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Cover illustration: Cover illustration: The floating plant *Cobbania corrugata* (Lesquereux) Stockey et al. from the Upper Cretaceous of North America inspected by an *Ornithomimus* dinosaur. The quarry in the Dinosaur Provincial Park, Alberta (Canada), produced numerous complete specimens of this plant and the most complete skeleton of the dinosaur (Reconstruction by Marjorie Legin). For details, see Bogner, J.: The free-floating Aroids (Araceae) – living and fossil, pp. 113–128 in this issue.

Umschlagbild: Umschlagbild: Ein *Ornithomimus* Dinosaurier betrachtet die Schwimmpflanze *Cobbania corrugata* (Lesquereux) Stockey et al. aus der Oberkreide Nordamerikas. Im Steinbruch des Dinosaur Provincial Park, Alberta (Kanada), wurden mehrere komplette Exemplare dieser Pflanze und ein nahezu vollständiges Skelett des Dinosauriers gefunden (Rekonstruktion Marjorie Legin). Für weitere Informationen siehe Bogner, J.: The free-floating Aroids (Araceae) – living and fossil, S. 113–128 in diesem Heft.

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The free-floating Aroids (Araceae) – living and fossil

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Abstract

The Lemnoideae (duckweeds) are a very early offshoot of the Araceae which evolved by neoteny and became especially adapted to aquatic life as free-floating plants. The systematic position of the genus *Pistia* is also discussed as well as a very different fossil free-floating plant, *Cobbania corrugata*, originally described as *Pistia corrugata* from the Upper Cretaceous. Morphological traits and molecular data both support a placement of the Lemnoideae as an early branch of Araceae and extant species illustrate extreme neoteny and the genus *Lemna* is known since the Oligocene. The fossil genus *Limnobiophyllum* is known since the Upper Cretaceous and died out in the Miocene; it was widely distrubuted in North America and Eurasia for approximately 50 Ma. The Lemnoideae with the tribes Lemneae and Wolffieae are highly reduced plants and the homologies of the organs are: the pouch of the *Spirodela*, *Landoltia* and *Lemna* frond is homologous to to the petiole sheath of typical Araceae; the frond´s distal part is homologous to the veined leaf blade; the shoot is reduced to just a vegetion point that produces new fronds as well as inflorescences; the membranous envelope around the inflorescence in the Lemneae can be interpreted as the spathe (the Wolffieae lacking a spathe); the spadix is reduced to a single bisexual flower in the Wolffieae and in one bisexual flower and one male flower (with one stamen only) in the Lemneae. The fossil genus *Limnobiophyllum* is much lesser reduced, has long stolons and simple as well as branched roots, whereas the Lemneae have only simply roots and the Wolffieae are rootless; the usually very short stipe (quite long in *Lemna trisulca*) of the new fronds of the Lemneae can be interpreted as a stolon. The genus *Limnobiophyllum*, the tribes Lemneae and Wolffieae show in their evolution a clear line to the reduction of their organs.

Key words: Lemnoideae (duckweeds), living, fossil, free-floating, *Pistia*, *Cobbania*, Araceae

