. 497-509)

Fig. 9.1. Spirodela

a. S. intermedia. No. 7355 from Surinam (locus classicus) of S. "biperforata"). The transparent preparation shows a flat form with small air spaces. 1 = pouch of the minus side, 2 = corner of the dorsal lobe of the prophyllum transgressing to the ventral side, 3 = ventral lobe of the prophyllum covering the point of attachment of the roots, 4 = rootcap, 5 = first daughter frond of the plus side.
b. S. intermedia. No. 7702 from Corrientes, Argentina. The fronds are slightly gibbous and have bigger air spaces than in a.
c. S. polyrrhiza. No. 8387 from Switzerland. 2 and 3 as under a.
d. S. punctata. No. 7536 from Canary Islands. 3 and 4 as under a.

Fig. 9.2. Lemna

a. L. gibba. Nr. 8291 from northern Iran. Fronds gibbous with big air spaces and five nerves. 1 = root sheath
b. L. disperma. No. 7816 from South Australia. Fronds gibbous.
c. L. minor. No. 8287 from Poland. The air spaces are much smaller than in L. gibba. The fronds show three nerves. At the apex a papilla is visible.
d. L. minor. Frond of the type collection of L. "rwandensis" from Ruanda. The size of the frond is at the upper limit of variation of L. minor.
e. L. japonica. No. 7432 from Honshu, Japan.
f. L. ecuadoriensis. From the type collection in Ecuador. Fronds slightly gibbous with a papilla at the apex.
g. L. obscura. Nr. 8044 from Louisiana, U.S.A. A very prominent papilla near the apex is visible.
h. L. turionifera. Nr. 7908 from Michigan, U.S.A. The prominent papilla near the apex is mostly not bigger than the papillae on the middle line which are not visible.

i. L. trisulca. No. 8193 from Utah, U.S.A. One root and three nerves are clearly visible.
k. L. trisulca. No. 7258 from Victoria, Australia. No root and only one nerve is present.
l. L. perpusilla. No. 8017 from Arkansas, U.S.A. Relatively big air spaces and the typical papilla at the apex are recognizable.
m. L. aequinoctialis. No. 8362 from Java, Indonesia. A prominent papilla at the apex and a broadly winged root sheath (l) are typical.
n. L. aequinoctialis. No. 8369 from Botswana. The very prominent papilla at the apex corresponds to the description of L. "angolensis", but the genetical and phenological variation is continuous to "normal" fronds of L. aequinoctialis.
o. L. aequinoctialis. No. 8413 from French Guiana. Similar thin fronds with a small papilla at the apex are often called L. "trinervis".
p. L. tenera. From Singapore. Vegetative fronds which float submerged in the water are very long and sabre-like.
q. L. tenera. From Singapore. Flowering fronds floating on the surface of the water look similar to fronds of L. aequinoctialis.
r. L. valdiviana. No. 7718 from Dominican Republic. The single nerve running near to the tip of the frond and distinctly surpassing the area of air spaces is typical.
s. L. valdiviana. No. 7673 from North Carolina, U.S.A. The area of air spaces is much larger than in s, but the angle between the tip of the nerve and the edge of the air space area is smaller than 90°.
t. L. minuscula. No. 6600 from California, U.S.A. In the full grown frond the area of air spaces surpasses the tip of the nerve. In the younger fronds the area of air spaces is not yet fully developed.
u. L. minuscula. No. 8370 from Switzerland.

Fig. 9.3. Wolffiella
a. W. hyalina. From Tanzania. The fronds are flowering; the appendage is unusually long. The length of the appendage is, like roots in the genus Lemna, dependent on the culture conditions.
b. W. hyalina. From the type collection in Chad, described as W. "Monodii". Along the edge of the frond some papillae are visible.
c. W. hyalina. No. 7376 from Egypt. The appendage is much shorter than in a. due to a high concentration of nutrients in the culture solution. A papilla near the apex is visible.
d. W. repanda. From Angola. The mother frond is flowering.
e. W. repanda. From the type locality in Angola. The fronds are flowering. A prominent papilla near the apex is visible.
f. W. rotunda. From the type locality in Zimbabwe. The lower side of the pouch with the tract of elongated cells is longer than the upper side but does not form a distinct prolongation (appendage) as in W. hyalina or W. repanda.
g. W. rotunda. From the type locality in Zimbabwe. The daughter frond shows asymmetrically situated flowers. The stomata are visible as small dots.
h. W. neotropica. No. 7225 from Rio de Janeiro, Brazil. The tract of elongated cells is slightly asymmetrical, the area of air spaces relatively small and not very pronounced.
i. W. Welwitschii. No. 8252 from Natal, South Africa. The tract of elongated cells is exactly in the median line of the lower wall of the pouch. The area of the air spaces is wider than long and distinctly visible.
k. W. Welwitschii. No. 7468 from Colombia.

l. W. lingulata. No. 7289 from Amazonas, Brazil. The tract of elongated cells is about halfway between the median line and the right edge of the pouch.
m. W. lingulata. No. 7464 from Venezuela. Small fronds like in the picture were described by HEGELMAIER as var. minor. The smallness is primarily caused by unfavourable conditions. The area of air spaces is at least as wide as long.
n. W. oblonga. No. 7167 from Louisiana, U.S.A. Much smaller than o and p. The area of air spaces fills three-quarters of the whole frond.
o. W. oblonga. No. 8031 from Louisiana, U.S.A. The area of air spaces is more expanded than in p. This characteristic is much dependent on culture conditions.
p. W. oblonga. No. 7732 from Sao Paulo, Brazil. The tract of elongated cells follows the left edge of the pouch. The area of air spaces is slightly longer than wide. HEGELMAIER attributed similar plants to W. lingulata var. minor (as the frond of fig. 9.3m).
q. W. gladiata. From Mexico. In nature the fronds are sometimes still narrower. These forms have been described as W."floridana".
r. W. gladiata. No. 7570 from North Carolina, U.S.A. Under our normal culture conditions the frond became relatively wider but the angle of the pouch is still much smaller than in W. oblonga and the area of air spaces fills nearly the whole frond.
s. W. denticulata. No. 7454 from Natal, South Africa. The fronds look similar to W. gladiata, but are nearly as wide at the tip as at the base and have a few small teeth (scarcely visible on the photograph).

Fig. 9.4. Wolffia
a. W. microscopica. No. 8359 from India. The frond is flowering and shows a very long cylindrical projection of the lower surface.
b. W. microscopica. No. 8359 from India. The frond with a flower in the center is shown from above.
c. W. elongata. From the type collection in Colombia. The shape of the frond and the position of the daughter frond are characteristic.
d. W. brasiliensis. No. 7149 from Texas, U.S.A. The typical papilla in the center of the upper surface is not visible (see fig. 2.24).
e. W. borealis. No. 7698 from Toronto, Canada. The pointed tip of the frond is characteristic for W. borealis.
f. W. borealis. No. 7354 from Indiana, U.S.A. The frond is very often narrower than that of W. brasiliensis.
g. W. australiana. No. 7631 from Victoria, Australia. W. australiana has a typical keel-like prolongation of the lower surface.
h. W. angusta. No. 7274 from New South Wales, Australia. The fronds are very small but relatively deep.
i. W. angusta. No. 7480 from Victoria, Australia. Whereas the mother frond is squashed on the side, the daughter frond shows the typical view from above.
k. W. arrhiza. No. 7219 from Cape, South Africa. W. arrhiza is nearly as deep as long.
l. W. arrhiza. No. 7158 from the Netherlands.
m. W. columbiana. No. 8046 from Louisiana, U.S.A.
n. W. columbiana. No. 7987 from Illinois, U.S.A. The relatively globular shape is characteristic.
o. W. globosa. No. 7233 from Cape, South Africa. Beside W. angusta W. globosa has the smallest fronds of the Lemnaceae.

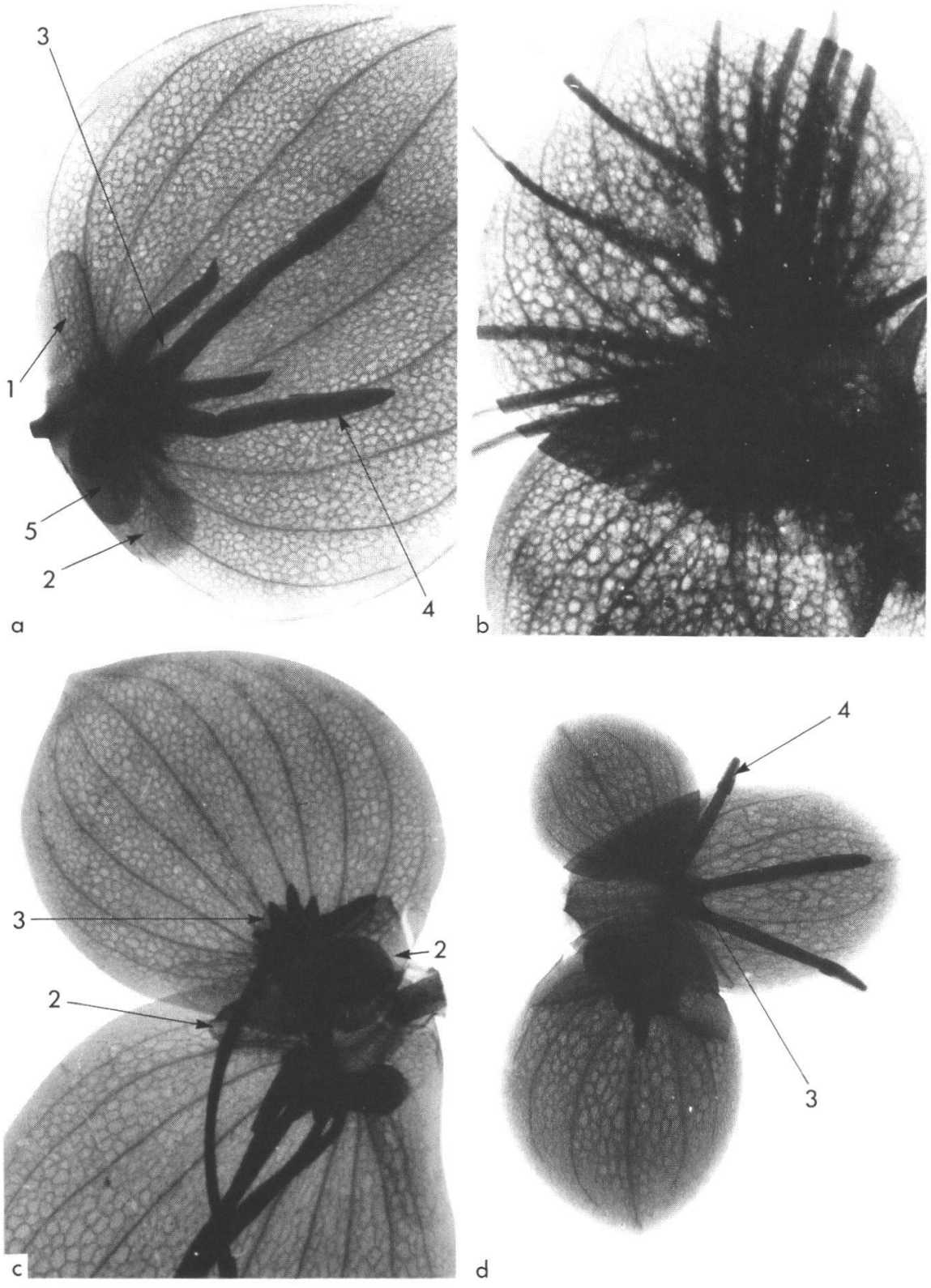
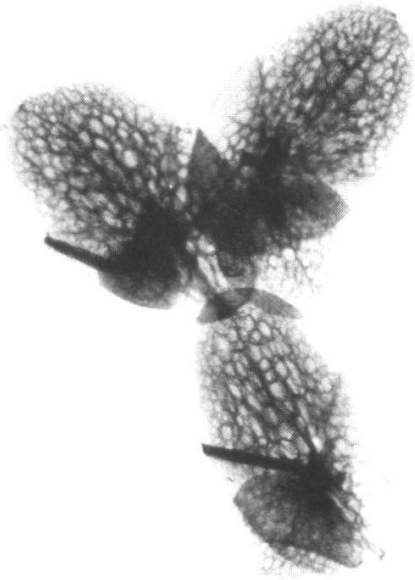


Fig. 9.1. Transparent photographs of Spirodela (x12) (see p. 494)
a. S. intermedia (from below). b. S. intermedia (from above)
c. S. polyrrhiza (from below) d. S. punctata (from below)

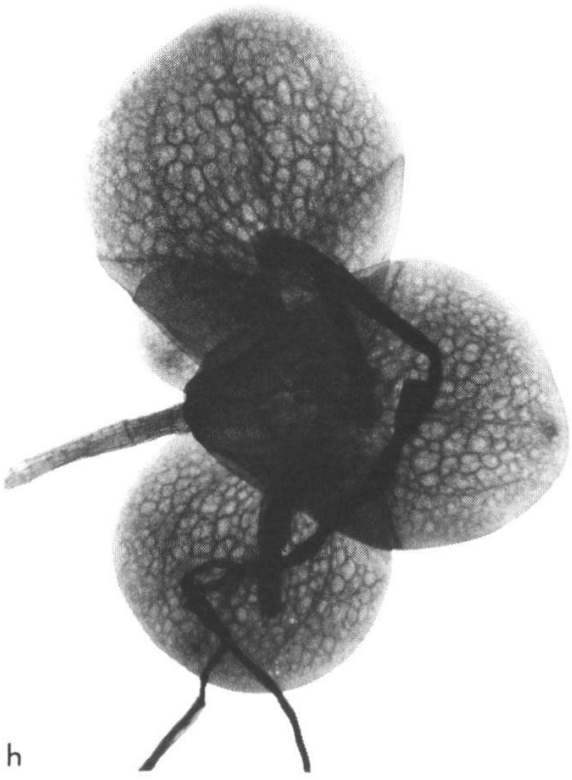
Fig. 9.2. Transparent photographs of Lemna (x12) (see p. 494)
a. L. gibba (from below)
b. L. disperma (from below)
c. L. minor (from below)
d. L. minor (from above)

e



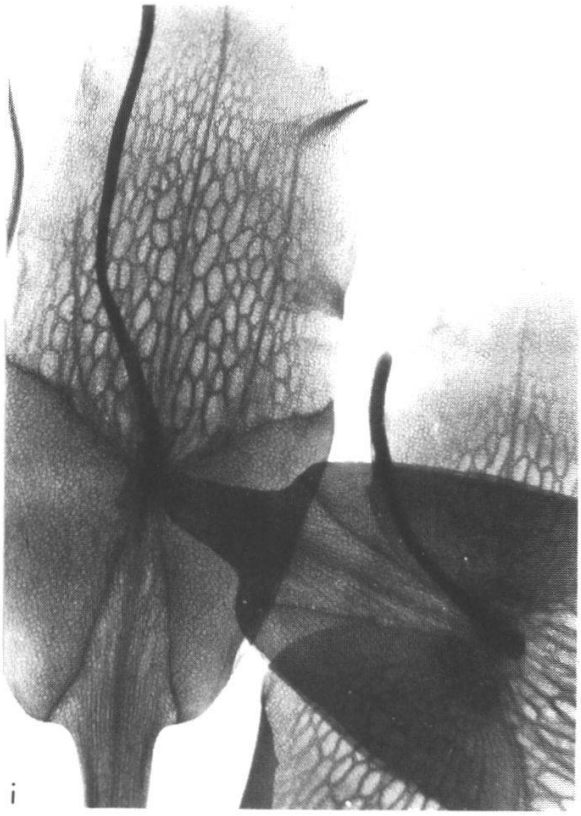
f

g



h

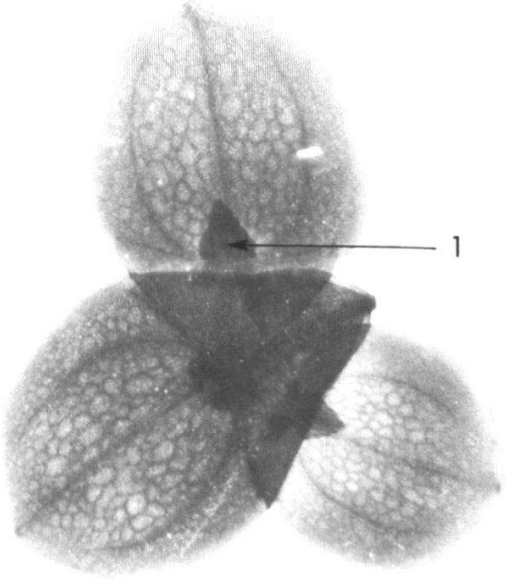
Fig. 9.2. (continued) Lemna (x12) (see p. 494)
e. L. japonica (from below)
f. L. ecuadoriensis (from above)
g. L. obscura (from above)
h. L. turionifera (from below)



i

k

l



m

Fig. 9.2. (continued) Lemna (x12) (see p. 495)
i. L. trisulca (from below)
k. L. trisulca (from below)
l. L. perpusilla (from below)
m. L. aequinoctialis (from below)

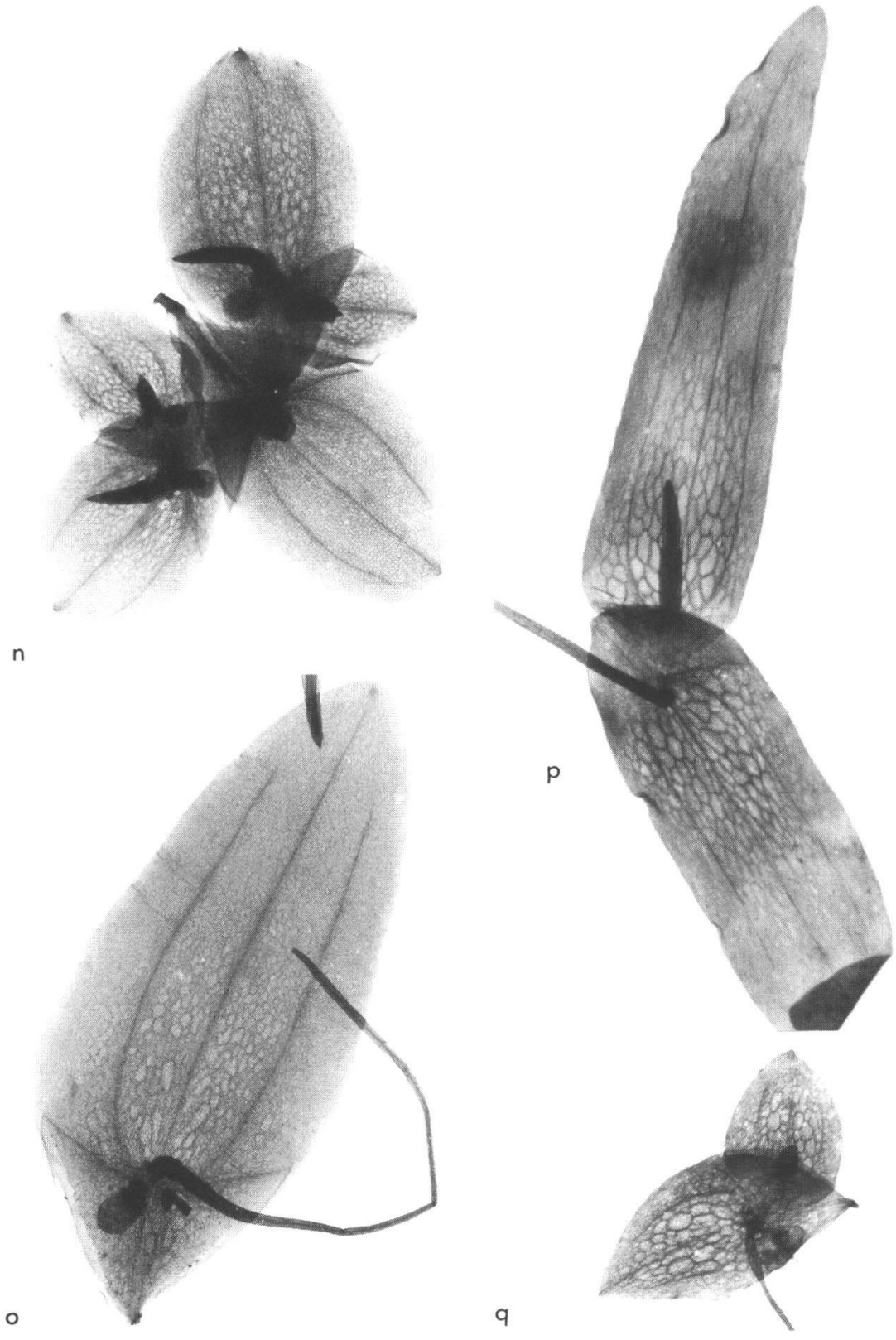
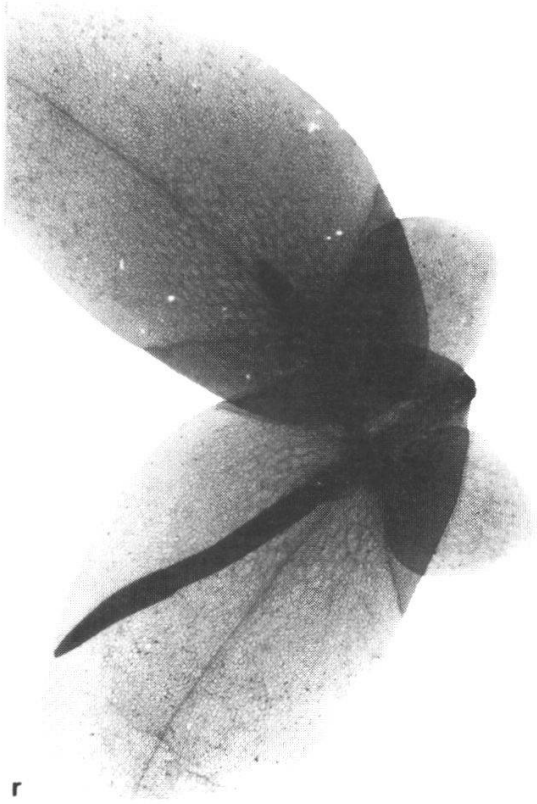
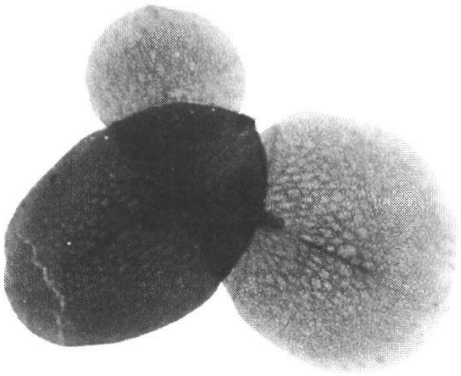


Fig. 9.2. (continued) Lemna (x12) (see p. 495)
n. L. aequinoctialis (from above)
o. L. aequinoctialis (from below)
p. L. tenera (from below)
q. L. tenera (from below)



r

s



t

u

Fig. 9.2. (continued) Lemna (x12) (see p. 495)
r. L. valdiviana (from below)
s. L. valdiviana (from below)
t. L. minuscula (from above)
u. L. minuscula (from below)

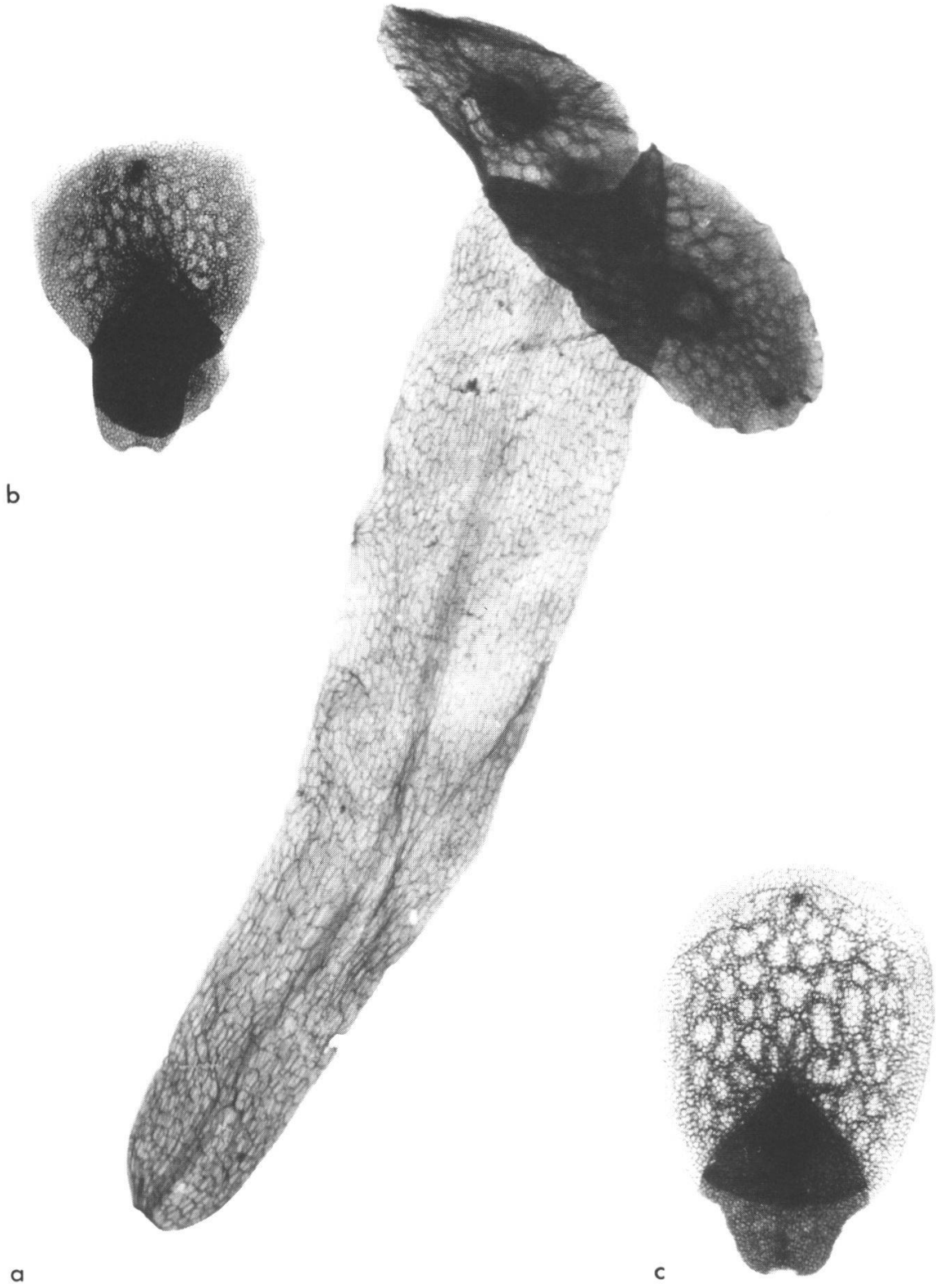
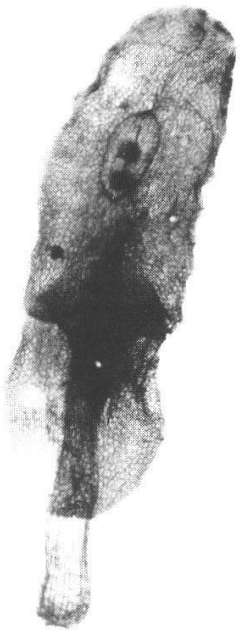
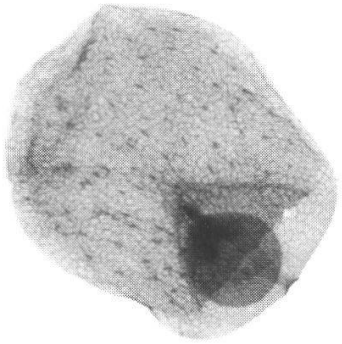


Fig. 9.3. Transparent photographs of Wolffiella (x18) (see p. 495)
a. W. hyalina (from the side) b. W. hyalina (from above)
c. W. hyalina (from below)

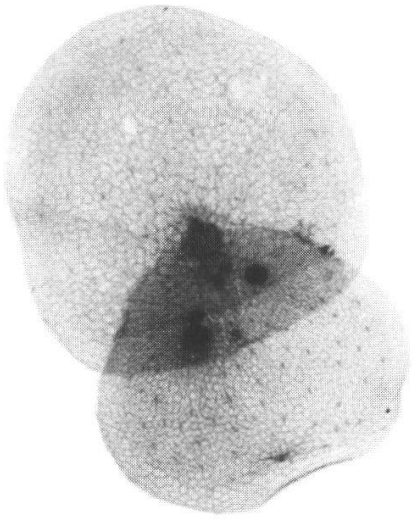


d

e



f



g

Fig. 9.3. (continued) Wolffiella (x18) (see p. 495)
d., e. W. repanda (from above)
f., g. W. rotunda (from above)

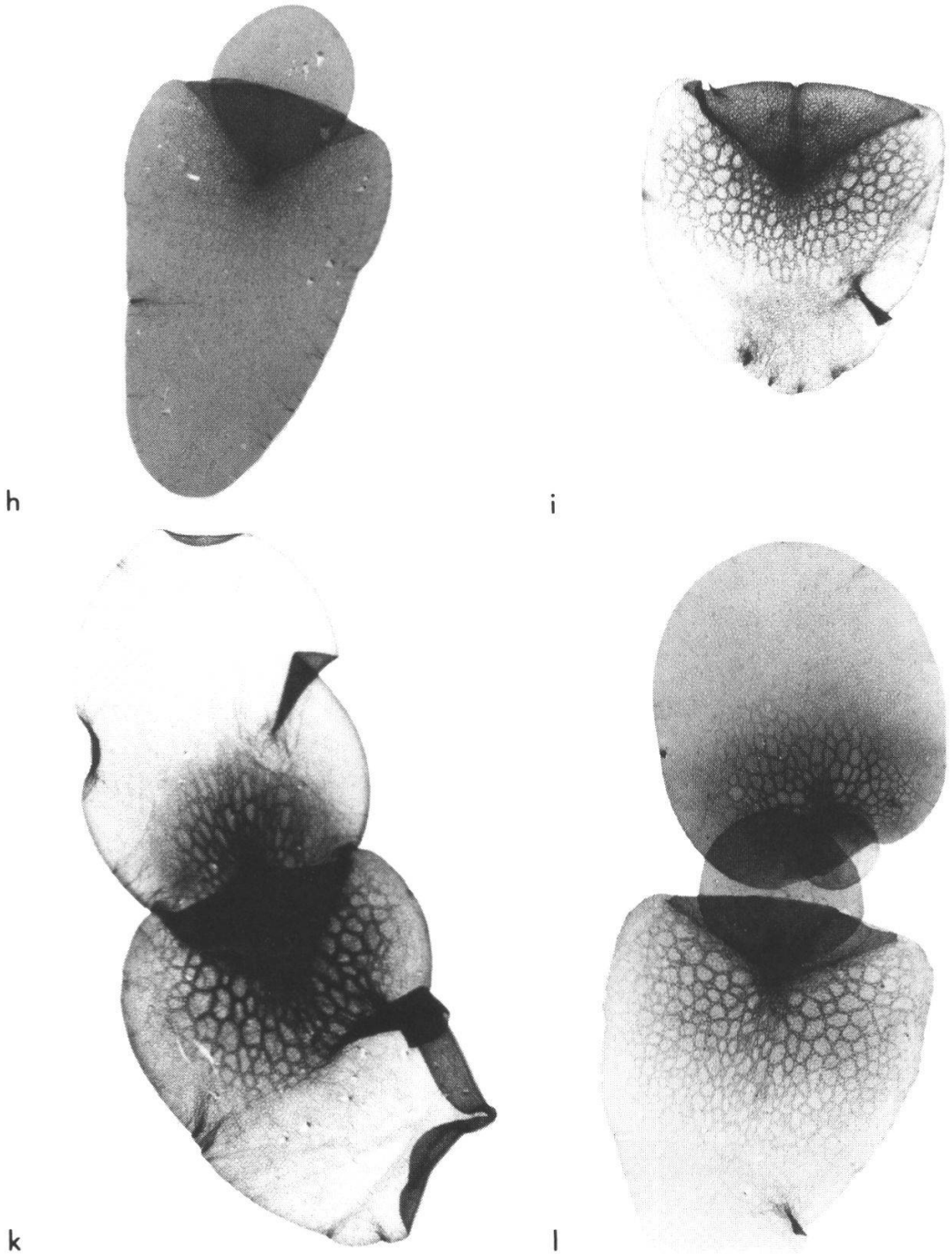
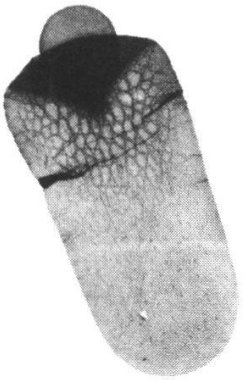
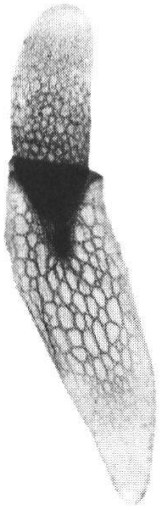


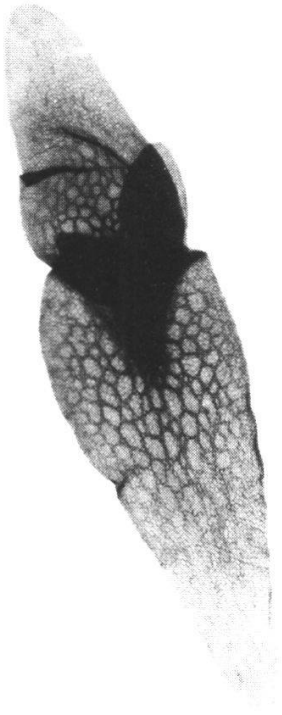
Fig. 9.3. (continued) Wolffiella (x12) (see p. 495 and 496)
h. W. neotropica
i. W. Welwitschii
k. W. Welwitschii
l. W. lingulata



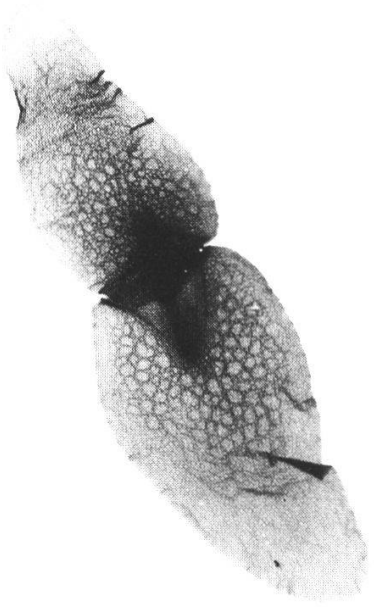
m



n



o



p

Fig. 9.3. (continued) Wolffiella (x12) (see p. 496)
m. W. lingulata n. W. oblonga
o. p. W. oblonga

Fig. 9.3. (continued) Wolffiella (x18) (see p. 496)

q., r. W. gladiata

s. W. denticulata

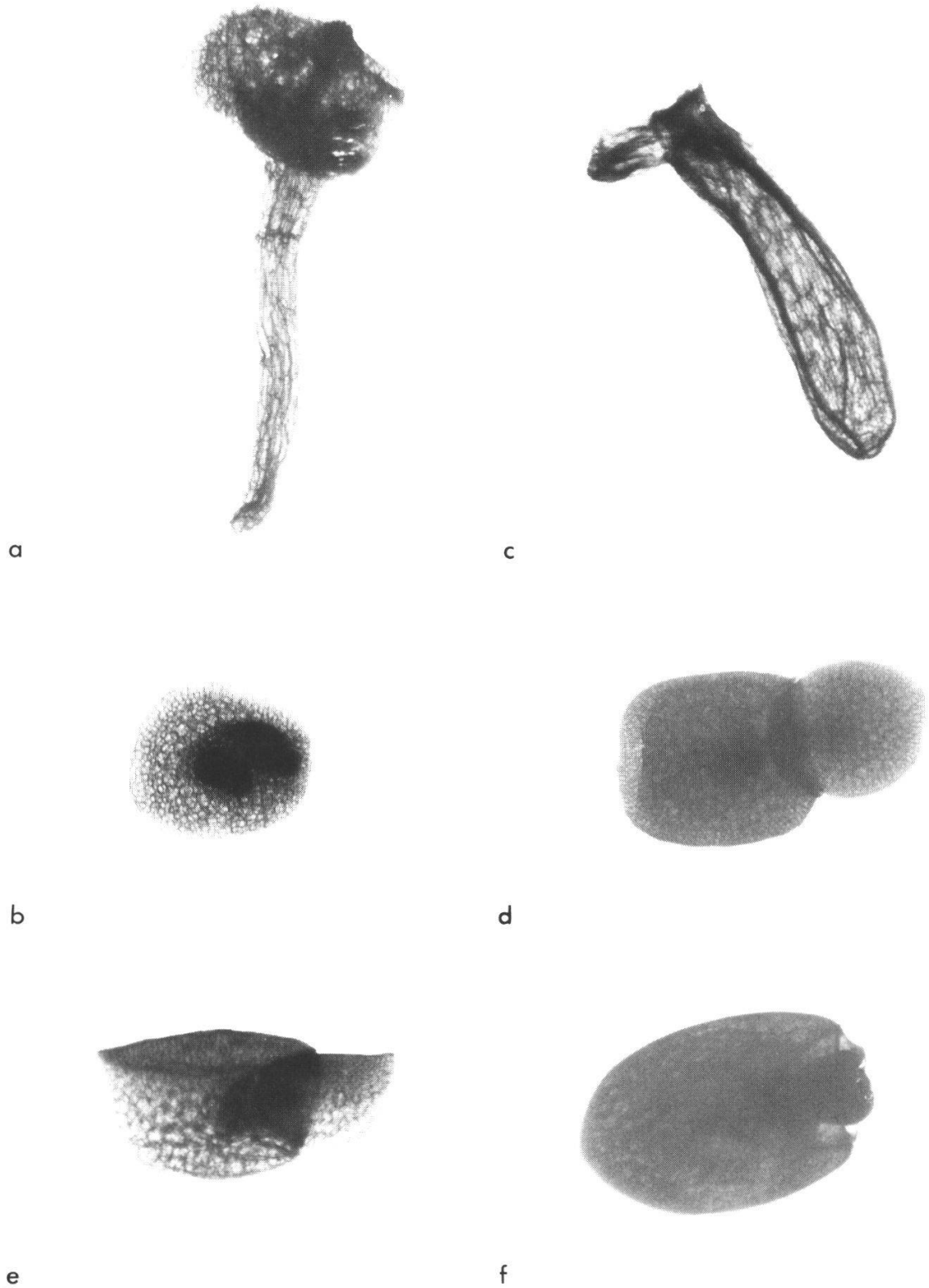


Fig. 9.4. Transparent photographs of Wolffia (x18) (see p. 496)
a. W. microscopica (from the side)
b. W. microscopica (from above)
c. W. elongata (from the side)
d. W. brasiliensis (from above)
e. W. borealis (from the side)
f. W. borealis (from above)