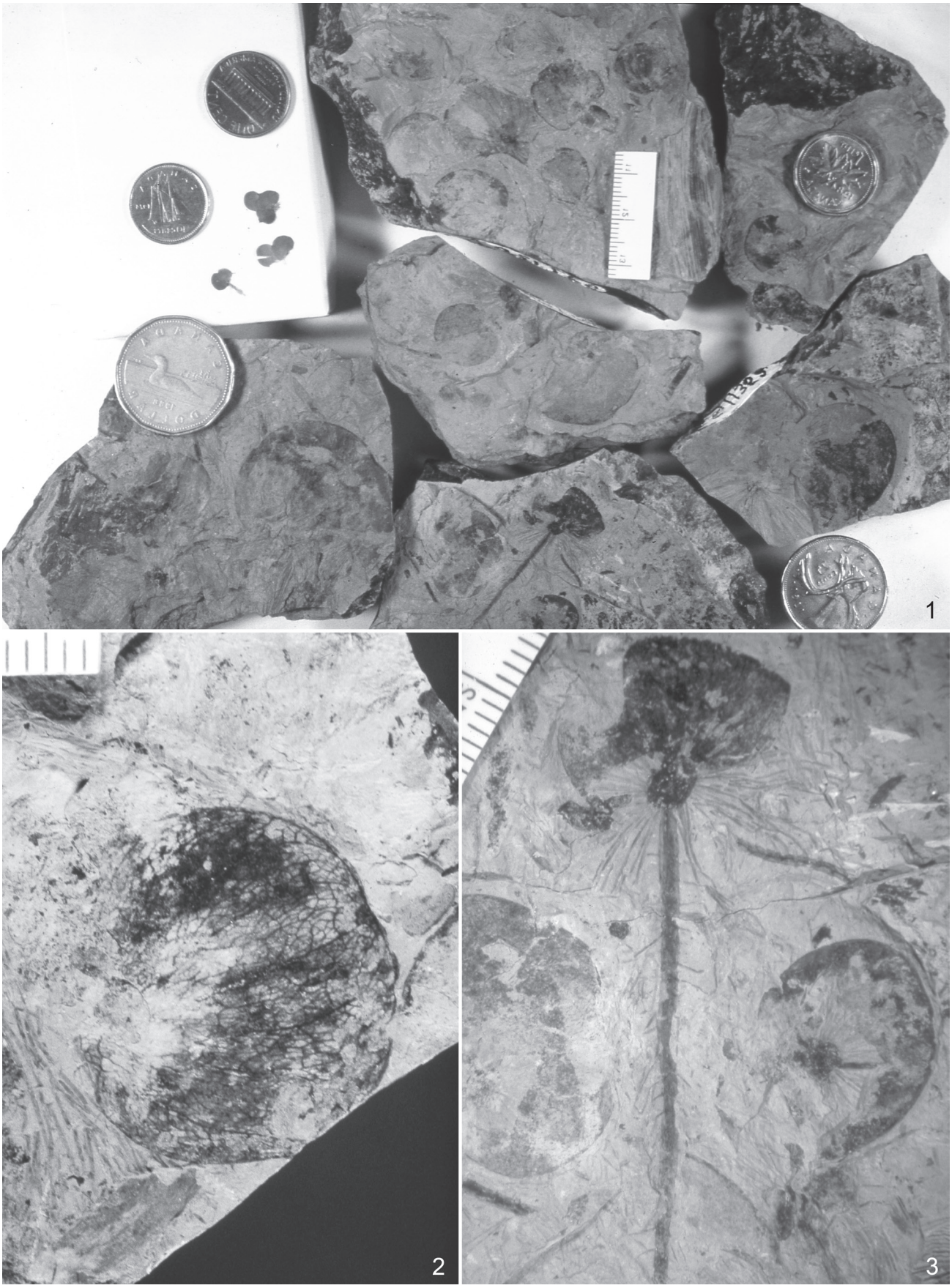
Zusammenfassung

Bei den Lemnoideae (Wasserlinsen) handelt es sich um eine sehr frühe Evolutionslinie der Araceae, die sich durch Neotenie entwickelt haben und besonders an das Wasserleben als freischwimmende Pflanzen angepasst sind. Die systematische Stellung der Gattung *Pistia* wird auch diskutiert sowie die sehr verschiedene *Cobbania corrugata*, die ursprünglich aus der Kreide als *Pistia corrugata* beschrieben wurde. Morphologische Merkmale und molekulare Daten unterstützen beide die Position der Lemnoideae als einen frühen Abzweig der Araceae; rezente Arten weisen eine extreme Neotenie auf und die Gattung *Lemna* ist seit dem Oligozän bekannt. Die fossile Gattung *Limnobiophyllum* trat bereits in der Oberkreide auf und starb im Miozän wieder aus; sie war weit verbreitet in Nordamerika und Eurasien für etwa 50 Millionen Jahre. Die Lemnoideae mit ihren Triben Lemneae sowie Wolffieae sind sehr stark reduzierte Pflanzen und die Homologien ihrer Organe können wie folgt interpretiert werden: die Tasche der Glieder von *Spirodela*, *Landoltia* und *Lemna* sind homolog der Blattscheide typischer Araceae; die Vorderseite der Glieder entspricht der Blattspreite mit den Blattnerven; der Spross ist extrem reduziert zu einem Vegetationspunkt, der neue Glieder und auch Blütenstände bildet; die häutige Hülle um den Blütenstand bei den Lemneae kann als Spatha interpretiert werden (bei den Wolffieae fehlt die Spatha); der Spadix weist eine extreme Reduzierung zu einer einzigen zwittrigen Blüte bei den Wolffieae auf und zu einer Zwitterblüte und einer männlichen Blüte (mit nur einem Staubgefäß) bei den Lemneae. Die fossile Gattung *Limnobiophyllum* ist viel weniger reduziert, hat lange Ausläufer (Stolonen) und einfache sowie verzweigte Wurzeln, während die Lemneae nur einfache Wurzeln haben und die Wolffieae wurzellos sind; der normalerweise sehr kurze Stiel (ziemlich lang bei *Lemna trisulca*) der neuen Glieder der Lemneae kann als Ausläufer (Stolon) betrachtet werden. Die Gattung *Limnobiophyllum* und die Triben Lemneae sowie Wolffieae zeigen in ihrer Evolution eine klare Linie zu einer starken Reduktion ihrer Organe.

Schlüsselwörter: Lemnoideae (Wasserlinsen), lebend, fossil, frei schwimmend, *Pistia*, *Cobbania*, Araceae

1. Introduction and history

The duckweeds were established as a family by S. F. Gray (1821) in the early nineteenth century and later authors have treated them nearly always as a separate family. Engler (1876, 1877) in his early works on Araceae, classified them as a subfamily of Araceae, the Lemnoideae. He was one of the first



Figures 1–3: *Limnobiophyllum scutaturm* (Dawson) Krassilov. **1:** Several fossil plates with coins in order to compare its size, (above left [below the two coins] three plants of extant duckweeds),1 x; **2:** Leaf, note the parallel primary veins and the reticulate secondary veins, 2.5 x; **3:** Note the plant (above) with branched root (middle) and simple roots (above left and right), 1.5 x. Photographs by G. Hoffman.

to include the duckweeds in the Araceae, but later changed his mind and considered them as a separate family (Engler 1889). In the nineteenth and twentieth centuries, monographs on the duckweeds were published by F. Hegelmaier (1868, supplement 1895), E. H. Daubs (1965), E. Landolt (1986), and Landolt & Kandeler (1987). Den Hartog & Van der Plas (1970) published a synopsis, as well as an important contribution to the „Flora Malesiana" (Van der Plas 1971), and S. C. Maheshwari (1956, 1958, and an unpublished thesis) presented several papers on embryological aspects of the group. All these authors interpreted the duckweeds as relatives of the Araceae, and usually placed them in the order Arales. Only A. Lawalrée (1945) viewed the duckweeds as belonging to the Helobiae/Alismatales with their closest relationship to *Najas* (Najadaceae).

In the past the Lemnoideae have been compared with the derived genus *Pistia*, but a basal phylogenetic placement within the Araceae fits better with the character combination of bisexual flowers, free filaments, aperturate pollen grains and the presence of sporopollenin. Fossils of duckweeds such as the genus *Limnobiophyllum* (Figs 1–3, 8, 11, 12, 16) are known already from the Upper Cretaceous: they were larger than their living descendants, had longer stolons, leaves with parallel primary veins and reticulate secondary veins, branched and simple roots, and seeds similar to those of *Spirodela*, *Landoltia* and *Lemna*; the pollen is also aperturate but with an annulate pore, unlike extant duckweeds in which the pollen is ulcerate (pore-like). A single fertile impression fossil even shows an inflorescence with four flowers (Fig. 4), each with six stamens; the spathe is not preserved.

Today, the *Lemna* clade, with its five genera, is considered as subfamily Lemnoideae of the Araceae. Engler (1876) included the Lemnoideae in the Araceae more than 130 years ago, based mainly on vegetative and inflorescence characters. .

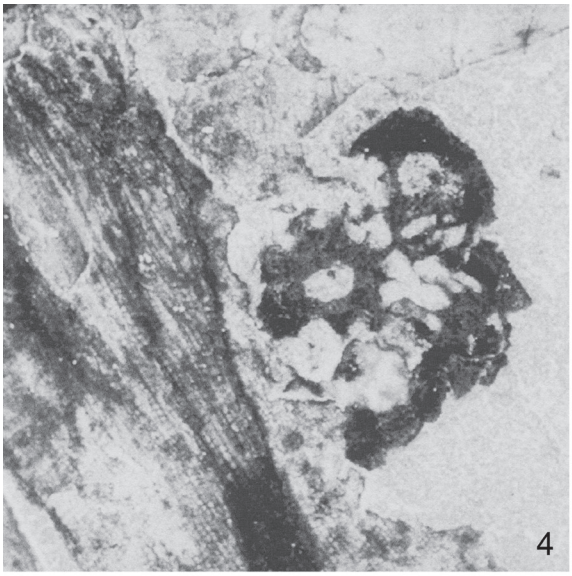
The *Lemna* clade consists of five genera divided into two tribes: the Lemneae, which includes *Spirodela* Schleiden (Fig. 22), *Landoltia* Les & D. J. Crawford (Figs 18, 21, 26), *Lemna* L. (Figs 17, 19, 20, 24); and the Wolffieae, which includes *Wolffiella* Hegelmaier (Figs 31, 32) and *Wolffia* Horkel ex Schleiden (Figs 23, 25, 29, 30). Placement of the Lemnaceae or duckweeds as a subfamily of the Araceae, the Lemnoideae, is strongly supported by molecular data (Barabé et al. 2002; Rothwell et al. 2004; Tam et al. 2004; Cabrera et al. 2008). The latest classification of the Araceae was given by Bogner & Petersen (2007) in volume 30 of the journal „Aroideana".

2. Fossil record of the Lemnoideae

Fossil Lemnoideae such as the genus *Limnobiophyllum* Krassilov (1973), are known from the Late Cretaceous until the Miocene. There are two species: *L. scutatum* (Dawson) Krassilov (Figs 1–4, 8) (Taylor et al. 2009), from North America and East Asia (Russian Far East and Northeast China) known from the Late Cretaceous to the Oligocene, and *L. expansum* (Heer) Kvaček (Figs 11, 12, 16) from European Miocene, although it died out in the Miocene (Fig. 34). The genus *Limnobiophyllum* lived for approximately 50 million years on the earth. Fossil seeds of *Lemna* are known from the Oligocene, Miocene, Pliocene and Quaternary deposits of Eurasia: *Lemna tertiaria* Dorofeev (Dorofeev 1963) from the Oligocene of Siberia, a whole plant from the Miocene described as *Lemna cestmirii* Kvaček (Kvaček 2003) and similar to *L. minor* L. from the Czech Republic, and extant species, e.g. *Lemna gibba* L., *L. minor* L. and *L. trisulca* L. from younger beds (Landolt 1998; Mai 1995; Velichkevich & Zastawniak 2006). The seeds of *Aracites interglacialis* Wieliczk. and *Aracites johnstrupii* (Hartz) P. Nikitin do not belong in the Araceae and are of uncertain affinity. The free floating genera *Limnobiophyllum*, *Lemna* and *Pistia* were distributed together in Eurasia at least during the Oligocene and Miocene, but it remains unclear why *Limnobiophyllum* died out during the Miocene.