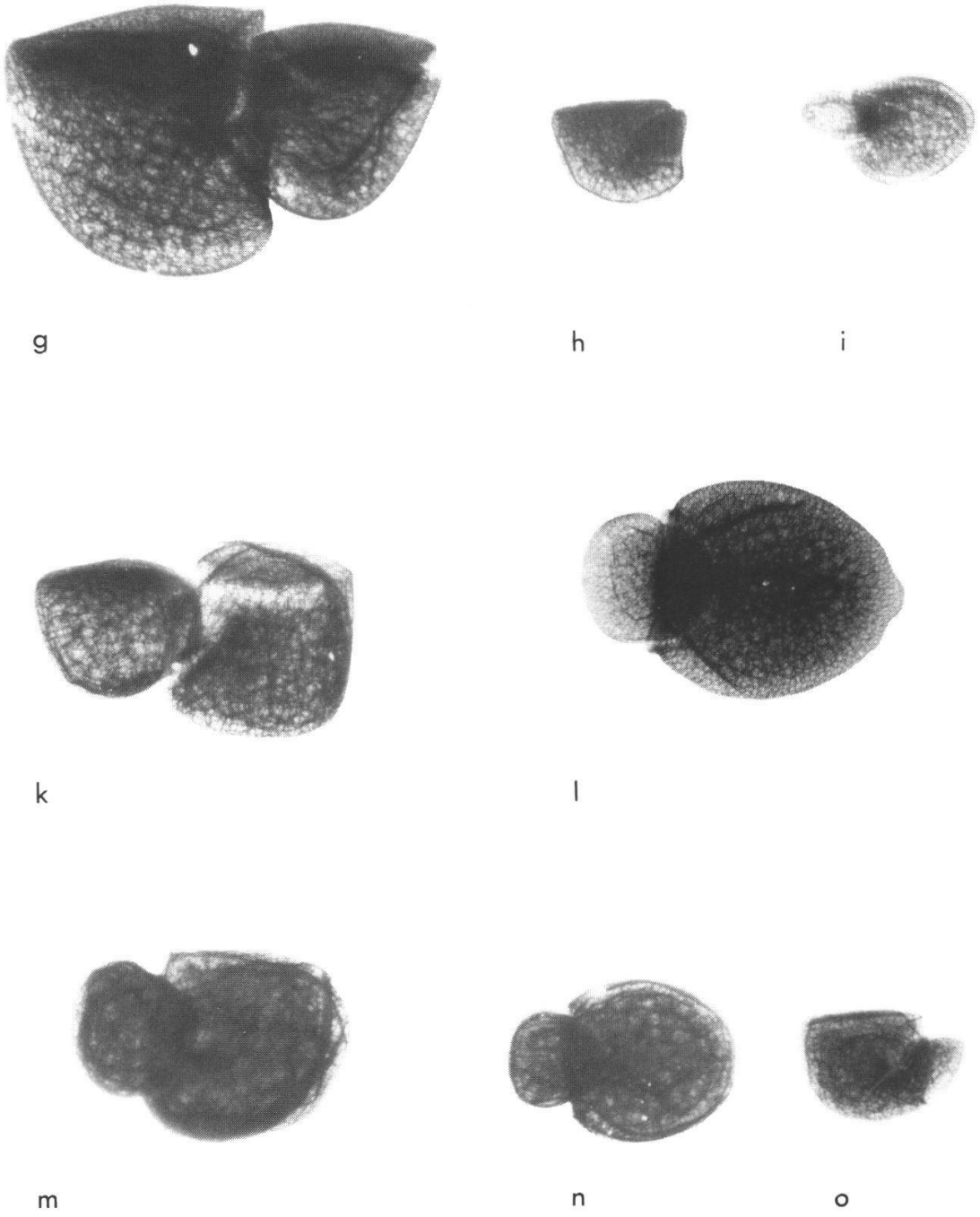


Fig. 9.4. (continued) Wolffia (x18) (see p. 496)

g. W. australiana (from the side)
h. W. angusta (from the side)
i. W. angusta (from above)
k. W. arrhiza (from the side)
l. W. arrhiza (from above)
m. W. columbiana (from the side)
n. W. columbiana (from above)
o. W. globosa (from the side)

Remarks to the plates I to XVI (p. 513-528)

Plate I.

a. Spirodela intermedia (No. 7178), from above (x6)
b. S. intermedia (No. 7747), from below (x6). The young fronds are slightly gibbous. In the lower young fronds, the three roots nearest to the base perforate the prophyllum.
c. S. polyrrhiza (No. 8403), from above (x6). In the center of the figure, a turion is formed. The small frond to the left of the turion has a red spot which is typical for S. polyrrhiza.
d. S. polyrrhiza (No. 6731), from below (x6). In the big frond in the upper part of the figure, two roots perforate the prophyllum which is very rare in S. polyrrhiza (mostly only one root perforates).

Plate II.

a. Spirodela punctata (No. 7273), from above (x6). The papules on the nerves are easily visible.
b. S. punctata (No. 7487), from below (x6). One to three roots per frond are visible, all perforating the prophyllum.
c. Turions of S. polyrrhiza (No. 8403), from above (left) and from below (right) (x12). The prophyllum at the base is recognizable. The turion to the left is already dying and the pigment cells become visible.
d. Turions of Lemna turionifera (No. 6753), from above (left) and from below (right) (x12). The rudimentary root and a dormant daughter frond can be seen.
e. Turions of Wolffia brasiliensis (No. 7150), from above (x12). The closed stomata are recognizable.
f. Turions of Wolffia arrhiza (No. 8272), from above (x12)

Plate III

a. Lemna gibba (No. 7218), from above (x8)
b. L. gibba (No. 7218) from below (x12). The frond is pronouncedly gibbous, the big air spaces are visible.
c. L. disperma (No. 7761), from above (x8). Two stamens of a flower and some papules especially at the apex are recognizable.
d. L. disperma (No. 7761), from below (x12). The fronds are slightly gibbous, the air spaces being much smaller than those of L. gibba. Two fronds show a flower primordium to the right of the base.

Plate IV

a. Lemna minor (No. 6591), from above (x8). Two flowers are visible, one with two stamens and one pistil, the other with one stamen.
b. L. minor (No. 6591), from below (x12). One flower with the two stamens and the relatively small air spaces are recognizable.
c. L. japonica (No. 8339), from above (x8), flowering.
d. L. japonica (No. 8339), from below (x12), with flowers. The fronds are slightly gibbous. The red colour around the root base is typical for L. japonica in contrast to L. minor.

Plate V

a. Lemna ecuadoriensis (No. 8896), from above (x8). Prominent papillas (especially at the apex) are typical.
b. L. ecuadoriensis (No. 8896), from below (x12). The strong coloration of the lower surface is striking.
c. L. obscura (No. 7143), from above (x8) with a prominent papilla at the apex.

d. L. obscura (No. 7143), from below (x12) slightly gibbous, with red spots around the base of the root and a flower (pistil protruding from the pouch, the two stamens still enclosed).

Plate VI

a. Lemna turionifera (No. 6753), from above (x8), forming turions. Some papillae are visible on the middle line.
b. L. turionifera (No. 6753), from below (x12). Fronds in a transitional stage to turions are formed.
c. L. trisulca (No. 7579), from above (x8). The narrow green stipe is called a stalk.
d. L. trisulca (No. 7579), from above (x8). The flowering fronds float on the surface of the water.

Plate VII

a. Lemna perpusilla (No. 8017), from above (x8). Flowers and fruits are present. The papilla at the apex is prominent.
b. L. perpusilla (No. 8017), from below (x8). The root sheath is narrowly winged, the root cap pointed.
c. L. aequinoctialis (No. 6746), from above (x8). Flowers with two stamens and a pistil as well as a prominent papilla at the apex are recognizable.
d. L. aequinoctialis, from below (x8), with flowers. A broadly winged root sheath and an acute root cap are typical.

Plate VIII

a. Lemna valdiviana (No. 7227), from above (x8).
b. L. minuscula (No. 6726), from above (x8). If nutrient and temperature conditions are near optimum, L. minuscula and L. valdiviana are difficult to distinguish. L. valdiviana looks a little more transparent.
c. Wolffiella hyalina (No. 7376), from above (x12). The little points are formed by the stomata cells.
d. W. hyalina (No. 7376), from below (x12). At the base of the frond, the lower wall of the pouch is elongated in a short appendage.

Plate IX

a. Wolffiella neotropica (No. 7279), from below (x12). At the base of the frond, the tract of elongated cells is clearly visible, it is near the middle line.
b. W. neotropica (from Rio de Janeiro), from above (x6). The fronds show a flower on the right side at the base.
c. W. Welwitschii (No. 7644), from above (x12). The tip of the frond is submerged in the water.
d. W. Welwitschii (No. 8254), from above. Two symmetrically arranged flowers can be seen near the base with a pistil (basewards) and a stamen (distally) each.

Plate X

a. Wolffiella lingulata (from California), from above (x12). The tip of the frond is bent downwards into the water. phot. W.P. Armstrong.
b. W. lingulata (from California), from above (x12). Each frond shows one flower on the right side near the base. A sugar containing droplet, on the stigma of the frond in the center, attracts attention. phot. W.P. Armstrong.
c. W. oblonga (from California), from above (x12). phot. W.P. Armstrong.
d. W. oblonga (No. 7997), from above (x12). Flowers, at the right side near the base, and the extended air space system can be seen.

Remarks to plates I to XVI (continued)

Plate XI

a. Wolffiella gladiata (No. 7590), from above (x6). The fronds often grow in star-like groups.
b. W. gladiata (No. 7590), from above (x12).
c. W. denticulata (No. 8251), from above (x12), growing in star-like groups.
d. W. denticulata (No. 8251), from above (x12). A flowering frond is located in the center.

Plate XII

a. Wolffia microscopica (No. 8359), from above (x32). In the center of the frond, a flowering pit with an anther is recognizable. phot. W.P. Armstrong.
b. W. microscopica (No. 8359), from the side (x32). On the surface a flower with a stamen and a pistil is visible. The frond is prolonged downwards into a cylindrical hyaline projection. phot. W.P. Armstrong.
c. Size of different Lemnaceae (x12). 1. Wolffiella hyalina; 2. Wolffia microscopica; 3. W. brasiliensis; 4. W. borealis; 5. W. arrhiza; 6. W. columbiana; 7. W. globosa. phot. W.P. Armstrong.
d. Size of Lemna minuscula (1) and Wolffia columbiana (2) (x12). phot. W.P. Armstrong.
e. Size of different Wolffia species (x12). 1. W. borealis; 2. W. columbiana; 3. W. globosa. phot. W.P. Armstrong.

Plate XIII

a. Wolffia brasiliensis (No. 7150), from above (x32). The daughter frond contains a pronounced papilla in the center, the mother frond shows instead a flowering pit with an anther towards the apex and a stigma basewards.
b. W. brasiliensis (No. 7150), from the side (x32). An anther is emerging out of the flowering pit.
c. W. borealis (No. 7908), from the side (x32). The two fronds are just separating.
d. W. borealis (from California), from above (x32). A vegetative mother and daughter frond are situated in the upper part; the light spots are caused by the stomata. In the lower center, a flowering frond shows the pit with a stamen (left) and a stigma (right). phot. W.P. Armstrong.

Plate XIV

a. Wolffia australiana, from above (x32). The stomata show up as light spots. phot. W.P. Armstrong.
b. W. australiana (No. 7819), from the side (x32). The mother frond shows the typical deep keel which dips in the water. The daughter frond is flowering with a stigma (left) and an anther (right).
c. W. angusta (No. 7274), from above (x32). Of the two flowering fronds in the center the lower shows the flowering pit, the upper the two-loculated anther.
d. W. angusta (No. 7274), from the side (x32). Both fronds are flowering. A seed is recognizable below the smaller frond.

(Remarks to plates XV and XVI see p. 529)

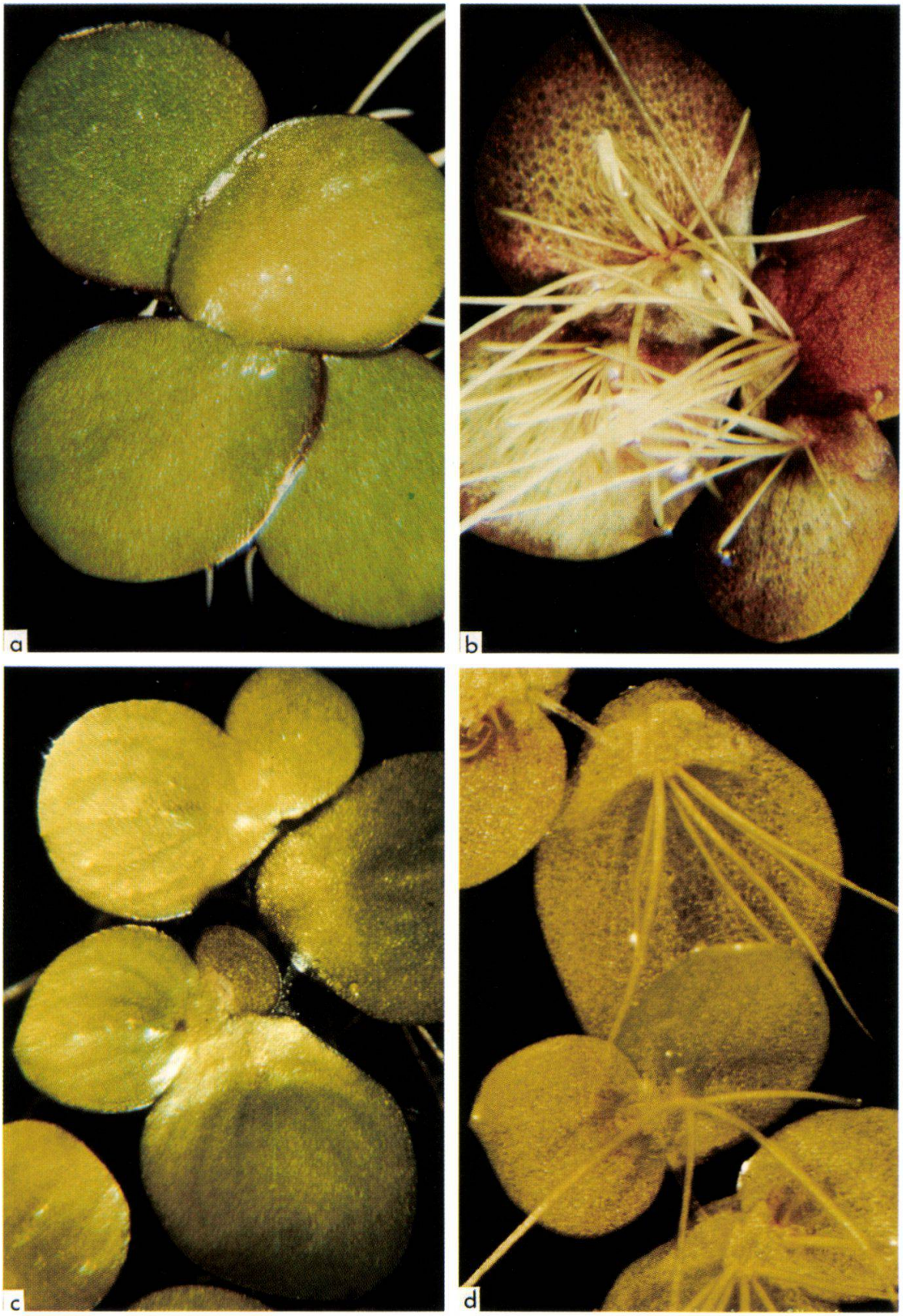


Plate I. a. b. Spirodela intermedia (x6); c. d. S. polyrrhiza (x6)

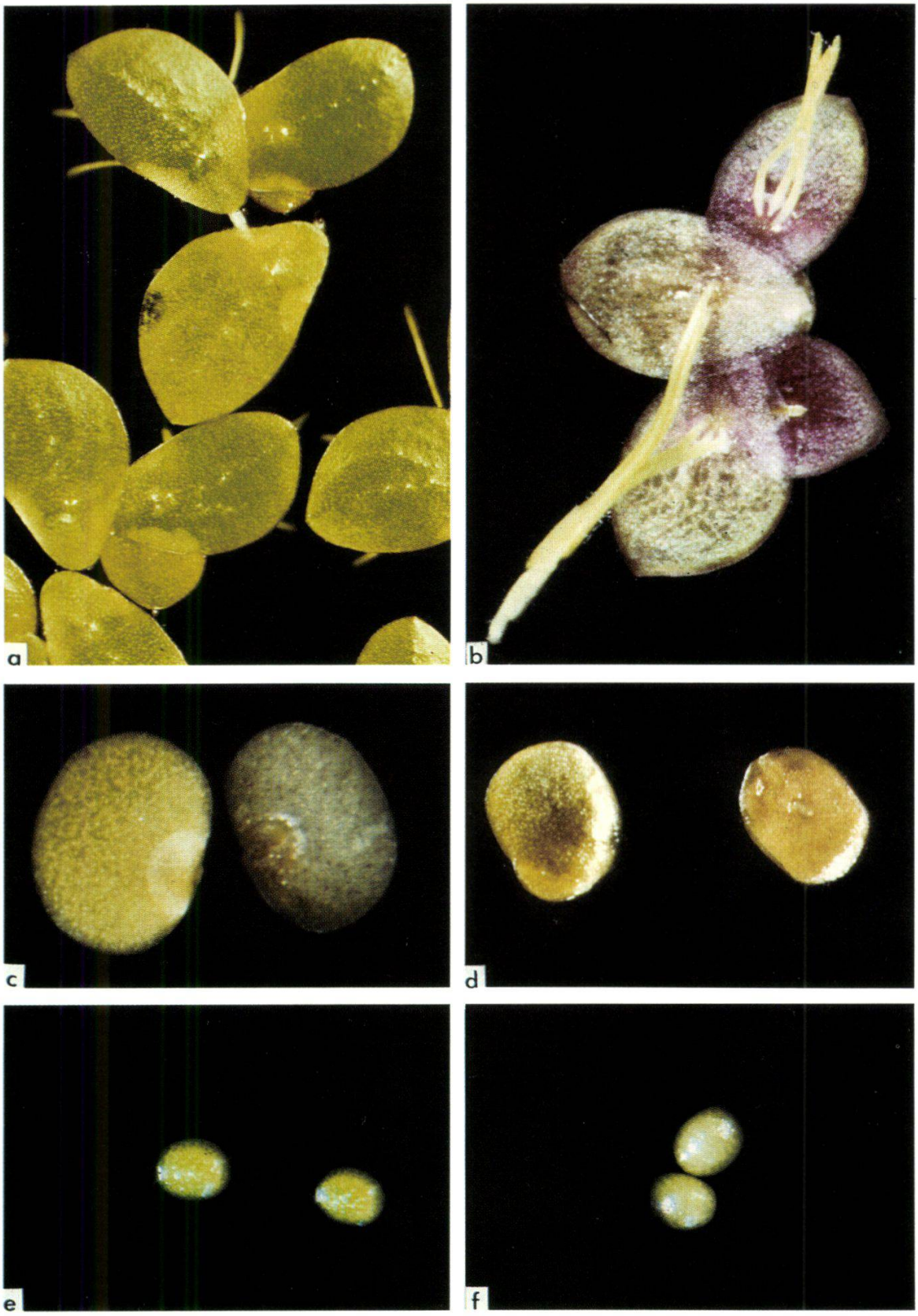


Plate II. a. b. Spirodela punctata (x6); c. to f. Turions of S. polyrrhiza, Lemna turionifera, Wolffia brasiliensis, W. arrhiza

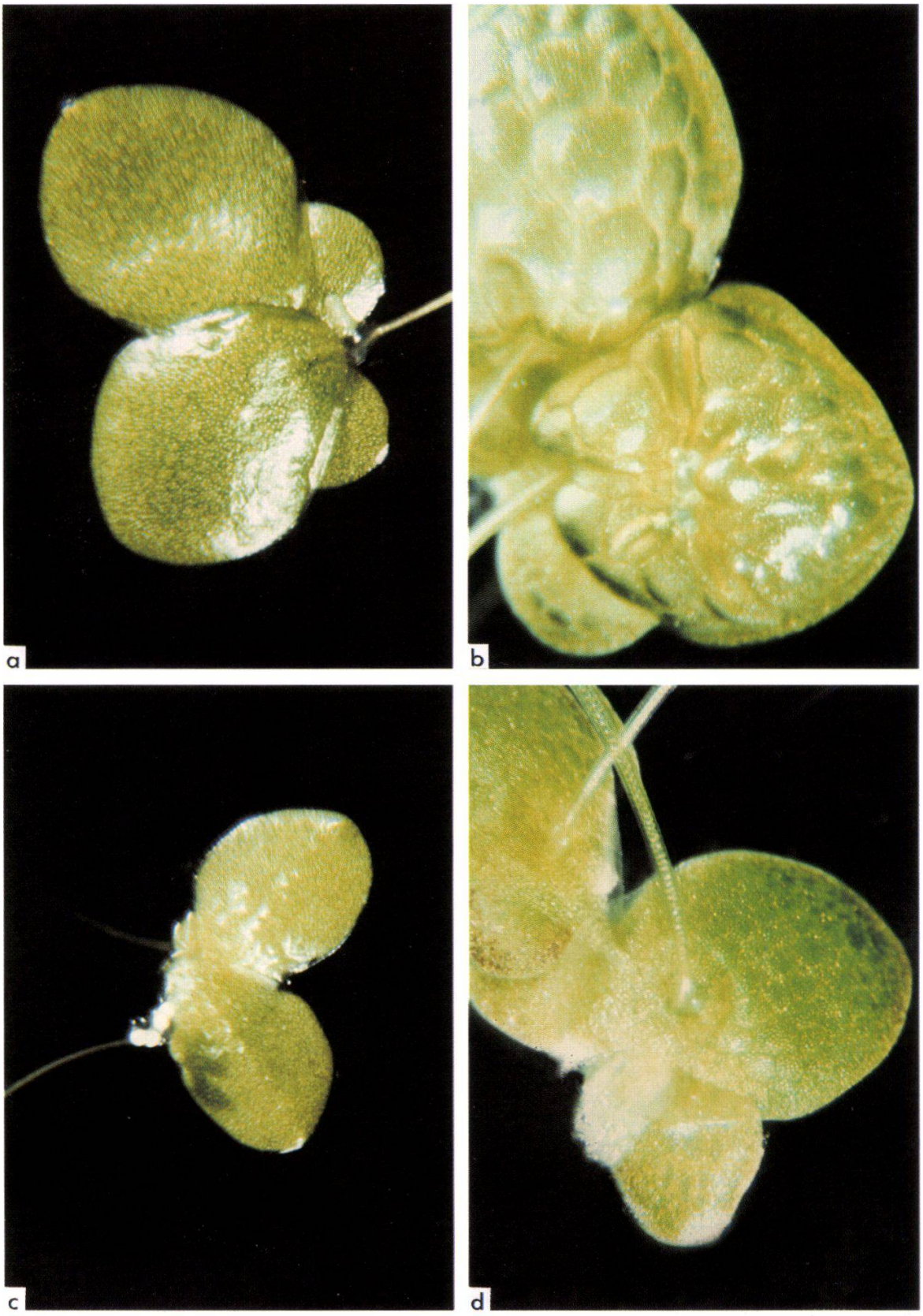


Plate III. a.b. Lemna gibba (x8, x12); c.d. L. disperma (x8, x12)

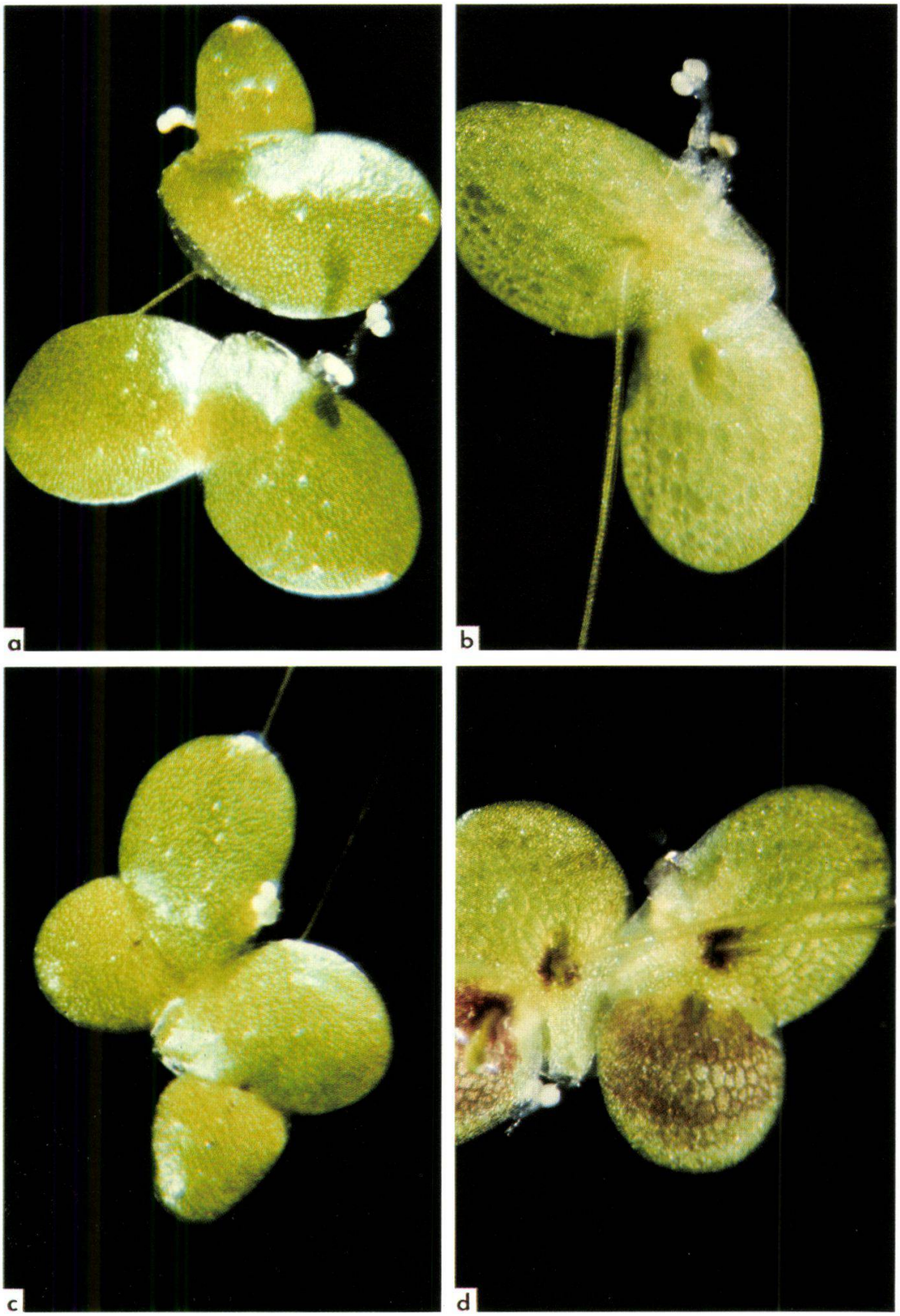


Plate IV. a.b. Lemna minor (x8, x12); c.d. L. japonica (x8, x12)

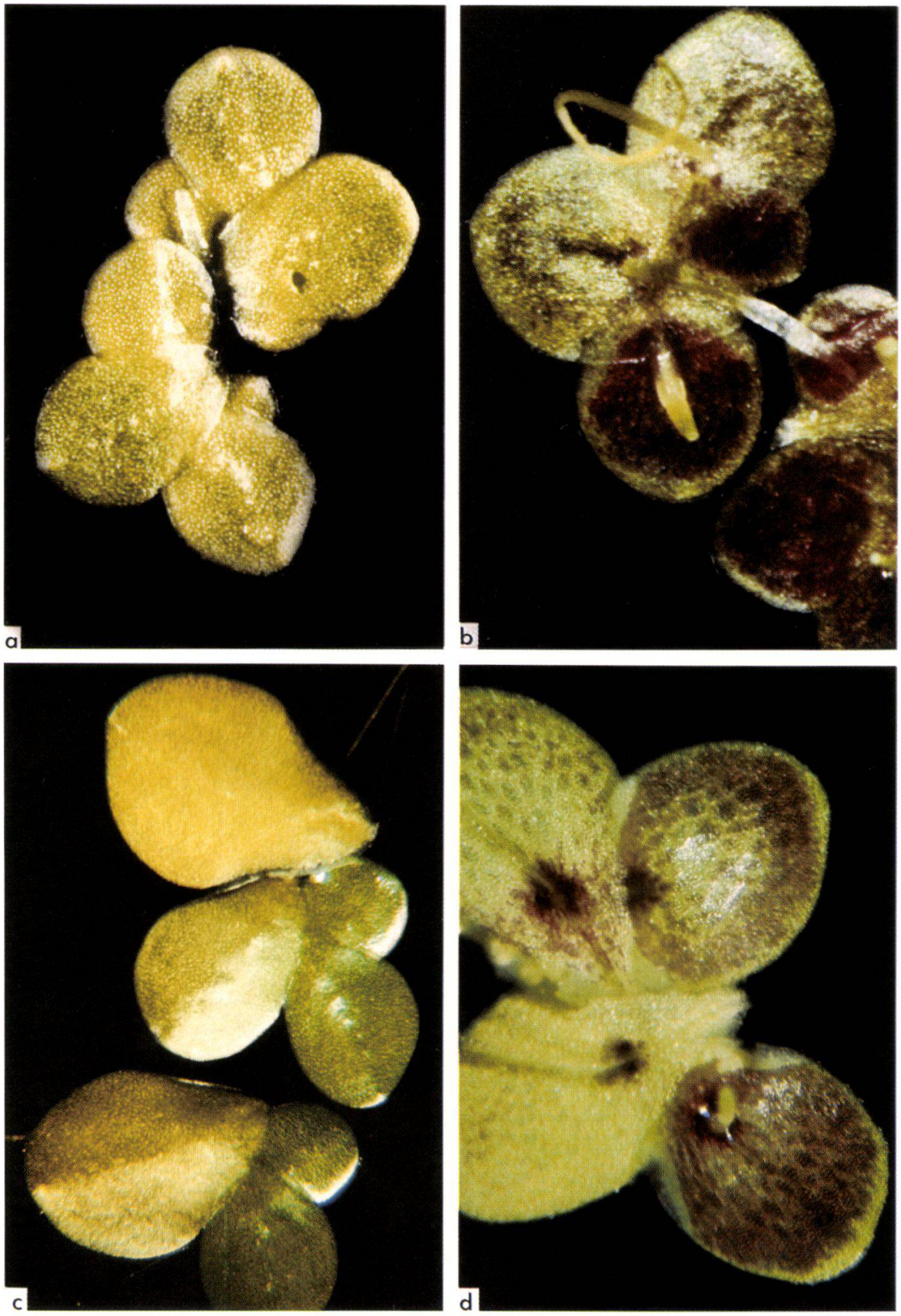


Plate V. a.b. Lemna ecuadoriensis (x8, x12); c.d. L. obscura (x8, x12)

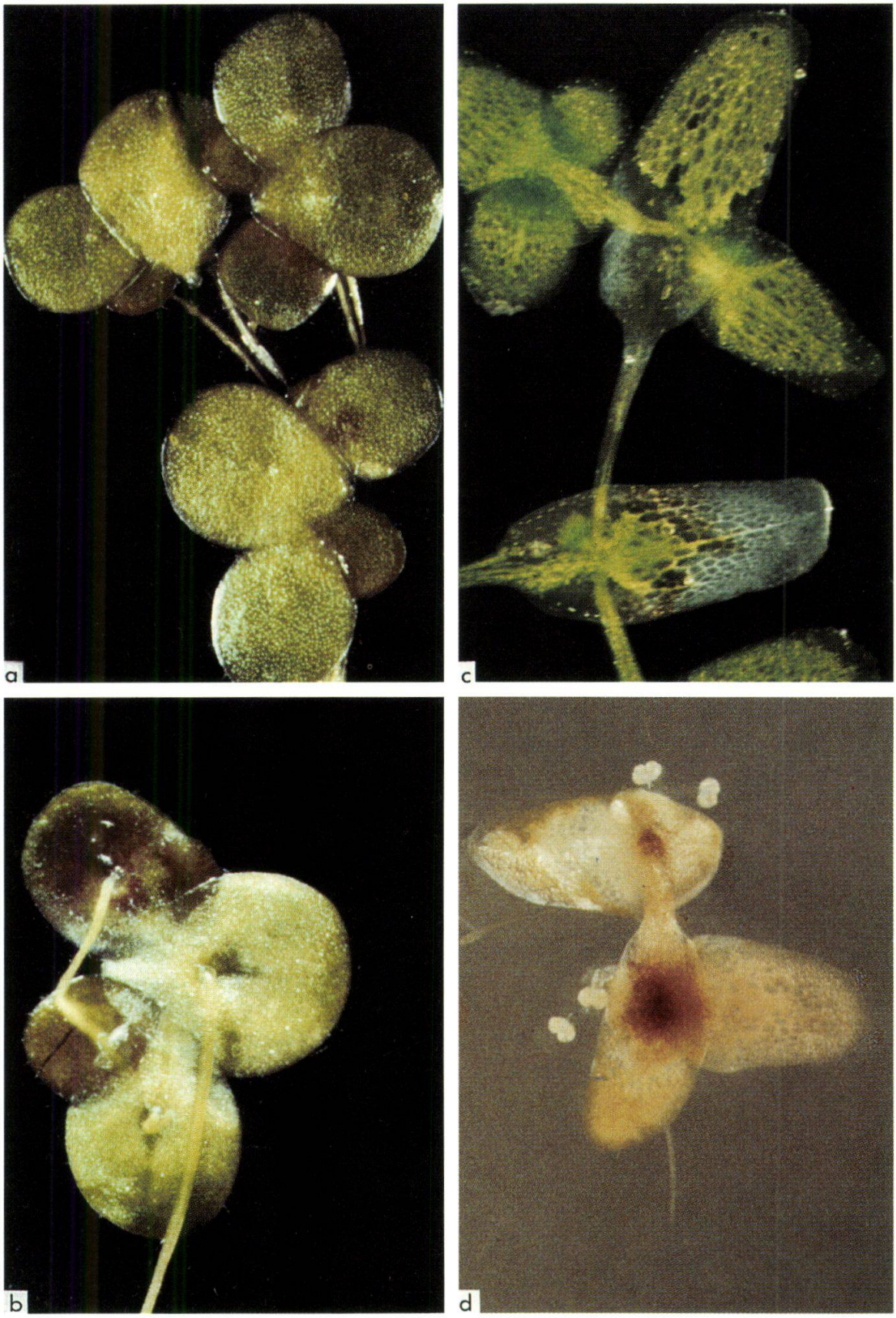


Plate VI. a.b. Lemna turionifera (x8, x12); c.d. L. trisulca (x8)