Apparently Lemnoideae are a very early offshoot of the Araceae which became adapted to water life as floating plants. The duckweeds living today are highly reduced and have evolved by extreme neoteny, especially in the Wolffieae. *Limnobiophyllum*, with its two species *L. scutatum* (Figs 1–3, 8) (Stockey et al. 1997) and *L. expansum* (Figs 11, 12, 16) (Kvaček 1995), are much larger and have stolons. There are two to three or four helically arranged, pubescent leaves with parallel primary veins (radiating from the base and curving towards the apex) and secondary veins between them which are reticulate. The roots are several, branched or simple. The flowers are bisexual and the seeds (Figs 13, 15) are very similar to those of *Spirodela*, *Landoltia* and *Lemna* and have a ribbed testa (the seeds were described as *Lemnospermum pistiforme* V. P. Nikitin; this kind of seed occurs in the same beds as *Limnobiophyllum scutatum* and *L. expansum* (Fig. 13) (Kvaček 2003). The pollen grains of *Limnobiophyllum* (Figs 5, 7) are globular with a spinulose exine, but the aperture is monoporate and the pore has an annulus (Stockey et al. 1997; Hesse & Zetter 2007). The Lemneae (*Spirodela, Landoltia, Lemna*) are always glabrous, have only primary veins (being too small to have