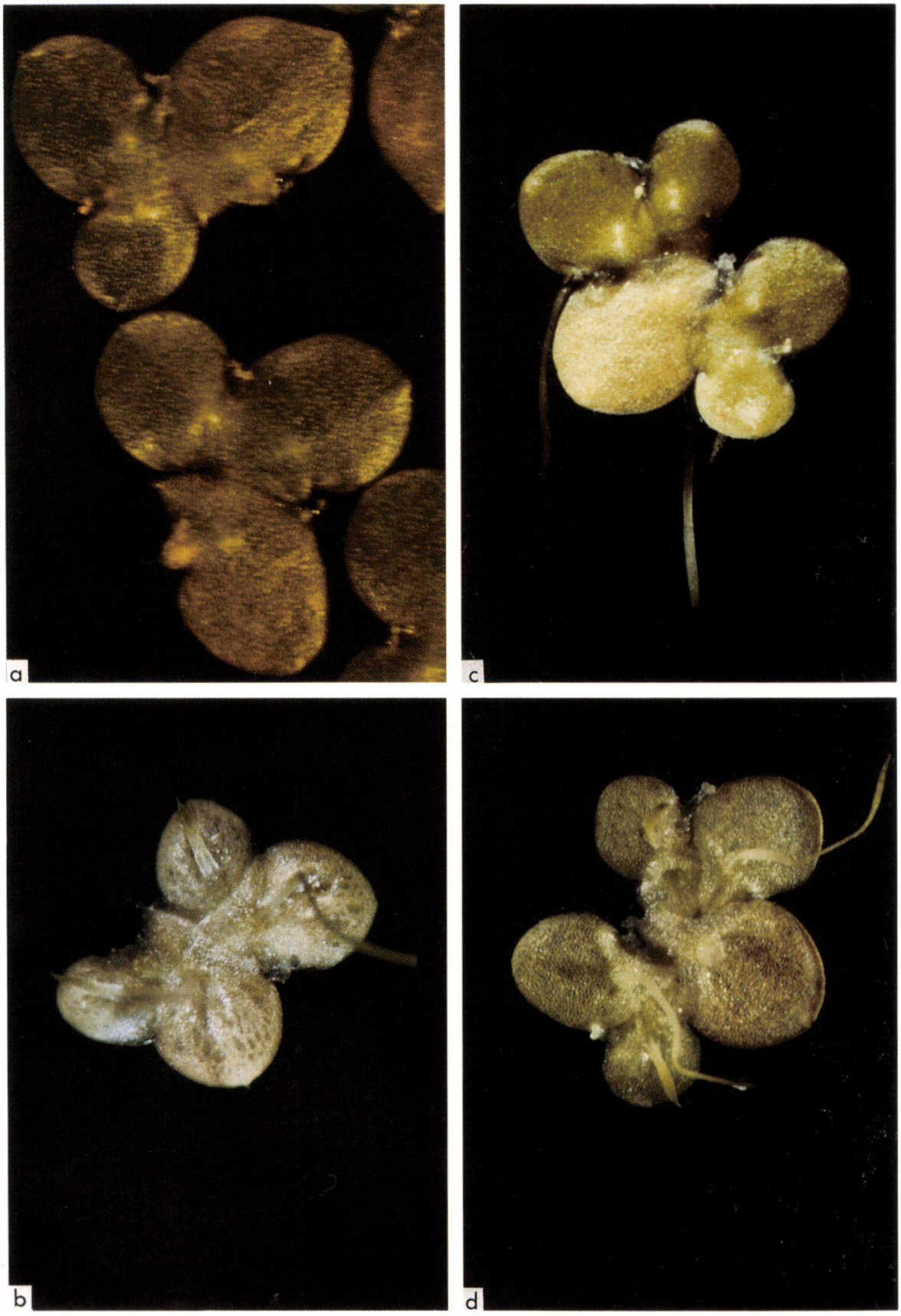


Plate VII. a.b. Lemna perpusilla (x8); c.d. L. aequinoctialis (x8)

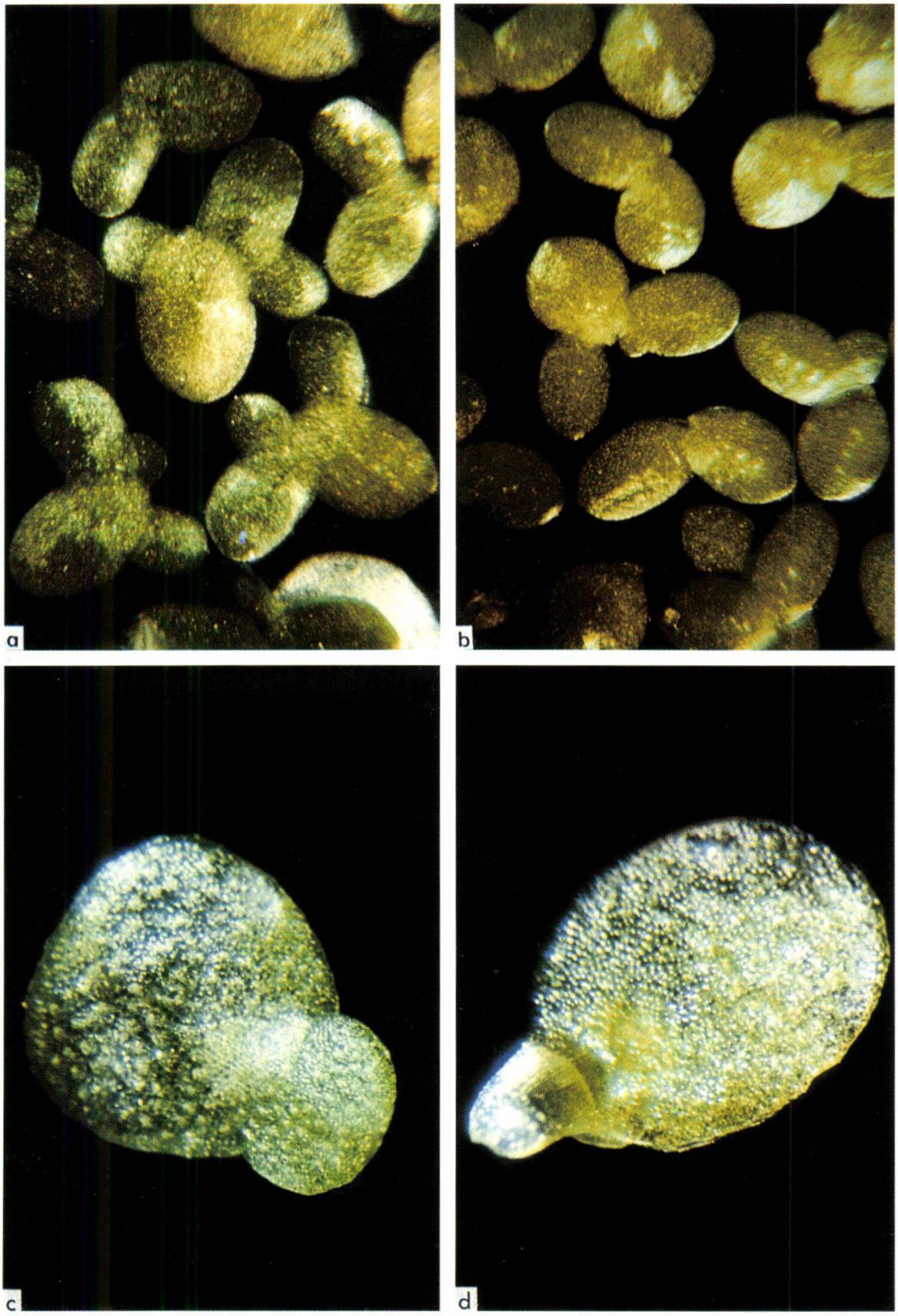


Plate VIII. a. Lemna valdiviana (x8); b. L. minuscula (x8);
c.d. Wolffiella hyalina (x16)

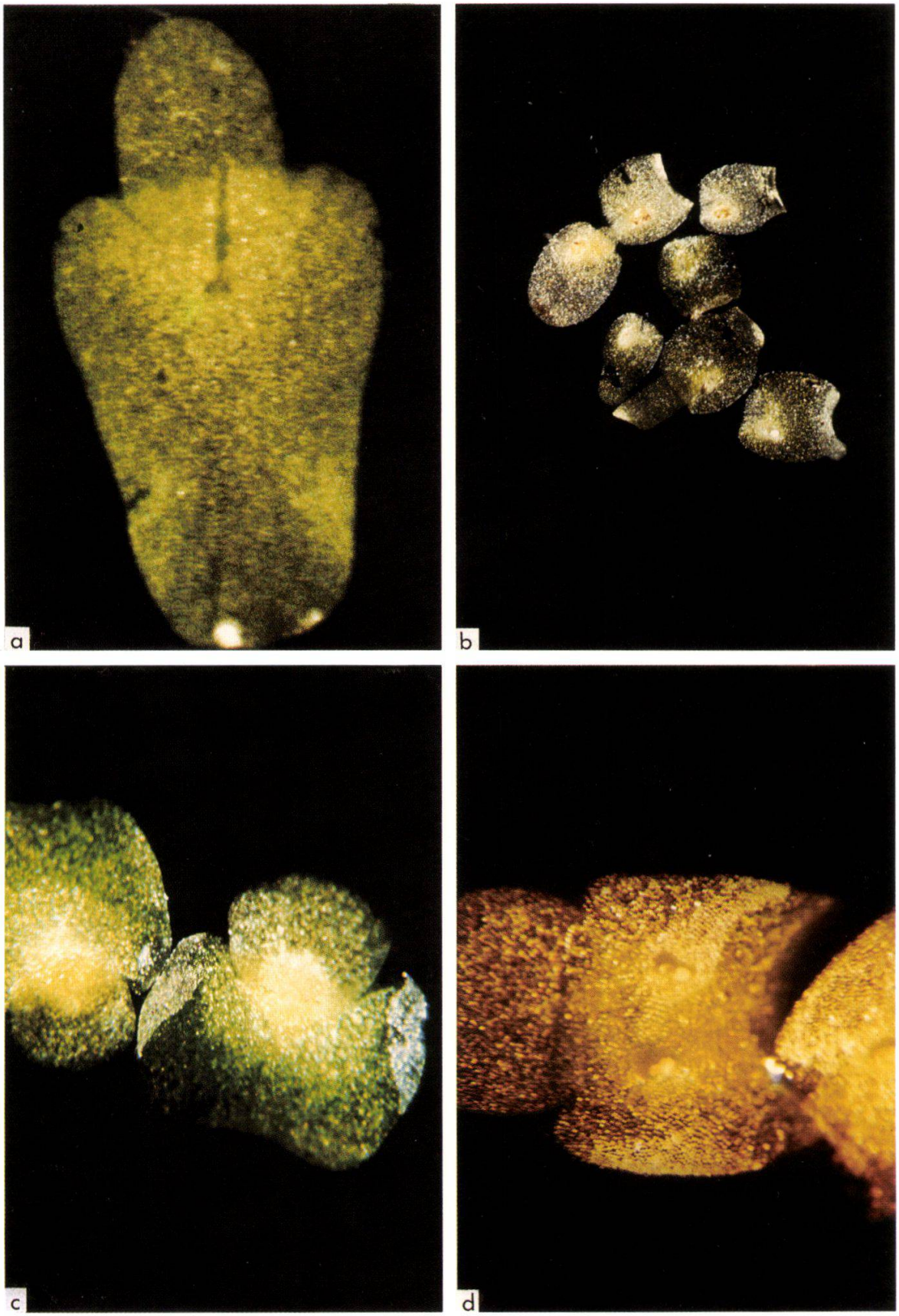


Plate IX. a.b. Wolffiella neotropica (x12, x6); c.d. W. Welwitschii (x12)

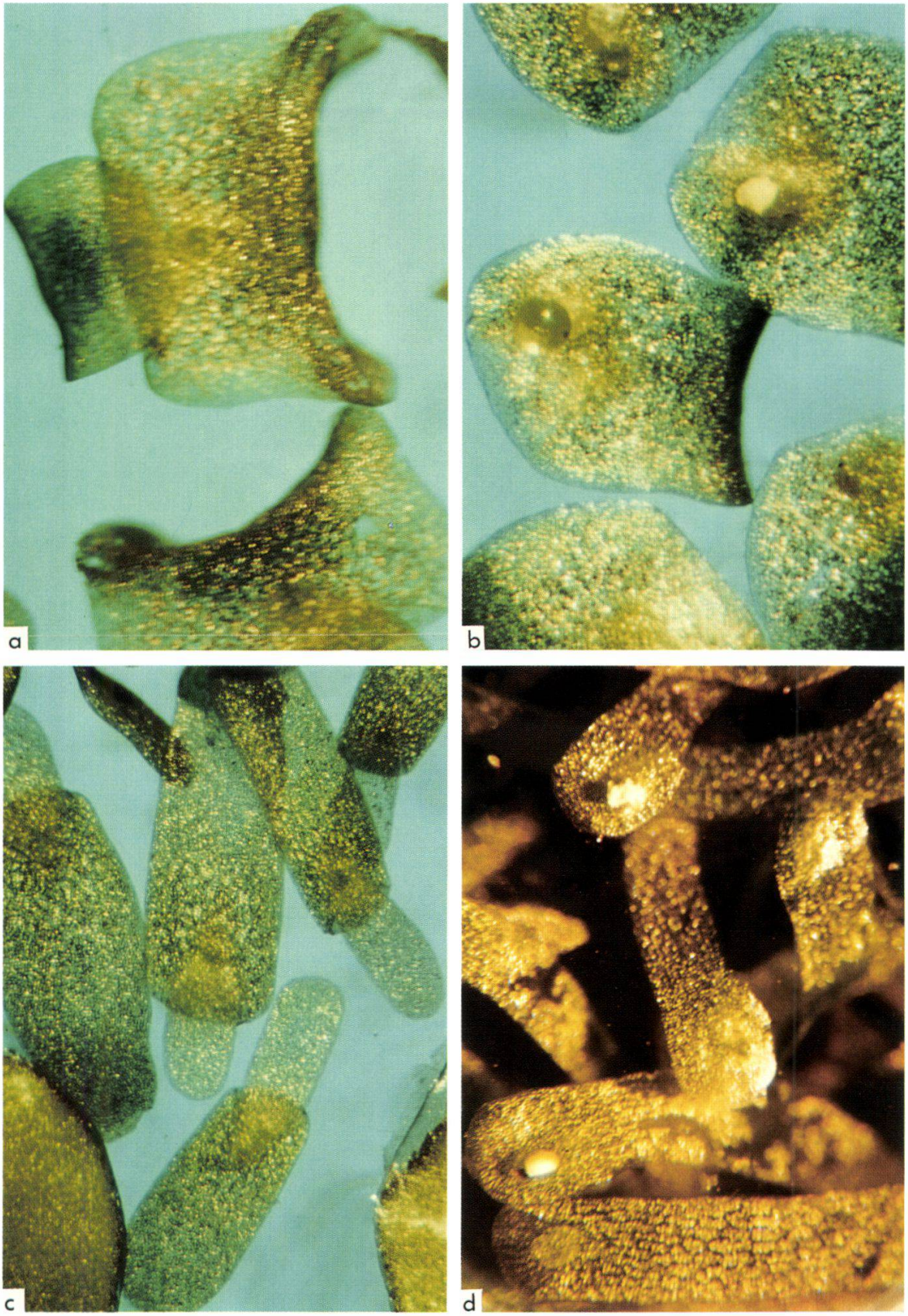


Plate X. a.b. Wolffiella lingulata (x12); c.d. W. oblonga (x12)

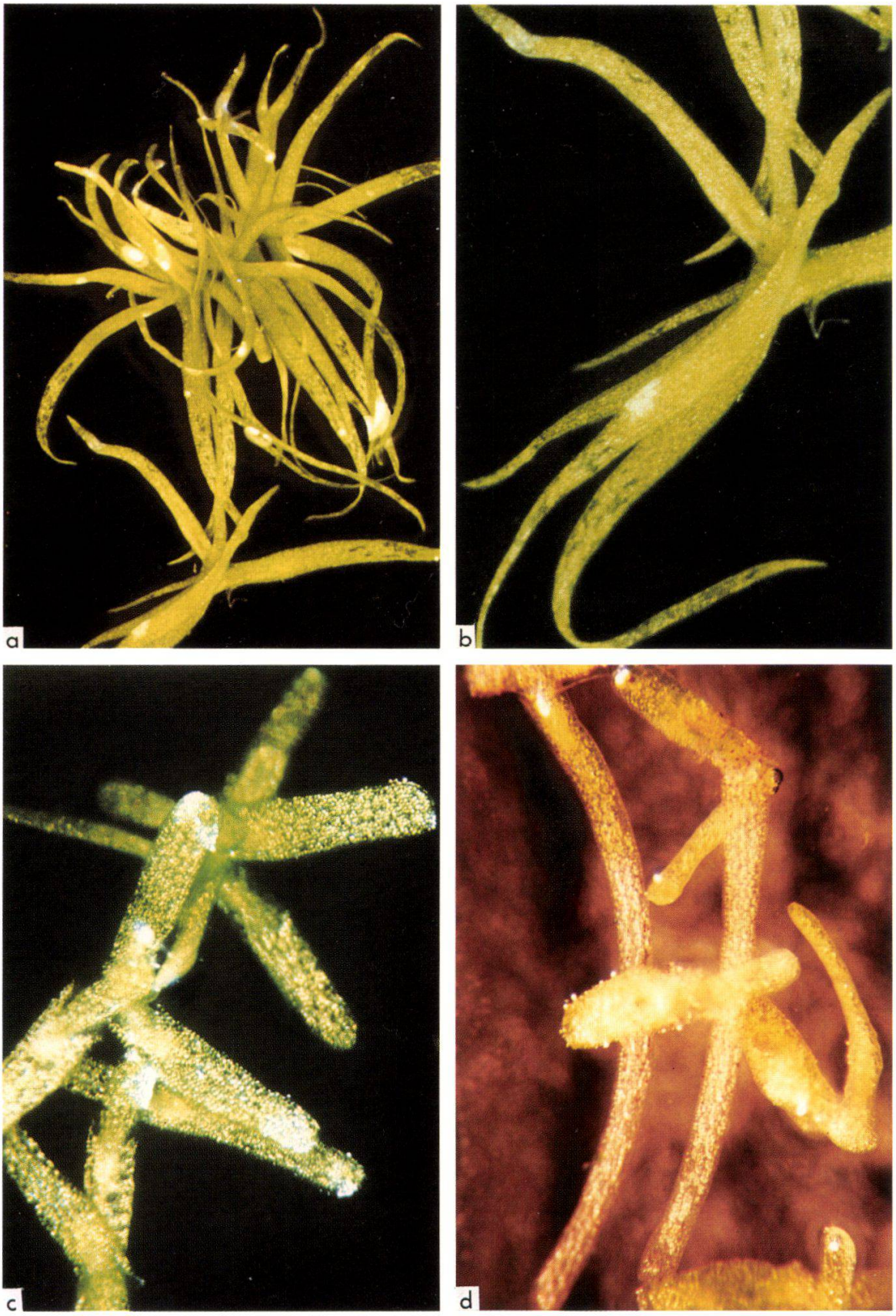


Plate XI. a.b. Wolffiella gladiata (x6, x12); c.d. W. denticulata (x12)