Figures 4–10 (on page 116): 4–5: *Limnobiophyllum scutatum* (Dawson) Krassilov. **4:** *Limnobiophyllum scutatum*, Plant with four clustered flowers, ca. 150 x; **5:** *Limnobiophyllun scutatum*, two pollen grains, note the spinulose exine and the pore with an annulus (the pollen grains were somewhat depressed during fossilisation), 2000 x; **6:** *Lemna trisulca* L., note the pollen grain with the spinulose exine and an ulcerate aperture (= pore-like aperture) without annulus (ulcerate aperture above left), ca. 2000 x; **7–8:** *Limnobiophyllum scutatum*, **7:** *Limnobiophyllum scutatum*, pore with annulus of the spinulose pollen grain, ca. 4200 x; **8:** *Limnobiophyllum scutatum*, reconstruction of the whole plant, 1.5 x; **9:** *Pistia stratiotes* L., pollen grain, note the inaperturate pollen grain with a plicate exine and strongly undulate frills running the length of the grain. ca. 2400 x; **10:** *Limnobiophyllum scutatum*, two stamens, each with two thecae, ca. 400 x. Photograph 4 by R. A. Stockey, SEM micrographs 5 and 7 by M. Hesse, 6 by M. Grayum, 8 reconstruction (drawing) by R. A. Stockey and G. Hoffman, 9 by W. Barthlott, 10 photograph by G. Hoffman.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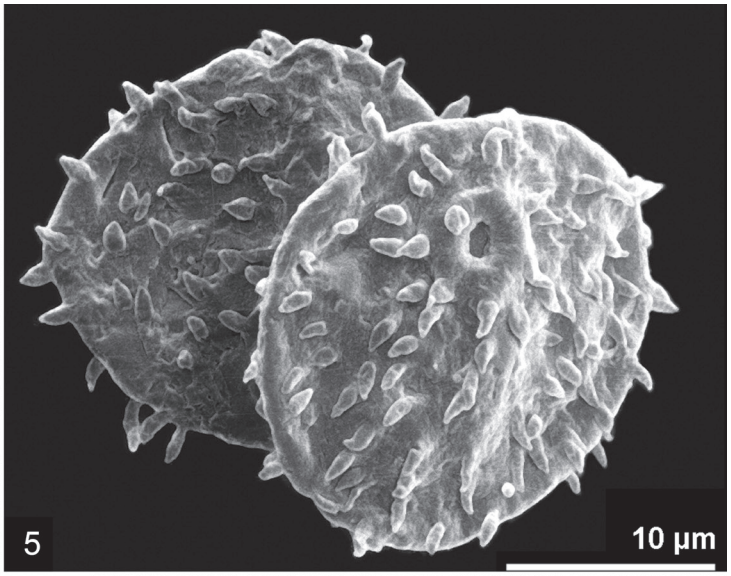
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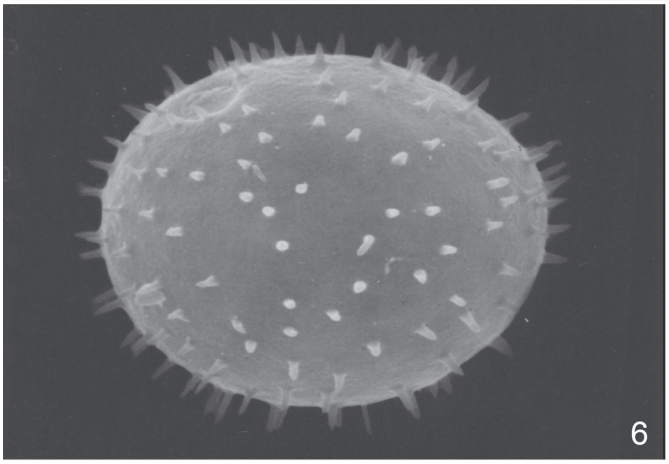
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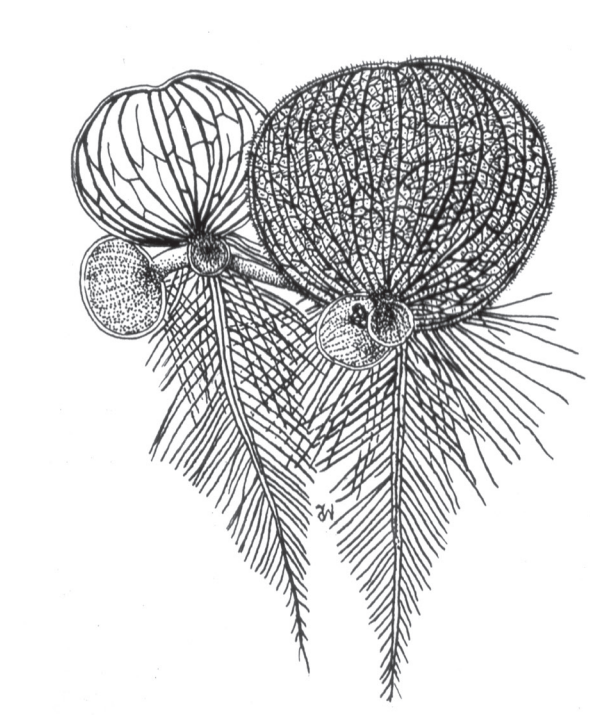
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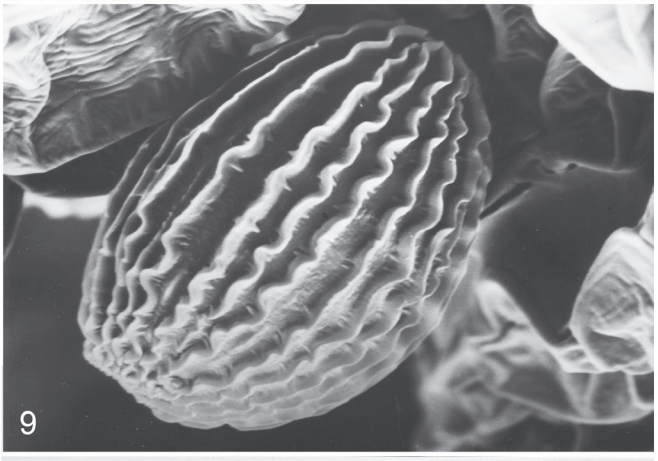
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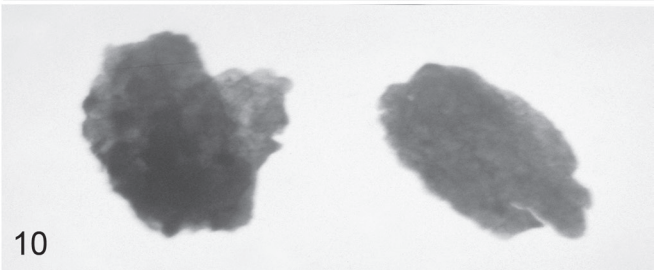
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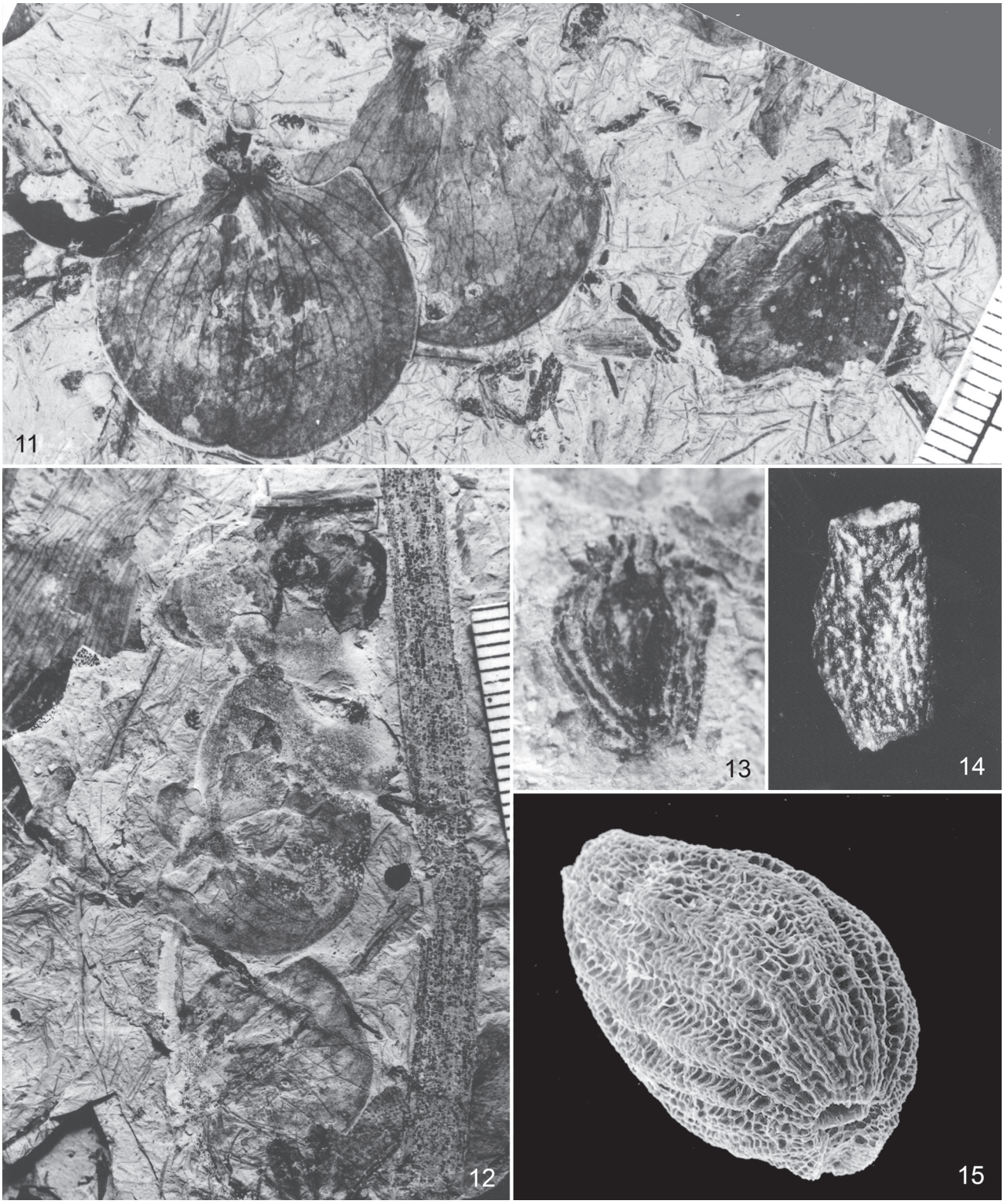
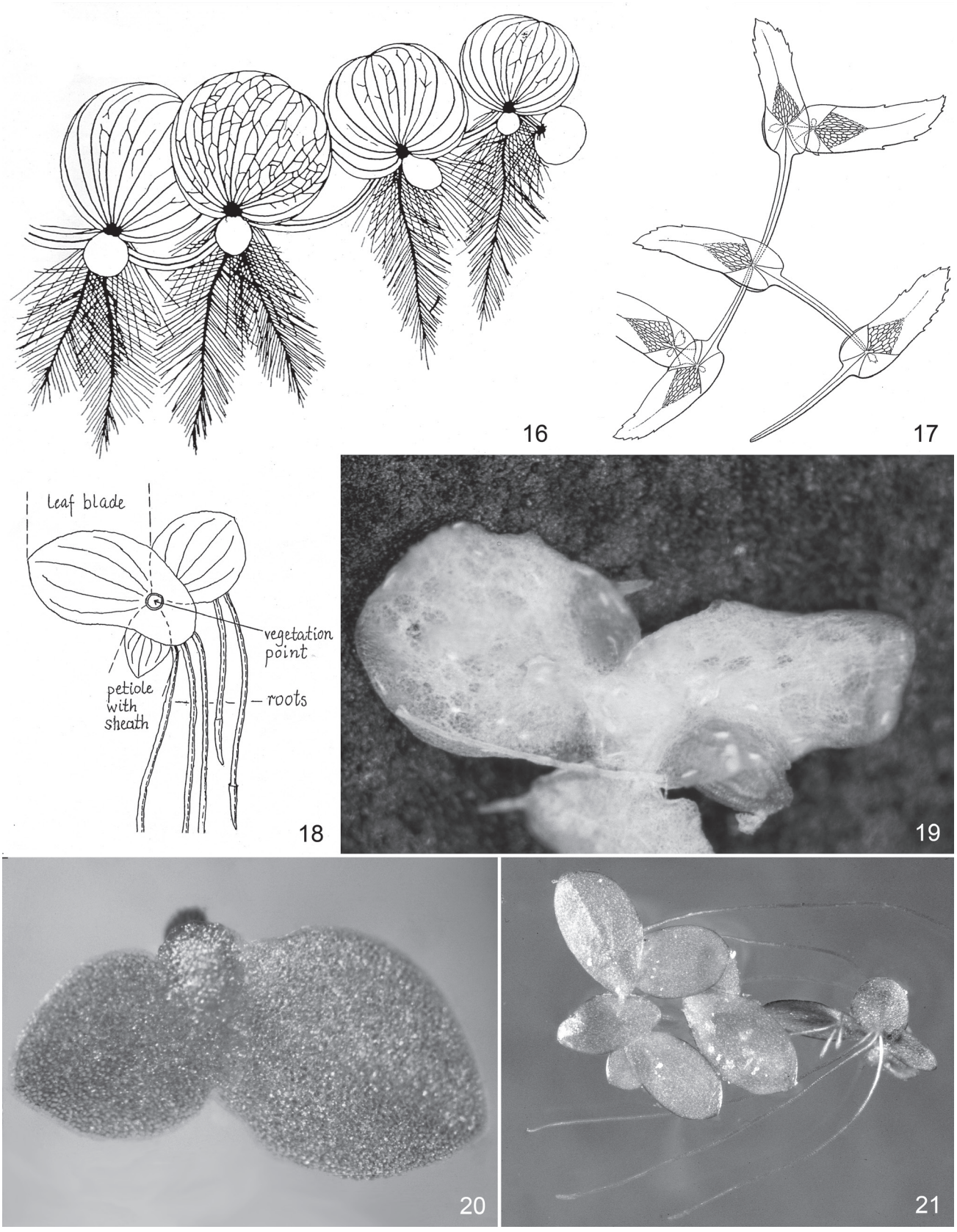