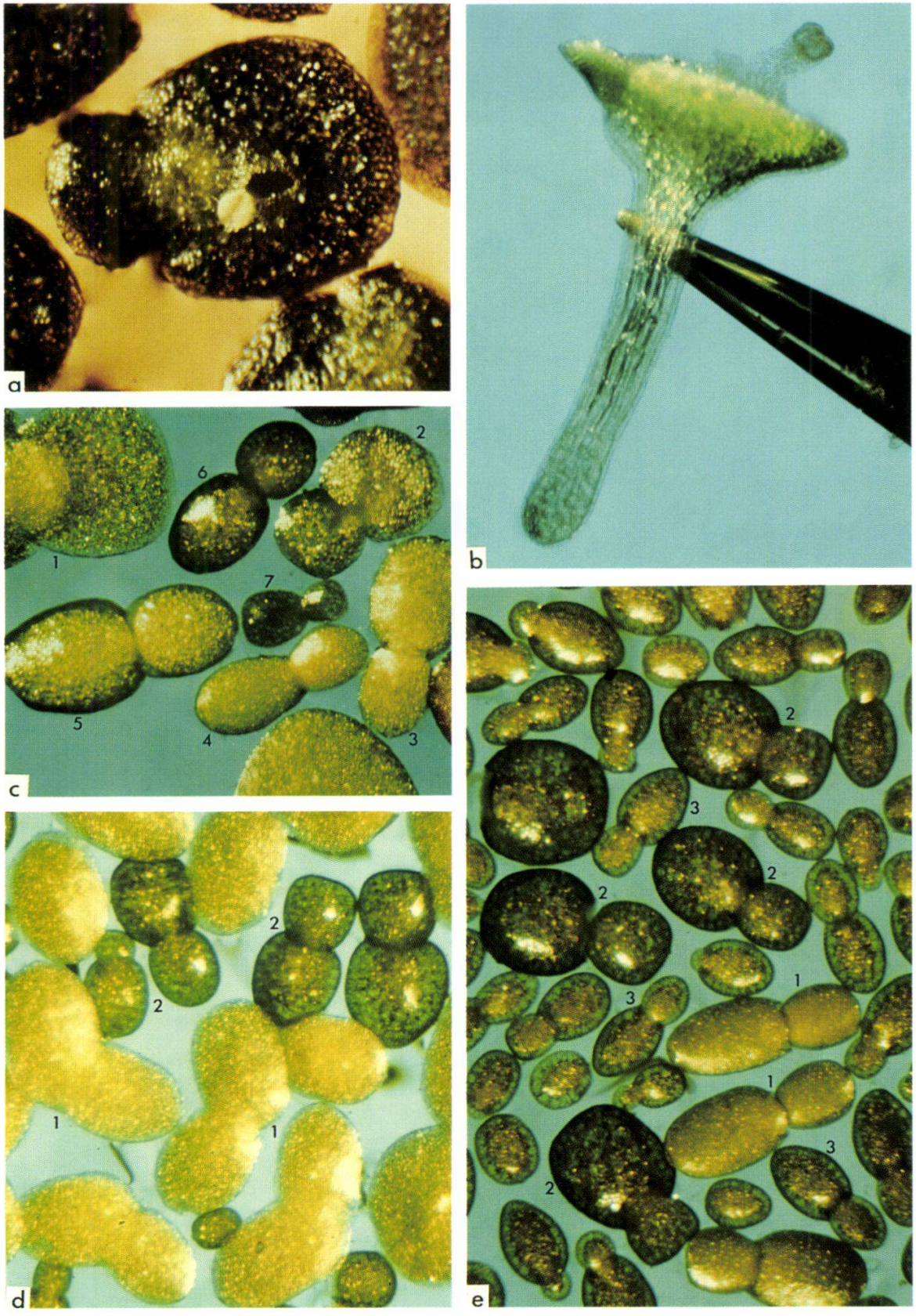


Plate XII. a.b. Wolffia microscopica (x32); c. to e. Relative size of Wolffia species.

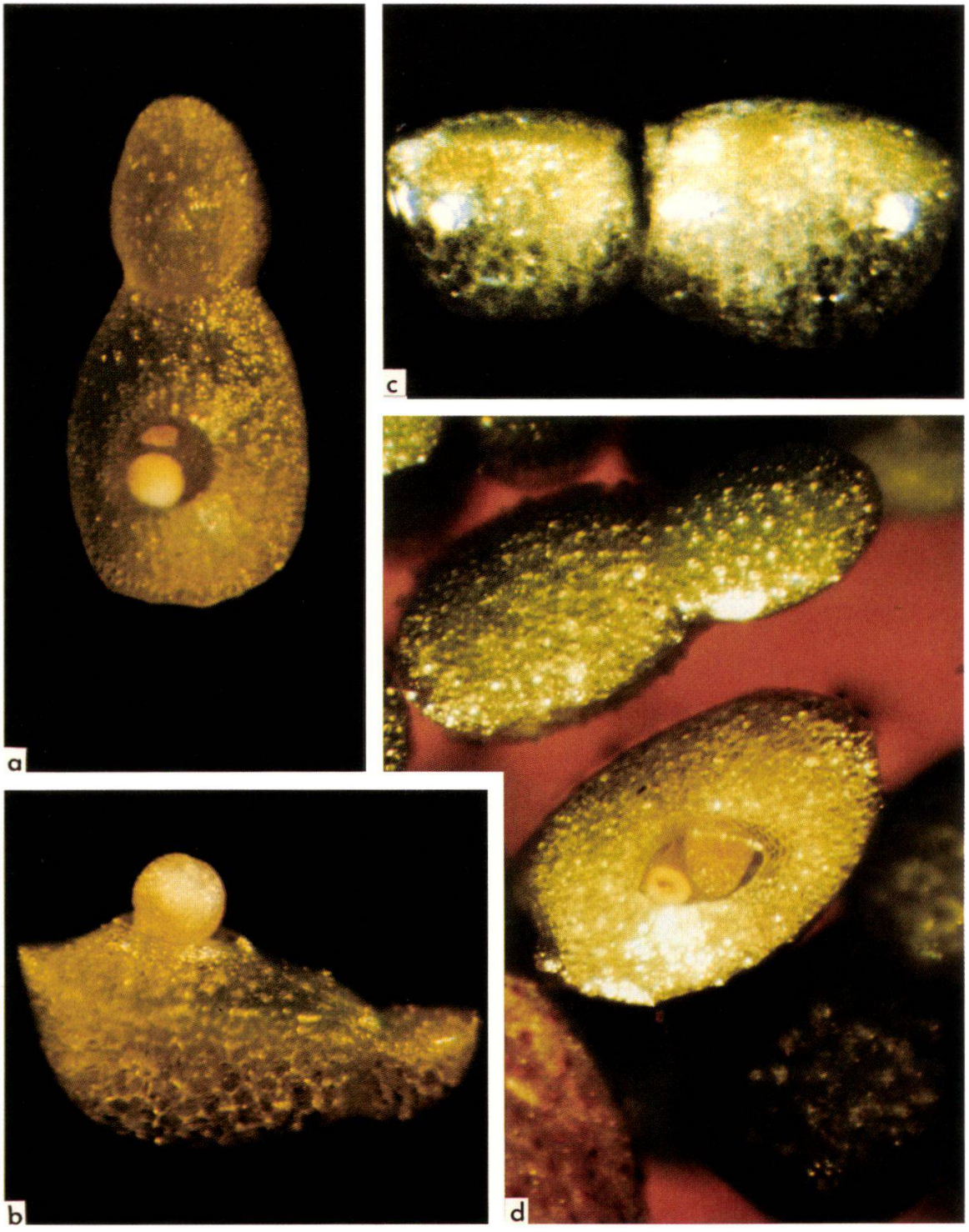


Plate XIII. a.b. Wolffia brasiliensis (x32); c.d. W. borealis (x32)

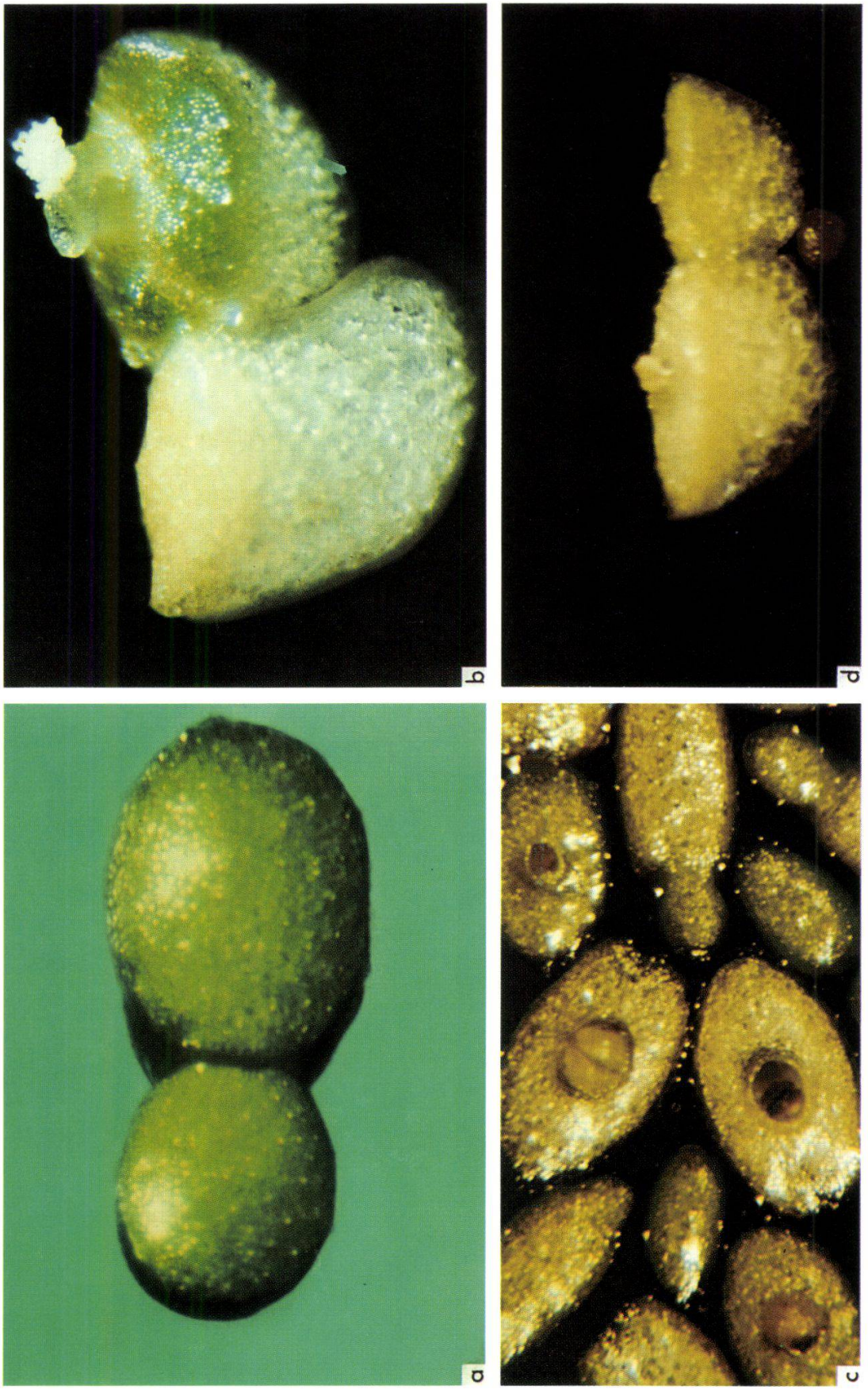


Plate XIV. a.b. Wolffia australiana (x32); c.d. W. angusta (x32)

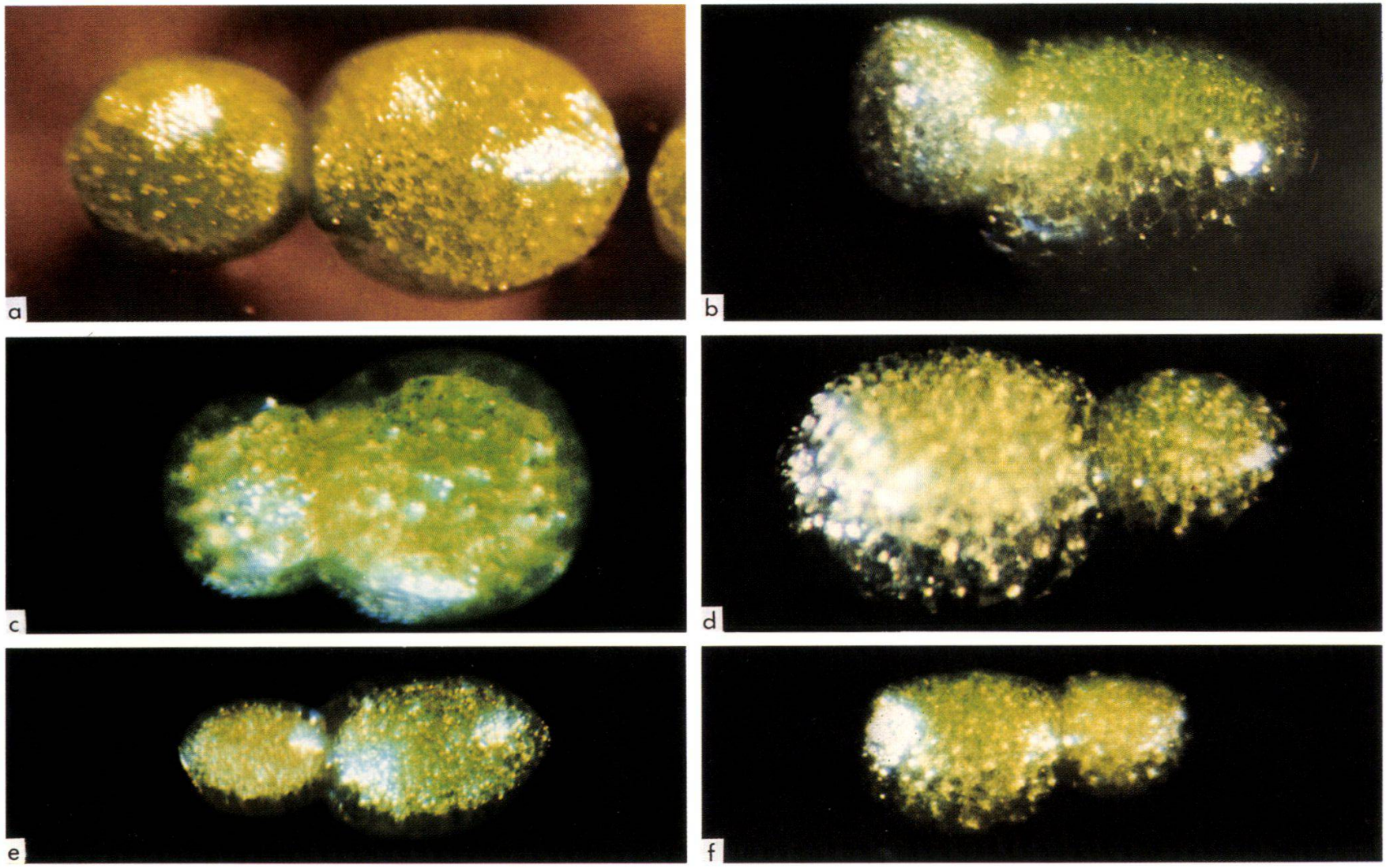


Plate XV. a.b. Wolffia arrhiza (x32); c.d. W. columbiana (x32); e.f. W. globosa (x32)

Plate XVI. Habitats of Lemnaceae
a. pond; b. flooded forest area; c. lake shore; d. moist rock

Remarks to plates I to XVI (continued)

Plate XV

a. Wolffia arrhiza (No. 7251), from above (x32). The stomata are visible as small light spots.
b. W. arrhiza (No. 7251), from the side (x32).
c. W. columbiana (No. 7898), from above (x32). The transparence especially at the edge is typical for W. columbiana.
d. W. columbiana (No. 7898), from the side (x32).
e. W. globosa (No. 7233), from above (x32). In shape and transparence, W. globosa is somewhere between W. arrhiza and W. columbiana, but distinctly smaller.
f. W. globosa, from the side (x32).

Plate XVI

a. San Digieto R., Cal., U.S.A.: a pond with thick layers of Wolffia borealis and W. columbiana. phot. W.P. Armstrong.
b. Flooded Salix humboldtii forest near Zarate, Entre Rios, Argentina. The dense mat on the water surface contains Spirodela intermedia, Lemna minuscula, Wolffiella lingulata, W. oblonga, Wolffia brasiliensis, Ricciocarpus natans, Azolla caroliniana, and Limnobium leviga-tum.
c. Laguna del Monte, Buenos Aires, Argentina. Between Scirpus californicus, Senecio bonariensis, Ludwigia peploides, and Ranunculus apiifolius the following species of the Lemna gibba - Wolffiella oblonga association occur: Lemna gibba, L. minuscula, Spirodela intermedia, Wolffiella oblonga, Wolffia brasiliensis, W. columbiana, Ricciocarpus natans, Azolla filiculoides, Ceratophyllum demersum.
d. Sao Conrado - Leblon, Rio de Janeiro, Brazil. Moist granitic rock in northern exposition with Lemna valdiviana and Azolla caroliniana.

9.3. SUBFAMILY OF WOLFFIOIDEAE

9.3.1. Description of the subfamily of Wolffioideae with key to the genera

Morphology

Fronds. Fronds thin or thick (three-dimensional), in various shapes, symmetrical or somewhat asymmetrical; with air spaces (Wolffiella) or without air spaces (Wolffia); no nerves and no tracheids; one terminal pouch or cavity at the base from which the daughter fronds originate; very few (rarely none) to numerous stomata on the upper surface of the frond; lateral walls of the epidermis cells straight; no crystal cells; stipe connecting daughter frond with mother frond very small, stays with mother frond after separation; no roots present.

Flowers and fruits. Usually one flower per frond (2 in W. Welwitschii and partly in W. rotunda), with no leaflet at the base, originating in a cavity on the upper surface; 1 stamen per flower, with 2 locules; pigment cells along the dehiscence line; filaments with or without tracheids; pollen grains with 0.4-1.0 µm long protuberances; 1 ovary with 1 orthotropous ovule; fruits not winged, no anthocyanin present; seeds 0.3-0.6 mm long, nearly smooth (undistinctly reticulate); outer seed coat with 2-4 subepidermal cell layers; embryo sac bisporic, endosperm with 1 cell layer.

Size and distribution

The subfamily of Wolffioideae consists of two genera (Wolffiella and Wolffia) and 18 species. The subfamily prefers warmer regions, avoiding areas with cold winters. The main distribution areas are South America (8 species), North America (8 species), and southern Africa (7 species).

Key to the genera of Wolffioideae

- Fronds flat with air spaces; daughter fronds emerging from a terminal flat pouch at the end of the mother frond; flower originating in a cavity at the side of the median line of the upper surface.