Figures 11–15. 11–13: *Limnobiophyllum expansum* (Heer) Kvaček. **11:** *Limnobiophyllum expansum*, plant with two leaves, note the venation with parallel primary veins and reticulate secondary veins, 2.5 x; **12:** *Limnobiophyllum expansum*, another specimen with a whole plant and with a branched root (left), 2.5 x; **13:** *Limnobiophyllum expansum*, seed, note the ellipsoid to ovoid shape with ribbed testa, 20 x; **14:** *Pistia sibirica* Dorofeev, seed, note the barel-like shape and the typical testa strucuture which is reticulate-alveolate (with small pits), 25 x; **15:** *Lemna gibba* L., seed, note the ovoid to ellipsoid shape with ribbed testa, ca. 100 x. Photographs 10–13 by Z. Kvaček, SEM micrograph 14 by Z. Kvaček, 15 by E. Landolt.



Figures 16–21. 16: *Limnobiophyllum expansum* (Heer) Kvaček, reconstruction of the whole plant, 2.5 x; **17:** *Lemna trisulca* L., whole plant, note the long stipe of the fronds which are homologous to the stolons, 4 x; **18:** *Landoltia punctata* (G. Meyers) Les & D. J. Crawford, diagramatic drawing in order to explain the homologies of the organs, 10 x; **19–20:** *Lemna aequinoctialis* Welwitsch, **19:** *Lemna aequinoctialis*, fruiting plant, note the mature seed (below right); the very thin pericarp decays at maturity and gives the seed free (therefore only fossil seeds are found and not fruits), 15 x; **20:** *Lemna aequinoctialis*, young plant (older seedling) grown from seed; part of the seed still visible (above in the middle), 15 x; **21:** *Landoltia punctata*, free-floating plants, one plant turned over to show the roots (usually there are three to four roots, 6 x. 16 reconstruction by Z. Kvaček, 17 drawing after F. van der Plas, 18 drawing by J. Bogner, photographs 19 and 20 by H.-J. Tillich, photograph 21 by A. Hartl.

secondary veins), simple roots (not branched) and pollen grains quite similar with a spinulose exine, but which are ulcerate, i.e. with a pore-like aperture but no annulus around the pore (Fig. 6). A single fertile impression of *Limnobiophyllum scutatum* shows an inflorescence with four bisexual flowers each with six stamens; the spathe is not preserved (Fig. 4). Since there is only one fossil with four bisexual flowers, it must be expected that the number of flowers is somewhat variable, suggesting a range of three to five flowers. Another single fossil shows a stamen with a long free filament and with pollen *in situ* (Fig. 10). Dispersed fossil pollen of the same type was described as *Pandaniidites* Elsink (Elsink 1968). Aerenchyma is present in *Limnobiophyllum* and in most duckweeds except *Wolffia*. Krassilov et al. (2005) described a third species of *Limnobiophyllum*, *L. dentatum* Krassilov, from the Cretaceous of Israel, but the venation of the single fossil, representing a leaf, is not well preserved, and I hold the opinion that this specimen cannot be determined with certainty; at best it should be considered *incertae sedis*.

3. Homologies of the organs

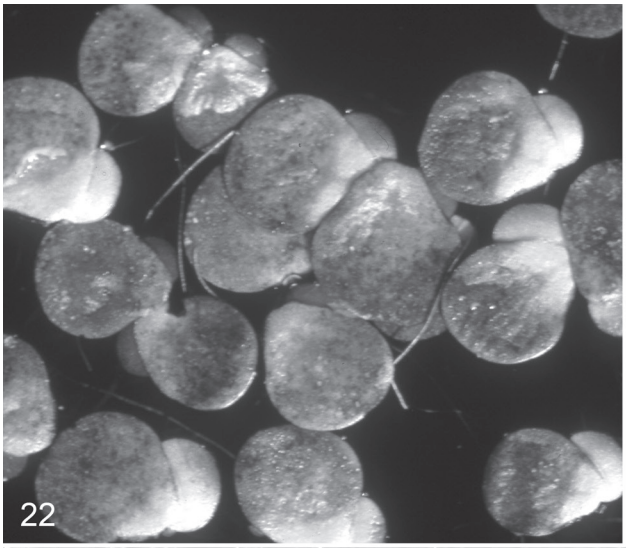
There are three morphological interpretations of the fronds of the Lemnoideae: 1. The frond corresponds to a leaf (e.g. Hoffmann 1840); 2. the frond corresponds to a shoot of leaf-like shape (e.g. Hegelmaier 1868; Brunaud 1974); 3. The basal part of the frond represents a shoot and the distal part a phyllome [= foliar organ] (e.g. Engler 1877; Hegelmaier 1895; Arber 1919; Kandeler, 1979). The flower structures have been interpreted either as a single flower (e.g. Lawalrée 1945; Landolt 1986) or as an inflorescence (e.g. Engler 1877, 1889; Maheshwari & Kapil 1963, and other authors), in which all flowers are reduced to either a single stamen or a single gynoecium.

The homologies of the organs of the Lemneae (*Spirodela, Landoltia, Lemna*) can be interpreted as follows (Fig. 18): the pouch (or pocket) of the frond is homologous to the sheath of the petiole of Araceae (which always have a sheathed petiole); the distal part of the frond is homologous to the veined leaf blade. The shoot is highly reduced, to just a vegetative point in the centre of the plant where new fronds and also the inflorescence(s) develop, also the root or roots are produce there. A stolon connects the daughter frond to the mother frond, seen particularly in *Lemna trisulca* L. (Fig. 17) where the daughter fronds have a long stipe at the base. This stipe is homologous to a stolon and was also interpreted as such an organ, but this stolon is usually very short in other species (e. g. *Spirodela polyrhiza*) or inconspicuous and not visible from outside of the pouch. The membranous envelope around the inflorescence (Fig. 28) can be interpreted as the spathe and the spadix is reduced to a single bisexual flower (with only one stamen) and one male flower (with one stamen) in the Lemneae. The scale at the roots in the genera *Spirodela* and *Landoltia* can be interpreted as a prophyll (a kind of cataphyll). The Wolffieae (*Wolffiella* and *Wolffia*) are more reduced (Figs 23, 25, 29): they are rootless and have fronds without veins. There is only one pouch where the daughter frond appears (Fig. 23), and the inflorescence is borne in a separate cavity on the upper side of the frond (Figs 23, 29); in *Wolffiella welwitschii* (Hegelmaier) Monod there are two cavities (Fig. 31), each of which containing an inflorescence, but there is no spathe, and the single flower is bisexual with one stamen (Hegelmaier 1868; Kuch et al. 2000; Landolt 1986, 1992). Furthermore, the single stamen is monothecal (Fig. 30) and therefore more reduced than in all other Araceae, including the Lemneae, where the anthers are bithecal and each theca has two pollen sacs and thus homologous to the basic angiospermous tetrasporangiate microsporophyll. The shape of the fronds in *Wolffia* is more or less globular to ellipsoid or ovoid boat-shaped (Figs 23, 25, 29), whereas in *Wolffiella* they are long (orbicular, oblong or linear) and flat (Figs 31, 32). The pollen grains have the same structure as in the other duckweeds and the seeds are also ellipsoid although the testa is not really ribbed but more or less reticulate to nearly smooth.

But there is a discrepancy in the flower structure of the Lemneae. The two stamens (rarely three stamens in *Spirodela polyrhiza* (L.) Schleiden [Lacor 1970]) reach maturity at different times (Fig. 28) (Hegelmaier 1868; Shih 1979; Landolt 1986); the Wolffieae have only one stamen. Lacor (1970) reported that in some flowers of *Spirodela polyrhiza* three stamens were found to be of unequal size; therefore these stamens also matures at different time. The maturation of stamens at different time is very unusual for Araceae with bisexual flowers; normally all stamens of a flower mature at the same time. In Araceae with unisexual flowers (Aroideae s.l. and Zamioculcadoideae) all female flowers mature simultaneously, followed by all male flowers, preventing self-pollination. Araceae are always protogynous, suggesting that the two stamens in Lemneae stem from two reduced flowers. Therefore my interpretation of the flowers of the Lemneae is that there is one bisexual flower with one stamen which matures earlier, and a second reduced flower (= male flower) with a single stamen or if sometimes are three stamens in *Spirodela* maturing also at different time, two male flowers must be there then. Ontogenetic studies of young inflorescences of *Lemna aequinoctialis* Welwitsch showed that the primordiae of the two stamens are of different size, the larger one matures earlier and the smaller one later. Developmental genetics may provide further support for this interpretation of the flower structure of the Lemneae.

Observations of bisexual-flowered Araceae indicate that the uppermost flowers of the spadix are often male, as for example in *Calla palustris* L. (with naked bisexual flowers) or *Orontium aquaticum* L. (with perigoniate bisexual flowers). On the other

Figures 22–26: (on page 120): 22: *Spirodela polyrhiza* (L.) Schleiden, free-floating plants, 4 x; **23:** *Wolffia neglecta* Landolt, flowering plants, note the cavity with the inflorescence on the upper surface of the frond containing one gynoecium (pistill) and one stamen, 35 x; **24:** *Lemna trisulca* L.in the natural habitat; this species is floating below the water surface, ca. 0.2 x; **25:** *Wolffia arrhiza* (L.) Horkel ex Wimmer, free-floating plants, 6 x; **26:** *Landoltia punctata* (G. Meyers) Les & D. J. Crawford, flowering plant, 30 x. Photographs 22 and 23 by Ch. Kasselmann, 24 by H. Herkner, 25 by J. Bogner, 26 by an anonymous photographer.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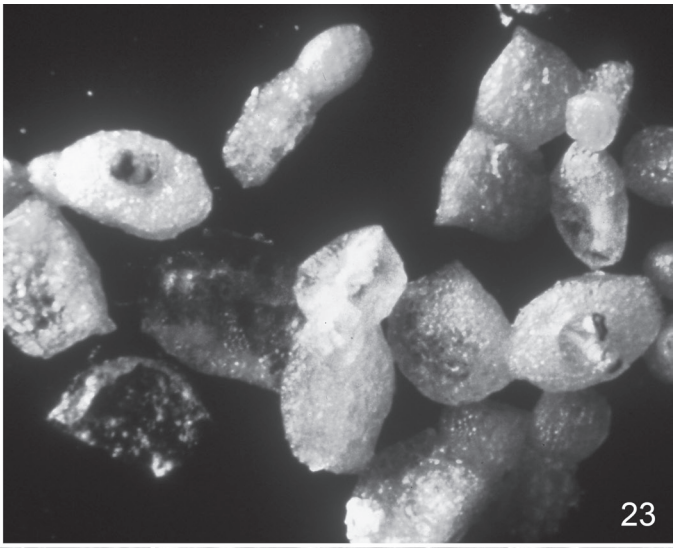
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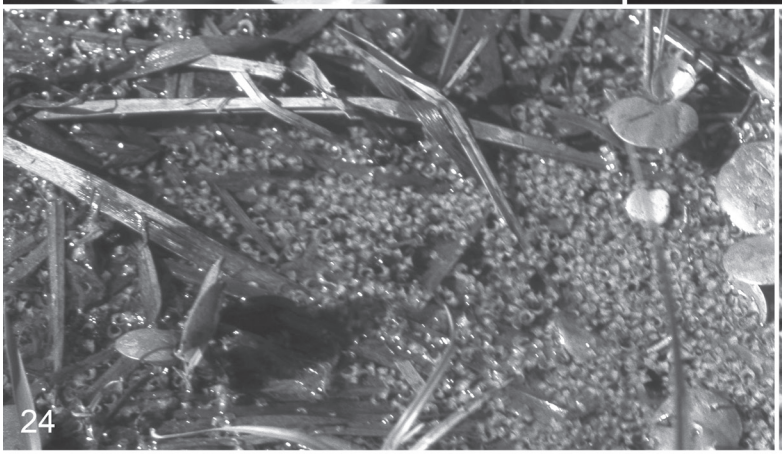
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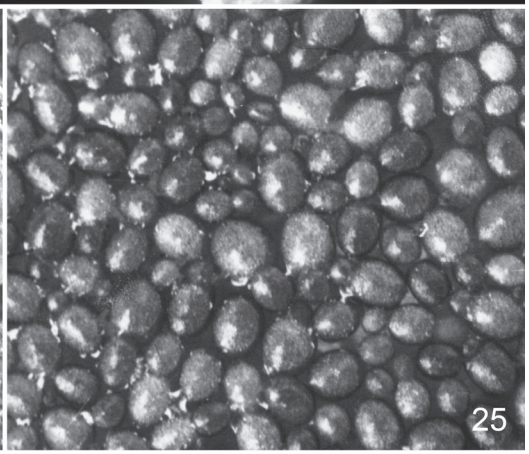
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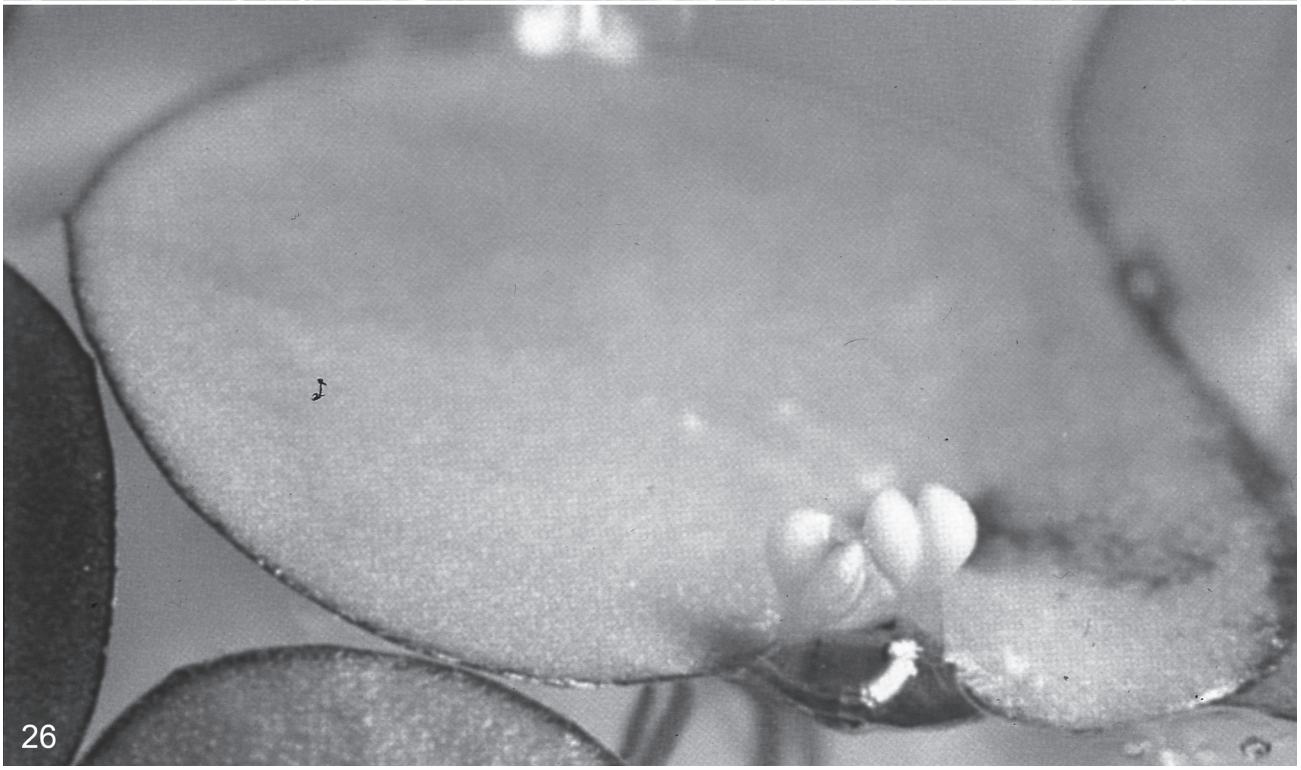
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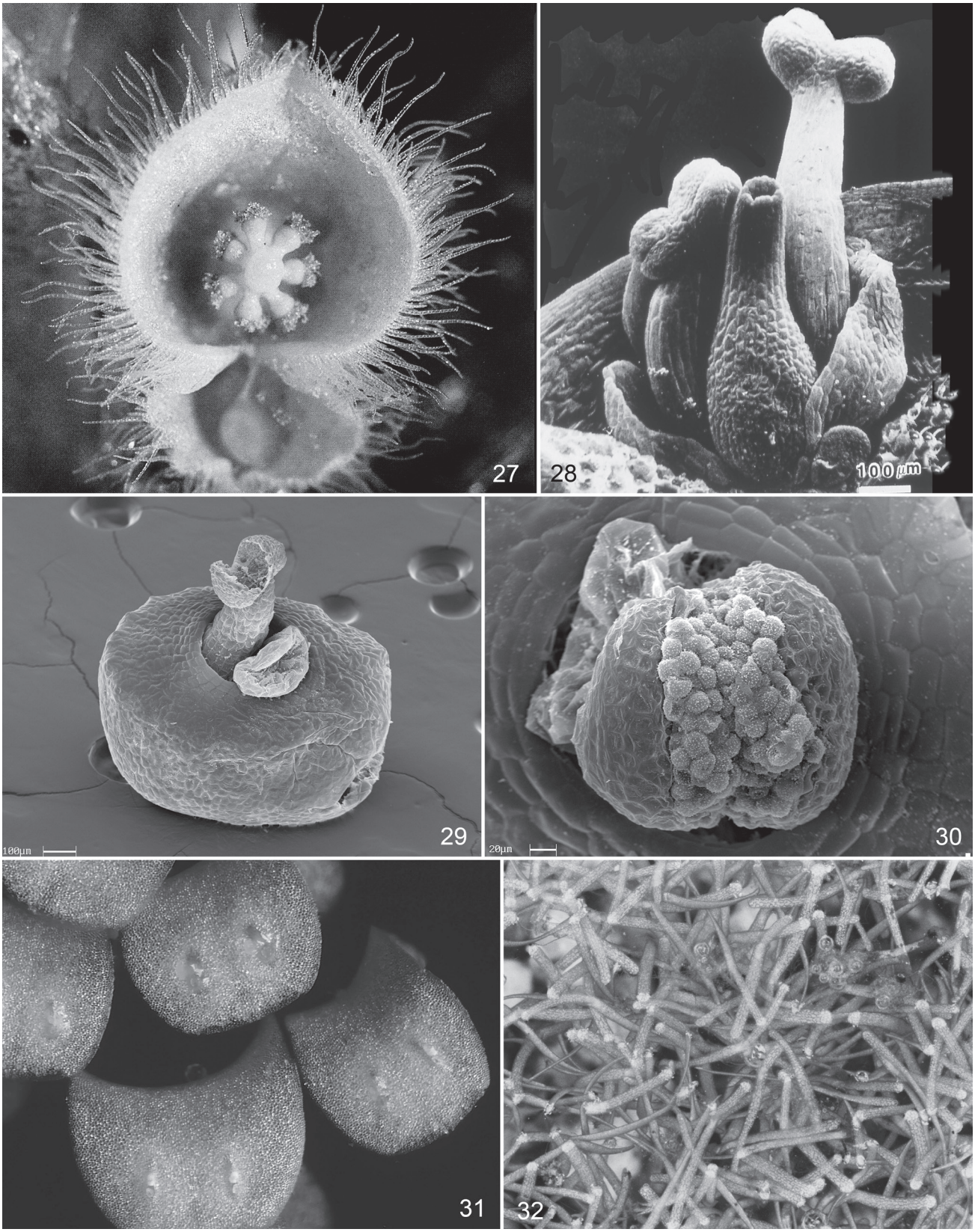