  Wolffiella

- Fronds three-dimensional (globular, ellipsoid, cylindrical, conical, boat-shaped or nutshell-shaped); daughter fronds emerging from a ter-

minal conical cavity at the base of the mother frond; flower originating in a cavity in or near the median line of the upper surface.

Wolffia

Remarks on the classification of the subfamily Wolffioideae

In his monography of Lemnaceae HEGELMAIER (1868) distinguished only one genus of Wolffia within his tribus Wolffieae; he designated one subgenus Wolffiella with 4 species due to their asymmetrical fronds. Later (1895), he upgraded the subgenus to a genus but called it a dubious genus. The species W. Welwitschii, W. hyalina and W. repanda had been left in the genus Wolffia because the fronds look symmetrical. MONOD (1949) placed all species with flat fronds in the genus Wolffiella as has been done in this work. DAUBS (1965) changed only W. Welwitschii to Wolffiella leaving the other two species with Wolffia. DEN HARTOG and VAN DER PLAS (1970) created two new genera, placing W. Welwitschii in a genus Wolffiopsis and combining W. hyalina and W. repanda together in a genus Pseudowolffia.

The only difference between Wolffiopsis and Wolffiella is based on symmetry: there are two symmetrical flowers in Wolffiopsis, one asymmetrical in Wolffiella. In Wolffiopsis the tract runs near the median line of the lower wall of the pouch; in Wolffiella it is situated between the median line and the edge of the pouch. KANDELER and HUEGEL (1974a) pointed out that the characteristic of the number of flowers might not be a good one since Lemna perpusilla is able to form two flowers per frond whereas most other species have only one flower. The subsequently discovered W. rotunda shows within the same population some one- and some two-flowered fronds. On the other hand, W. Welwitschii can rarely be seen with one flower per frond (fig. 2.40). Also, the characteristic of symmetry is not very distinct. Within the genus Wolffiella, a series of species from very asymmetrical to symmetrical position of the track can be observed: W. gladiata, W. oblonga, W. lingulata, W. neotropica and W. Welwitschii. It is the opinion of the present author that W. Welwitschii does not even deserve the state of a separate section.

Pseudowolffia is distinguished from Wolffiopsis by the former's lack of pigment cells, existence of only one flower per frond, an appendage originating from the lower wall of the pouch, and the high number of stomata. W. rotunda connects the genus Pseudowolffia with Wolffiella Welwitschii and other Wolffiella species: it has no pigment cells and has 1-2

flowers per frond but no appendage. On the other hand, W. neotropica and W. rotunda are provided with numerous stomata as are the two species of Pseudowolffia. The only characteristic distinguishing Pseudowolffia is the appendage. Therefore, W. hyalina and W. repanda might form a section of their own within the genus Wolffiella; at least the difference between these two species and the genus Wolffia is much greater than the difference between the two species and Wolffiella rotunda.

9.3.2. Genus Wolffiella Hegelmaier

9.3.2.1. Description of the genus Wolffiella with key to the sections

Morphology

Fronds. Fronds thin, orbicular to ovate and floating on the surface of the water or linear, ribbon-, sabre- or tongue-shaped and floating below the surface of the water (except when flowering and fruiting), 1 to several coher together or form morning-star like balls; pigment cells in some species present; one layer of air spaces present; either throughout the whole frond or only around the node; at the base with one terminal, triangular and flat pouch out of which the daughter fronds emerge; lower wall of the frond with a tract of elongated cells forming the connection between node and point of attachment of the daughter frond; in some species (W. hyalina, W. repanda), this lower wall elongates after separation from the mother frond into a ribbon-like appendage.

Flowers and fruits. 1-2 flowers per frond, originating in a cavity at the side of the median line of the upper frond surface.

Size and distribution

The genus Wolffiella comprises three sections with eight species. The distribution of the genus is restricted to warm temperate, subtropical and tropical America (5 species) and Africa (4 species). W. hyalina is introduced into India.

Key to the sections of the genus Wolffiella

- Fronds floating on the surface of the water; orbicular to ovate, sometimes polygonal; no pigment cells present in the vegetative tissue.
  - Lower wall of the pouch elongated in a ribbon-like appendage which is 1-8 mm long and bent vertically down; fronds with 2 papules on the upper surface. sect. Stipitatae

- Lower wall of the pouch not elongated; fronds without papules. sect. Rotundae
- Fronds floating below the surface of the water (except flowering and fruiting fronds and, occasionally vegetative fronds of W. neotropica); linear, ribbon-, sabre- or tongue-shaped; with pigment cells in the vegetative tissue. sect. Wolffiella

Remarks on the taxonomy of the genus Wolffiella

The genus can be divided into two groups: 1. an African group of species that float on the water surface and have no pigment cells within the vegetative tissue (W. hyalina, W. repanda, W. rotunda); within this group W. rotunda is isolated as it has no appendage; it forms a connection to the second group; 2. a group of submersed species, with pigment cells; it consists of three clearly distinct species one of Southern Africa (W. denticulata), one of tropical America (W. neotropica), and one of tropical Africa and America (W. Welwitschii) and one group of 3 closely related American species sometimes difficult to distinguish.

9.3.2.2. Section Stipitatae Hegelmaier

Morphology

Fronds. Fronds float on the surface of the water, coher 1-2 together, with more than 60 stomata; without pigment cells; with one papule near the tip and one above the node; tract of elongated cells situated in the median line of the lower wall of the pouch; lower wall of the pouch elongated towards the basal section in a ribbon-like appendage which is bent downwards.

Flowers and fruits. Flowering fronds similar to vegetative ones; 1 flower per frond; in the filament one row of tracheids (the only known section of the genus with tracheids); stigma without pigment cells.

Size and distribution

Two African species belong to the section Stipitatae.

Key to species of the section Stipitatae

- Fronds with distinct air spaces, spreading throughout 1/2-4/5 of the distance between the node and the tip; appendage 0.6-1.8 mm wide, 1/2-4/5 as wide as the frond. W. hyalina
- Fronds with indistinct air spaces restricted to the area around the

node; appendage 0.2-0.5 mm wide, 1/4-1/2 as wide as the frond.

W. repanda

Remarks on the taxonomy of the section Stipitatae

The two species in this section are not as distinctly separated as it could be assumed from the description of HEGELMAIER (1868). HEGELMAIER did not know of the large variability in morphological characteristics caused by the influence of external factors. Especially variable is the length of the appendage of W. hyalina.

JOVET-AST (1968) treated the Lemnaceae of Ennedi (Chad) in a very careful publication. She described a new species under the name of W. Monodii, which was clearly separated from W. hyalina occurring in the same region. The main differentiating characteristics are the form of the frond (trapezoid in W. Monodii, ovate in W. hyalina), the length of the appendage (as long as or shorter than the frond length in W. Monodii, 1-2 times as long as in W. hyalina) and the diameter of the pollen grain (20 µm in W. Monodii, 28 µm in W. hyalina). Four clones of W. hyalina were compared in our laboratory (2 from Egypt, 1 from Tanzania, 1 from Malawi). Under normal growth conditions (Hutner solution 1/5), the appendage was 1/2-1 times as long as the frond; in diluted nutrient solution, the fronds developed an appendage which was 1-2 times as long as the frond. The length of the appendage is, similar to the root length of Lemna, dependent on the composition and concentration of the nutrient solution. The form of the fronds varies between ovate and trapezoid, depending on the clone and the external conditions. The two "species" W. hyalina and W. Monodii grow in neighbouring pools according to JOVET-AST (1968) and are not mixed together; therefore, it is possible that the morphological differences between the two "species" are due either to differences in the water composition or just to the fact that the two pools are populated by two different clones. The difference in pollen diameter can be explained by a different chromosome number (different chromosome numbers are found within the same populations of Lemnaceae, cf. URBANSKA 1980) or by different nutritional states of the plants. There is no characteristic of W. Monodii that is not within the variation range of W. hyalina. W. Monodii must be regarded as a plant population of W. hyalina with a special combination of characteristics. A picture of W. Monodii is given in fig. 9.3b.

17. Wolffiella hyalina (Delile) Monod (fig. 9.3a,b,c; plate VIIIc,d)

Morphology

Fronds. Fronds 1-3 mm long, 0.8-2.0 mm wide, ovate to trapezoid, with some one-celled teeth along the margin or without; air spaces distinct, spread throughout 1/2-4/5 of the distance between the node and the tip, up to 7 cell layers thick at the base; angle of the pouch 90°-120°; appendage 0.5-5.0 mm long, 0.6-1.8 mm wide, 3/4-5 times as long as wide, 1/2-4 times as long as the frond, 1/2-4/5 as wide as the frond.

Flowers and fruits. Plants often flowering and fruiting. Seeds 0.35-0.40 mm long, 0.25-0.3 mm thick.

Distribution

Subtropical and tropical regions of Africa with rather dry climate; introduced in Central India (fig. 6.16).

18. Wolffiella repanda (Hegelmaier) Monod (fig. 9.d,e)

Morphology

Fronds. Fronds 0.5-1.8 mm long, 0.4-1.2 mm wide, ovate with several one-celled teeth along the margin; air spaces indistinct, restricted to the area around the node (spread throughout up to 1/2 of the distance between the node and the tip), up to 4 cell layers thick at the base; angle of the pouch 70°-90°; appendage 3-8 mm long, 0.2-0.5 mm wide, 6-20 times as long as wide, 1/2-7 times as long as the frond, 1/4-1/2 as wide as the frond.

Flowers and fruits. Plants often flowering and fruiting. Seeds 0.3-0.35 mm long, 0.22-0.27 mm thick.

Distribution

Subtropical and tropical regions of Southwest Africa with rather dry climate (Angola, Botswana) (fig. 6.16).

9.3.2.3. Section Rotundae sect. nov.

Morphology

Fronds. Vegetative and reproductive fronds similar. Fronds float on the surface of the water, coher 1-2 together, with many stomata; without pigment cells; no papules present; tract of elongated cells situated in the median line of the lower wall of the pouch; lower wall not elongated in an appendage.

Flowers and fruits. Flowering fronds similar to the vegetative ones; 1-2 flowers per frond; stigma without pigment cells.

Size and distribution

W. rotunda with only one known locality in eastern Africa is the only species of the section.

Remarks on the taxonomy of the section Rotundae

W. rotunda is the only species of this section. It forms a connection between the sections Stipitatae and Wolffiella.

19. Wolffiella rotunda Landolt (fig. 9.3f,g)

Morphology

Fronds. Fronds 1-3 mm long, nearly as wide as long, without teeth along the margin; air spaces not very distinct, restricted to the area near the node; angle of the pouch 90°-120°.

Flowers and fruits. Fruits not known.

Distribution

Tropical regions of Africa with rather dry climates; restricted to Kariba Gorge, Zimbabwe (fig. 6.16). Unfortunately, the Kariba Gorge has been dammed since 1958. This species may therefore be endangered or even extinct.

9.3.2.4. Section Wolffiella

Morphology

Fronds. Vegetative fronds mostly float below the surface of the water, coher 1-50 together; 0-35 stomata (number of stomata higher in flowering than in non-flowering fronds); pigment cells present; without papules; tract of elongated cells situated in the median line or near the angle of the lower wall of the pouch; lower walls not elongated in an appendage.

Flowers and fruits. Some flowering fronds similar to while others differ from the vegetative ones; 1-2 flowers per frond; stigma with pigment cells.

Size and distribution

Six American and African species are included in the section Wolffiella.

Key to the species of the section Wolffiella

- Fronds with 20-35 stomata; air spaces not very distinctly visible. W. neotropica
- Fronds with 0-8 stomata; air spaces distinctly visible.
  - Tract of elongated cells running along the median line of the lower wall of the pouch; 2 flowers per frond. W. Welwitschii
  - Tract of elongated cells running between the medium line and the edge or along the edge of the lower wall of the pouch.
    - Fronds rounded or pointed at the tip but without teeth, 1-20 times as long as wide.
      - Fronds 1-8 times as long as wide; angle of the pouch 45-120°.
        - Angle of the pouch 70-120°; tract of elongated cells running between the median line and the edge of the lower wall of the pouch; area of air spaces within the frond rarely longer than wide. W.lingulata
        - Angle of the pouch 45-90°; tract of elongated cells running along or close to the edge of the lower wall of the pouch; area of air spaces within the frond very often longer than wide. W. oblonga
      - Fronds 4-20 (usually 6-15) times as long as wide; angle of the pouch 25-50°. W. gladiata
    - Fronds truncated or rounded at the tip, with 2-4 teeth, 6-15 times as long as wide. W. denticulata

Remarks on the taxonomy of the section Wolffiella

Three species of the section (W. Welwitschii, W. neotropica and W. denticulata) are relatively easy to distinguish from each other and from the rest of the section. Within the section there is an evolution from strictly symmetrical to asymmetrical fronds: W. Welwitschii - W. neotropica - W. lingulata - W. oblonga - W. gladiata - W. denticulata. In W. Welwitschii with two flowers (all the other species with only one flower, laterally situated), the tract of elongated cells follows the median line, and flowering and vegetative fronds are nearly similar. In W. lingulata, the tract is shifted to one side and the flowering fronds are smaller than most of the vegetative ones; in W. oblonga, W. gladiata and W. denticulata the tract follows the edge of the lower wall of the pouch and the flowering fronds in the same sequence of species are more and more different from the vegetative fronds; in addition, the vegeta-

tive fronds are smaller and grow in cooler climates. W. denticulata is distinguished sharply from the other species by the few teeth at the tip of the frond, as well as by its isolated distribution area in South Africa. A somewhat different place is taken by W. neotropica: the tract of elongated cells nearly follows the median line, but the flowering fronds look quite different from the vegetative ones; furthermore, it is characterized by the numerous stomata.

The three species W. lingulata, W. oblonga and W. gladiata are sometimes very difficult to recognize. Especially unclear are the limits between W. lingulata and W. oblonga. There is a great variability in some of the most important differentiating characteristics such as angle of the pouch, extension of the air spaces within the frond, and width of the frond. Also, the position of the tract of elongated cells overlaps in the two species; if it is near the edge it might belong to either species. The tract changes its position towards the edge (more laterally) if cultivated in diluted nutrient solutions; in addition, the fronds get wider (own cultivation experiments). Identification with certainty is possible only for the fronds with relatively extreme characteristics: these are summarized in table 9.4. Especially in California, Mexico and Argentina, it is sometimes very difficult to decide whether a sample of Wolffiella consists of either W. oblonga or W. lingulata in different developmental forms or if there is a mixture of both species present. THOMPSON (1896) proposed that the characteristic of the position of the point of attachment of the stipe of the daughter frond (which corresponds to the position of the tract of elongated cells) is important for the distinction of the species. However, MASON (1938) thinks that this characteristic is variable. From his observations in the field and in non-clonal cultures, he concluded that only W. lingulata is present in California and that this plant may develop different forms during the course of the years due to different external conditions; forms which look more like W. lingulata or more like W. oblonga. HEGELMAIER (1895) was not sure, too, whether he should keep the distinction between the two species. On the other hand, there are regions where only one well-characterized species occurs: e.g. W. oblonga in northern Florida, northern Louisiana, Prov. Buenos Aires; W. lingulata in tropical lowlands. It might be presumed that MASON (1938) investigated a partial mixture of both species. The author's own observations in northern Argentina (cf. LANDOLT and ZARZYCKI in prep.) led to the conclusion that

mixed populations of both species are very common. The problem of distinguishing between the two species still has to be further investigated.

Small plants of Wolffiella with limited air space area were named by HEGELMAIER (1878) as W. lingulata var. minor. The area of the air spaces in W. oblonga is very variable; under some growth conditions, the air spaces extend to the tip of the frond, under other conditions, they are only around the node. In W. lingulata, the extension of the air spaces does not vary much as the area containing air spaces is rarely longer than wide. HEGELMAIER (1868) was of the opinion that the area of air spaces in W. oblonga was always longer than half of the frond length which is not true. His W. lingulata var. minor therefore very often includes small fronds of W. oblonga or mixtures of both species. Already THOMPSON (1898) and DEN HARTOG and VAN DER PLAS (1970) incorporated the var. minor into W. oblonga (cf. fig. 9.3m,p).

SMITH (1880), THOMPSON (1896) and HEGELMAIER (1895) distinguished a special variety of W. gladiata (var. floridana J.D. Smith) with narrower

Table 9.4. Characteristics typical for species of the Wolffiella oblonga group

Characteristics	Wolffiella		
	lingulata	oblonga	gladiata
Fronds wider than 2.5 mm	+		
Fronds 1-2 times as long as wide	+		
Fronds 2-4 times as long as wide	+	+	
Fronds 4-8 times as long as wide		+	+
Fronds more than 8 times as long as wide			+
Area containing air spaces more than 1 1/2 times as long as wide		+	+
Tip pointed		+	+
Angle of the pouch more than 90°	+		
Angle of the pouch 70-90°	+	+	
Angle of the pouch 60-70°		+	
Angle of the pouch 40-60°		+	+
Angle of the pouch less than 40°			+
Tract exactly following the edge		+	+
Distance from the point of attachment to the nearer edge of the pouch at least 1/5 of the whole distance between the edges	+		

and more elongated fronds than the typical W. gladiata. THOMPSON later (1898) elevated the variety to the rank of species. DAUBS (1965) and DEN HARTOG and VAN DER PLAS (1970) followed this treatment. W. gladiata was described by HEGELMAIER (1868) from material of Mexico City. The fronds were characterized as ribbon-shaped or sabre-like and 6-11 times as long as wide. The fronds of W. floridana are said to be 10-20 times as long as wide. Under culture conditions (own investigations), all clones of W. floridana from the USA showed fronds which are 4-10 times as long as wide; they are identical to the type collection material from Mexico (cf. fig. 9.3q,r). However in nature, there is rather frequently a length-width ratio of 10-20 in many populations from the USA. Plants from Argentina or Uruguay named W. gladiata all belong to W. oblonga as can be easily seen from our plants grown under controlled conditions. In general, the length- width ratio of the fronds seems to be higher in cold rather than warm water. This is probably valid for all species of the group as well as for L. valdiviana.

20. Wolffiella neotropica Landolt (fig. 9.3h; plate IXa,b)

Morphology

Fronds. Vegetative fronds mostly submerged, coher 2-3 together, wide tongue-shaped to ovate, rounded at the tip, nearly as wide at the tip as at the base, 2-8 mm long, 1.0-5.5 mm wide, 1 1/4-3 times as long as wide, without teeth, with 20-35 stomata; air spaces present near the node but indistinct; angle of the pouch 100-120°; tract of elongated cells running near the median line of the lower wall of the pouch. Reproductive fronds floating on the surface of the water, 1.0-3.5 mm long, 0.7-1.5 mm wide; point of attachment of the daughter frond after separation not conspicuous.

Flowers and fruits. Plants probably occasionally flowering and fruiting. Flowering fronds much smaller than most of the vegetative ones. One flower per frond. Seed 0.30-0.36 mm long, 0.20-0.25 mm thick.