Figures 27–32. 27: *Pistia stratiotes* L., inflorescence, note the constricted and hairy spathe, the synandria (above) each consisting of two connate stamens and (below) the single gynoecium (pistill), 8 x; **28:** *Lemna aequinoctialis* Welwitsch, inflorescence, note the gynoecium (pistill) in the middle, two stamens right and left of different size, surronded by an envelope which is homologous to the spathe, 100 x; **29–30:** *Wolffia elongata* Landolt. **29:** *Wolffia elongata*, flowering plant, note the single stamen and the stigma in a cavity, Landolt no. 9188, from Colombia, 35 x; **30:** *Wolffia elongata*, opened theca with pollen grains, from Landolt no. 9188, ca. 300 x; **31:** *Wolffiella welwitschii* (Hegelmaier) Monod, flowering plants, note the two cavities each with one flower consisting of only one gynoecium (pistill) and one stamen on the upper surface of the fronds, 10 x; **32:** *Wolffiella denticulata* (Hegelmaier) Hegelmaier, free-floating plants, 5 x. Photograph 27 by K. Horst, SEM micrograph 28 by C. Y. Shih, 29 and 30 by A. Kocyan; photograph 31 by Ch. Kasselmann, 32 by J. Bogner.

hand, as already mentioned, the fossil *Limnobiophyllum scutatum* has clearly bisexual flowers and molecular studies strongly support the view that the duckweeds have bisexual flowers since they are nested among bisexual-flowered subfamilies. E. Landolt (1986, 1998) also considered duckweed flowers to be bisexual, an interpretation with which I agree

4. The position of *Pistia*

In the past, the Lemnoideae have often been compared morphologically and anatomically with the genus *Pistia* (Figs 33, 38), and a closer relationship was usually inferred. However, the Lemnoideae have a more basal position in the Araceae between the subfamilies Orontioideae and Pothoideae (Cabrera et al. 2008), whereas *Pistia* belongs to the advanced Aroideae s. l. which have unisexual flowers, inaperturate pollen grains (Fig. 9), and variously modified spathes. The main characters distinguishing *Pistia* from the Lemnoideae are barrel-shaped, subtruncate seeds with an reticulate-alveolate testa (Fig. 14), ellipsoid inaperturate pollen grains with a plicate exine and strongly undulate frills running the length of the grain (Fig. 9), pollen lacking sporopollenin, and male flowers consisting of two stamens connate into a synandrium; there is only one naked female flower consisting of a single gynoecium, the spathe is well-developed and has a constriction (Fig. 27). By contrast, Lemneae have ellipsoid seeds with a ribbed testa (Fig. 15), globular to ellipsoid aperturate pollen grains with a spinulose exine (ulcerate in Lemneae [Fig. 6] and Wolffieae, but monoporate in the fossil *Limnobiophyllum* [Figs 5, 7]) and sporopollenin, stamens with free filaments, bisexual flowers, the spathe represented by a membranous envelope lacking a constriction (Fig. 28). *Pistia* also has well-developed leaves which are shortly petiolate and hairy, whereas the Lemneae have quite reduced fronds (see above) which are glabrous (but also with hairs (pubescent) in *Limnobiophyllum*). Molecular data support the view that *Pistia* is not closely related to the duckweeds (Barabé et al. 2002; Rothwell et al. 2004; Cabrera et al. 2008).