Distribution

Tropical regions of South America with warm and humid climate (fig. 6.16).

21. Wolffiella Welwitschii (Hegelm.) Monod (fig. 9.3i,k; plate IXc,d)

Morphology

Fronds. Fronds submerged, with the basal part near the surface of the water, the tip bent downwards, coher 2-3 together, at the base saddle-like, wide tongue-shaped, rounded at the tip, nearly as wide at the tip as at the base, 3-7 mm long, 2.5-5.0 mm wide, 1 1/4-2 times as long as wide, without teeth, with 0-12 stomata (especially along the lateral margins of the base); air spaces distinct; the area containing air spaces not longer than wide; angle of the pouch 100-120°; tract of elongated cells running along the median line of the lower wall of the pouch; point of attachment of the daughter frond after separation not conspicuous.

Flowers and fruits. Plants often flowering and fruiting. Flowering fronds similar to the vegetative ones. Two flowers per frond. Seed 0.45 mm long, 0.3 mm thick.

Distribution

Tropical regions of Africa and America with warm semi-arid climates (fig. 6.17).

22. Wolffiella lingulata (Hegelm.) Hegelmaier (fig. 9.3 l,m; plate Xa,b)

Morphology

Fronds. Fronds submerged, with the basal part near the surface of the water and the tip bent downwards, coher 2-4 together, at the base saddle-like, wide tongue-shaped or ovate, rounded at the tip, sometimes narrower at the tip than at the base, 3-9 mm long, 0.8-5.0 mm wide, 1 1/2-4 times as long as wide, without teeth, with 0-10 stomata (especially along the lateral margins of the base); air spaces distinct; the area containing air spaces rarely longer than wide; angle of the pouch 70-120°; tract of elongated cells running between the median line and the edge of the lower wall of the pouch but never in the edge of the pouch; point of attachment of the daughter frond after separation not conspicuous.

Flowers and fruits. Plants often flowering and fruiting. Flowering fronds narrower than most vegetative ones; 1 flower per frond; seeds 0.41-0.44 mm long, 0.29 mm thick.

Distribution

Tropical and subtropical regions of America with mild winters (fig. 6.18).

23. Wolffiella oblonga (Phil.) Hegelmaier (fig. 9.3n,o,p; plate Xc,b)

Morphology

Fronds. Fronds submerged, the basal part near the surface and the tip bent downwards, coher 2-8 together (often grouped star-like), occasionally somewhat contorted, the base straight, narrow tongue-shaped to ribbon-like, rounded at the tip or pointed, usually narrower at the tip than at the base, 1.2-7.5 mm long, 0.4-2.5 mm wide, 3-8 times as long as wide, without teeth, with 0-8 stomata (especially along the lateral margins of the base); air spaces distinct, the area containing air spaces mostly longer than wide and sometimes spreading throughout the whole frond; angle of the pouch 45-90°; tract of elongated cells running along or near the edge of the lower wall of the pouch; point of attachment of the daughter frond after separation prominent.

Flowers and fruits. Plants occasionally flowering and very rarely fruiting. Flowering fronds rather similar to the vegetative ones. One flower per frond; seeds 0.35-0.40 mm long, 0.25-0.29 mm thick.

Distribution

Warm temperate and subtropical regions with mild winters and not very hot summers (fig. 6.19).

24. Wolffiella gladiata (Hegelm.) Hegelmaier (fig. 9.3q,r; plate XIa,b)

Morphology

Fronds. Vegetative fronds submerged, the basal part near the surface of the water and the tip bent downwards, coher 3-50 together (usually grouped star-like), the base straight; narrow, sabre-shaped, pointed at the tip, tapering to the tip, 3-9 mm long, 0.25-0.80 mm wide, 4-20 (usually 6-15) times as long as wide, without teeth, 0-8 stomata (along the lateral margins of the base); air spaces distinct, the area containing air spaces much longer than wide, spreading throughout most of the frond; angle of the pouch 25-50°; tract of elongated cells running along the edge of the lower wall of the pouch; the point of attachment of the daughter frond after separation very prominent. Reproductive fronds much

wider at the base than the vegetative ones and float on the surface of the water, the distal part immersed in the water.

Flowers and fruits. Plants occasionally flowering and rarely fruiting. Flowering fronds shorter and wider than the vegetative ones. One flower per frond; seeds 0.3-0.4 mm long, 0.18-0.30 mm thick.

Distribution

Temperate regions of North America with relatively humid climate and mild winters (fig. 6.20).

25. **Wolffiella denticulata (Hegelm.) Hegelmaier** (fig. 9.3s; plate XIc,d)

Morphology

Fronds. Vegetative fronds submerged, the basal part near the surface of the water and the tip bent downwards, coher 2-7 together (often grouped star-like); narrow, ribbon-shaped, truncated or rounded at the tip, with 2-4 short triangular teeth, 2-7 mm long, 0.3-0.8 mm wide, 6-15 times as long as wide, with 0-5 stomata (along the lateral margins of the base); air spaces distinct, the area containing air spaces much longer than wide, spreading throughout most of the frond; angle of the pouch 25-40°; tract of elongated cells running along the edge of the lower wall of the pouch; the point of attachment of the daughter frond after separation very prominent. Reproductive fronds wider and shorter than the vegetative ones, float on the surface of the water, coher together with a submerged vegetative frond.

Flowers and fruits. Plants rarely flowering and fruiting. Flowering fronds much shorter and wider than the vegetative ones, coher together with a vegetative frond; 1 flower per frond; ripe fruits not known.

Distribution

Subtropical region of South Africa with relatively humid climate and very mild winters (no frosts) (fig. 6.20).

9.3.3. Genus Wolffia Horkel

9.3.3.1. Description of the genus Wolffia with key to the sections

Morphology

Fronds. Fronds thick, globular, ovoid, cylindrical, conical, boat-shaped or nutshell-shaped, floating on or near the surface of the water or sometimes (in a resting stage) below the surface of the water, 1 or 2 coher together; pigment cells in some species; no air spaces; at the base one terminal conical cavity out of which daughter fronds emerge; tract of elongated cells along the median line of the lower side of the cavity, only very short and indistinct.

Flowers and fruits. Flowering fronds similar to vegetative ones; 1 flower per frond, originates in a cavity more or less on the median line of the upper surface of the frond. No tracheid cells are present in the filament.

Size and distribution

The genus consists of 8 species which can be grouped into 4 sections: 1. Pseudorrhizae; 2. Elongatae; 3. Pigmentatae; 4. Wolffia. The genus is distributed all over the warmer regions of the world, with a center in northern South America (three sections represented).

Key to the sections of the genus Wolffia

- Fronds with an orbicular to polygonal flat upper surface; the lower surface tapering into a conical appendage. sect. Pseudorrhizae
- Fronds without a conical appendage.
  - Fronds cylindrical, 2-4 times as long as thick, the distal part submerged. sect. Elongatae
  - Fronds globular to ovoid, boat-shaped or nutshell-shaped
    - Fronds nutshell-shaped, 1/2-1 times as deep as wide; with pigment cells in the vegetative tissue. sect. Pigmentatae
    - Fronds globular to ovoid or boat-shaped, 1-3 times as deep as wide; without pigment cells in the vegetative tissue. sect. Wolffia

Remarks on the taxonomy of the genus Wolffia

The section Pigmentatae contains the species with the most primitive characteristics. The main difference to the section Wolffia is the pres-

ence of pigment cells in the frond parenchyma. The two other sections are somehow more distinct. Especially section Pseudorrhizae is morphologically as well as geographically (India) rather isolated.

9.3.3.2. Section Pseudorrhizae sect. nov.

Morphology

Fronds. Fronds floating on the surface of the water; upper surface suborbicular with 5-10 teeth along the margin, the lower surface tapering downwards into a cylindrical projection; with 5-30 stomata; without pigment cells; without turions.

Flowers and fruits. Stigma with pigment cells.

Size and distribution

W. microscopica is the only known species of this section. It is restricted to the Indian subcontinent.

Remarks on the taxonomy of the section Pseudorrhizae

W. microscopica is not closely related to any other group. The systematic position within the Wolffioidae is unclear.

26. Wolffia microscopica (Griffith) Kurz (fig. 9.4a,b; plate XIIa,b)

Morphology

Fronds. Fronds 0.4-1.0 mm long, 0.3-0.8 mm wide, 1-1 1/2 times as long as wide, pale green; projection 0.4-3.0 mm long.

Flowers and fruits. Plants probably often flowering and fruiting. Seeds 0.3 mm long, 0.2 mm thick.

Distribution

Subtropical and tropical region of India with warm climate and a dry season (fig. 6.21).

9.3.3.3. Section Elongatae sect. nov.

Morphology

Fronds. Fronds with the basal part floating just below the surface of the water; the distal part bent downwards, cylindrical; without pigment cells; with 0-5 stomata on the upper surface of the basal part; daughter fronds growing downwards from the cavity at an acute angle; turions not known.

Size and distribution

W. elongata is the only known species of this section.

Remarks on the taxonomy of the section Elongatae

There might be some relationship to W. columbiana from which it is clearly distinct by the cylindrical submerged distal part of the frond (W. columbiana is globular).

27. Wolffia elongata Landolt (fig. 9.4c)

Morphology

Fronds. Fronds 1.0-2.5 mm long, 0.3-0.6 mm thick, 2-4 times as long as thick, light green.

Flowers and fruits. Not known.

Distribution

Tropical region of northwestern South America and Curaçao with warm and rather dry climate (fig. 6.21).

9.3.3.4. Section Pigmentatae sect. nov.

Morphology

Fronds. Fronds floating on the surface of the water; nutshell-shaped (the lower surface hemispherical, the upper surface only slightly convex), wider than deep; the largest horizontal sectional area at the surface of the water; bright green on the upper surface; 50-100 stomata; pigment cells present; form turions under unfavourable conditions.

Flowers and fruits. Stigma with pigment cells.

Size and distribution

The section comprises one Panamerican and one North American species.

Key to the species of the section Pigmentatae

- Fronds 1-1 1/2 times as long as wide, rounded at the tip, with a prominent papule in the center of the upper surface (in some smaller fronds, occasionally no papule). W. brasiliensis
- Fronds 1 1/3-2 times as long as wide, with a point at the tip bent upwards; without a papule. W. borealis

Remarks on the taxonomy of the section Pigmentatae

HEGELMAIER (1868, 1895) recognized only one species within this group:

W. brasiliensis. However, he separated the North Amnerican plants as var. borealis Engelmann. THOMPSON (1898) distinguished a new species (W. papulifera) which had a very typical prominent papule in the middle of the upper surface. He called the var. borealis W. punctata Griseb. DAUBS (1965) and DEN HARTOG and VAN DER PLAS (1970) followed this treatment, thus distinguishing three species within the group. But, plants of the type collection of W. brasiliensis are identical with W. papulifera. The same is true for the type collection of W. punctata. Therefore W. punctata and W. papulifera are synonymous to W. brasiliensis. There are only two species within the group. The fronds of W. brasiliensis lack the typical papules under certain external factors (e.g. warm water temperatures). Also, flowering and fruiting fronds do not show a papule. Furthermore, the papules are sometimes not visible in herbarium samples; therefore it is recommended to boil the dried fronds in order to obtain their typical shape. The typical point at the apex of W. borealis is more easily recognizable in boiled specimens, too. Both species have much smaller cells below the upper epidermis than in the lower part of the body which makes the fronds bright green above and pale green below.

28. Wolffia brasiliensis Weddell (fig. 9.4d; plate XIIIa,b)

Morphology

Fronds. Fronds broad-ovate to suborbicular from above, 0.5-1.6 mm long, 0.7-1.5. mm wide, 1-1 1/2 times as long as wide, 1/3-2/3 as deep as wide, rounded at the tip, with a prominent papule in the middle of the upper surface (tent-shaped) (in some smaller fronds, sometimes no papule); 1-2 layers of small cells below the epidermis.

Flowers and fruits. Plants occasionally flowering and rarely fruiting. Seeds 0.40-0.45 mm long, about 0.4 mm thick.

Distribution

Tropical, subtropical and warm temperate regions of America (fig. 6.22).

29. Wolffia borealis (Engelm.) Landolt (fig. 9.4e,f; plate XIIIc,d)

Morphology

Fronds. Fronds ovate from above, 0.7-1.5 mm long, 0.5-1.0 mm wide, 1 1/3-2 times as long as wide, 2/3-1 times as deep as wide, with a point at the tip bent upwards; without a papule; 3-4 layers of small cells below the epidermis.

Flowers and fruits. Plants very rarely flowering; fruits not known.

Distribution

Temperate regions of North America with rather mild winters and not very hot summers (fig. 6.23).

9.3.3.5. Section Wolffia

Morphology

Fronds. Fronds floating on or just below the surface of the water; spherical to ellipsoid or boat-shaped, convex on the upper surface; without prominent papules, but often with small one-celled teeth (visible especially along the margins of the upper surface); the greatest horizontal sectional area at or below the surface of the water; bright green to pale and transparent green on the upper surface; with 2-100 stomata; without pigment cells; forming turions under unfavourable conditions.

Flowers and fruits. Stigma without pigment cells.

Size and distribution

The section Wolffia contains five vicariant species, mainly restricted to Australia (W. australiana and W. angusta), southeastern Asia (W. globosa), Africa, Europe, and western Africa (W. arrhiza) and America (W. columbiana). In Australia there is a climatic vicariance between a species of temperate climate (W. australiana) and a species of tropical-subtropical climate (W. angusta).

Key to the species of the section Wolffia

- Fronds 2-3 times as deep as wide, boat-shaped, with the greatest width at the surface of the water.
  - Fronds 0.3-0.8 mm wide, 1 1/3-2 times as long as wide, with 50-80 stomata, deep green on the upper surface. W. australiana
  - Fronds 0.2-0.5 mm wide, 1 2/3-2 1/2 times as long as wide, with 8-10 (rarely up to 25) stomata, whitish green on the upper surface with more intensely green margins. W. angusta
- Fronds 1-1 1/2 times as deep as wide, spherical to ellipsoid, with the greatest width slightly below the surface of the water.
  - Fronds with 10-100 stomata, on the upper surface relatively deep green (not transparent). W. arrhiza
  - Fronds with 1-15 (rarely up to 30) stomata, on the upper surface mostly transparently green.

- Fronds 1-1 1/3 times as long as wide, 0.4-1.2 mm wide.
  W. columbiana
- Fronds 1 1/3-2 times as long as wide, 0.3-0.5 mm wide.
  W. globosa

Remarks on the taxonomy of the section Wolffia

Apart from the two Australian species, the group is very difficult to classify morphologically. W. arrhiza, W. globosa and W. columbiana are separated from the other species by the lesser depth of the fronds (up to only 1 1/2 times as deep as wide). The morphological differences between the three species are small; the centers of distribution are different. However, there are regions with both species: Africa with W. arrhiza and W. globosa, North America with W. columbiana and W. globosa (probably introduced), and South America with W. columbiana and W. arrhiza (eastern Brazil). W. columbiana and W. globosa have both fewer stomata than W. arrhiza; W. columbiana, in addition, shows only a very small area of the frond above the surface of the water; W. globosa develops smaller and relatively narrower fronds than the other two species. But all these characteristics are modifiable according to external conditions. In addition, there are genetical differences within the species which lead to an overlapping of characteristics. In Florida, there are clones of W. columbiana which have up to 30 stomata and therefore resemble W. arrhiza. The delimitation of the three species needs further investigations. The size of the epidermis cells is not characteristic for a species (as was supposed by MASON 1957), but the upper subepidermal cells are distinctly smaller than the lower parenchymatic cells in all species except W. columbiana.

30. Wolffia australiana (Bentham) den Hartog and van der Plas
(fig. 9.4g; plate XIVa,b)

Morphology

Fronds. Fronds boat-shaped, with the greatest width at the surface of the water, 0.5-1.3 mm long, 0.3-0.8 mm wide, 1 1/3-2 times as long as wide, 2-3 times as deep as wide, with 50-80 stomata, bright green on the surface.

Flowers and fruits. Plants very rarely flowering. Seeds 0.4-0.5 mm long, 0.4 mm thick.

Distribution

Temperate regions of Australia and New Zealand with mild winters (fig. 6.23).

31. Wolffia angusta Landolt (fig. 9.4h,i; plate XIVc,d)

Morphology

Fronds. Fronds boat-shaped, with the greatest width at the surface of the water, 0.5-0.8 mm long, 0.2-0.4 mm wide, 1 2/3-2 1/2 times as long as wide, 2-3 times as deep as wide, with 8-10 (rarely up to 25) stomata, whitish green on the surface with more intensely green margins.

Flowers and fruits. Plants occasionally flowering and rarely fruiting. Seeds 0.3-0.4 mm long, about 0.25 mm thick.

Distribution

Subtropical and tropical regions of Australia and southeastern Asia with rather humid climates (fig. 6.24).

32. Wolffia arrhiza (L.) Horkel (fig. 9.4k,l; plate XVa,b)

Morphology

Fronds. Fronds spherical to ellipsoid, with the greatest width just below the surface of the water, 0.5-1.5 mm long, 0.4-1.2 mm wide, 1-1 1/3 times as long as wide, 1 1/4-1 1/2 times as deep as wide, with 10-100 stomata, bright green on the surface (not transparent).

Flowers and fruits. Plants occasionally flowering and rarely fruiting. Seeds 0.4-0.5 mm long, about 0.4 mm thick.

Distribution

Temperate, subtropical and tropical regions of Europe, Africa, western Asia and eastern Brazil with relatively mild winters and not very hot summers (fig. 6.24).

33. Wolffia columbiana Karsten (fig. 9.4m,n; plate XVc,d)

Morphology

Fronds. Fronds nearly spherical, with the greatest width distinctly below the surface of the water, 0.5-1.4 mm long, 0.4-1.2 mm wide, 1-1 1/3 times as long as wide, 1-1 1/3 times as deep as wide, with 1-10 (rarely up to 30) stomata, pale and transparently green on the surface.

Flowers and fruits. Plants occasionally flowering and rarely fruiting. Seed size not measured.

Distribution

Temperate and subtropical regions of America with mild winters and not very hot summers (fig. 6.25).

34. Wolffia globosa (Roxburgh) Den Hartog and van der Plas
(fig. 9.4 o; plate XVe,f)

Morphology

Fronds. Fronds ellipsoid, with the greatest width slightly below the surface of the water, 0.4-0.8 mm long, 0.3-0.5 mm wide, 1 1/3-2 times as long as wide, 1-1 1/2 times as deep as wide, with 1-10 (rarely up to 30) stomata, rather pale and somewhat transparently green on the surface.

Flowers and fruits. Plants occasionally flowering and rarely fruiting. Seed size not measured.

Distribution

Warm temperate, subtropical and tropical regions of eastern and southern Asia, Africa and North America (probably introduced), with mild winters (fig. 6.26).