Fossil fruits and seeds of the genus *Pistia*, described as *Pistia sibirica* Dorofeev (Fig. 14), are known from the Oligocene and Miocene of Eurasia (Dorofeev 1963; Mai 1995; Kvaček & Bogner 2008). The first monographer of the Araceae, H. W. Schott (1794–1865) did not treat the duckweeds nor did he include *Pistia* in his final major work (Schott 1860); *Pistia* had already been established in a separate family, the Pistiaceae, by C. Agardh in 1822. Engler (1876, 1877, 1889, 1920) included *Pistia* in a separate subfamily, the Pistioideae, within the Araceae. Today *Pistia* is included in the enlarged subfamily Aroideae s. l. (Mayo et al. 1997; Bogner & Petersen 2007).

5. Taxonomic change

Kvaček (2003) described a subfamily for the fossil genus *Limnobiophyllum*, Limnobiophylloideae, but this fossil genus should better be placed within the Lemnoideae as a separate tribe:

Tribe Limnobiophylleae (Kvaček) Bogner, stat. et comb. nov.

Basionym: Limnobiophylloideae Kvaček, 2003, Courier Forschungsinstitut Senckenberg 241: 262.

Type: *Limnobiophyllum scutatum* (Dawson) Krassilov, 2003

6. Other affinities

As shown in this paper, the Lemnoideae and *Pistia* of the Aroideae s. l. certainly belong to the family Araceae, but there is very probably a third independent evolutionary line of free-floating plants associated with the Araceae. This species originated in the Late Cretaceous of North America and East Asia (Russian Far East and Northeast China in the region of the Amur River or Heilongjiang River [Chinese name of the Amur]; see Stockey et al. 2007; Sun et al. 2007; Akhmetiev, pers. comm.), but apparently died out before the Cretaceous/Tertiary boundary, according to existing specimens. The fossils were first already described in the nineteenth century as *Pistia corrugata* Lesquereux (1876, 1878), but certainly do not belong to the genus *Pistia* because of distinct differences in leaf venation (Figs 35–39, 41). The plant consists of a rosette of leaves with stolons and branched roots (Fig. 40). The petiole has a sheath (Fig. 39[left]) and the leaf blades are trumpet-shaped (Fig. 39), pubescent and contain aerenchyma. The leaf venation is completely reticulated in veins of all orders (Figs 37, 39, 41), with three collective veins along the margins (Fig. 36), but a midvein (midrib) is lacking (Figs 35, 37, 39, 41). These fossils have recently been studied comprehensively by Stockey et al. (2007) and were transferred to a separate genus as *Cobbania corrugata* (Lesquereux) Stockey, Rothwell & Johnson. This species is very distinct from all other known free-floating plants. No reproductive organs are known with certainty; fruits and ellipsoid seeds with a smooth testa have been found associated but not attached to fossil plants in the Dinosaur Park, Alberta, Canada. The exact systematic position of *Cobbania corrugata* thus remains unknown. Reproductive organs are said to have been found in the Russian Far East (Krassilov, pers. comm..) but these fossils have not yet been studied.

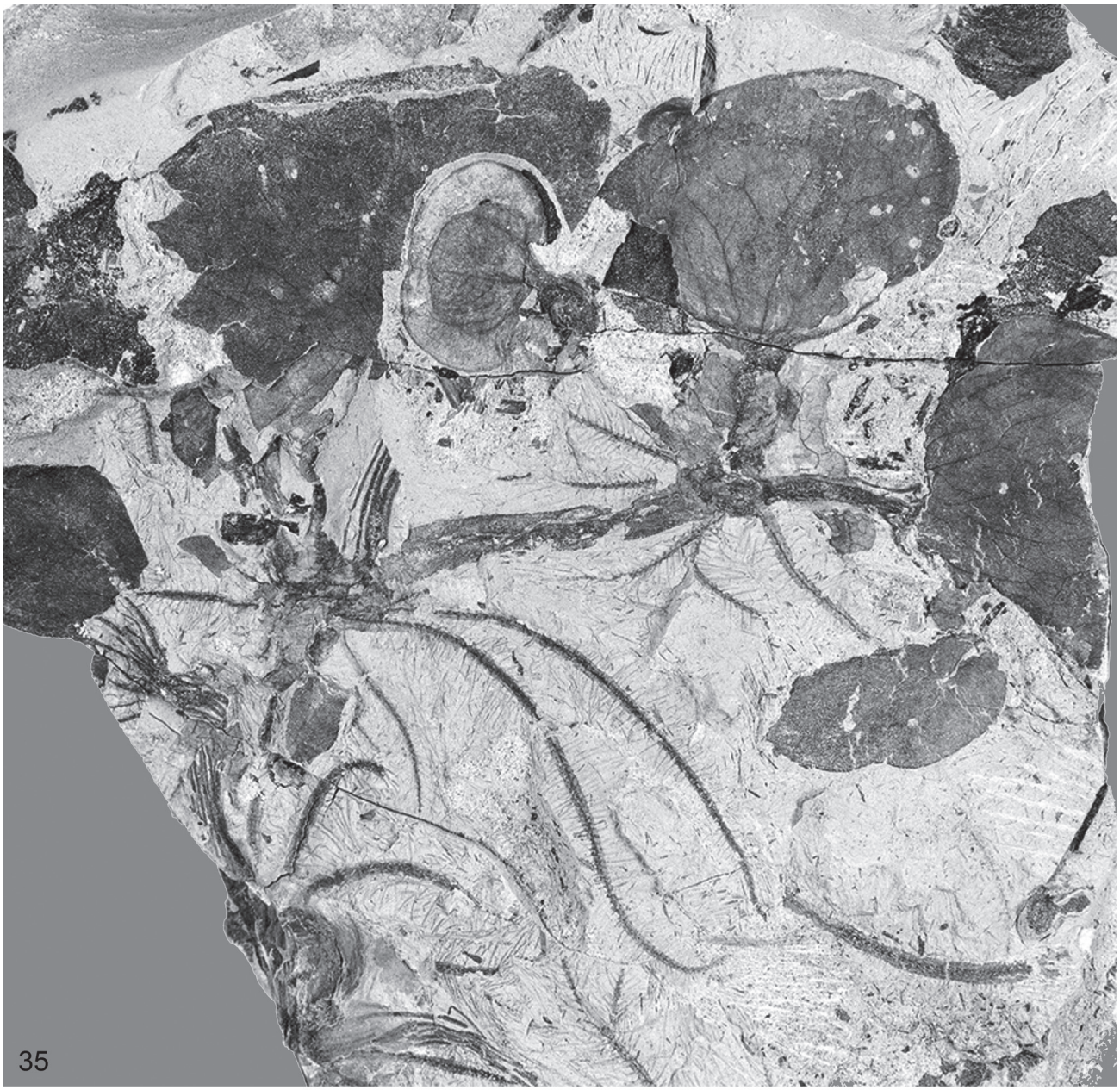
7. Remarks

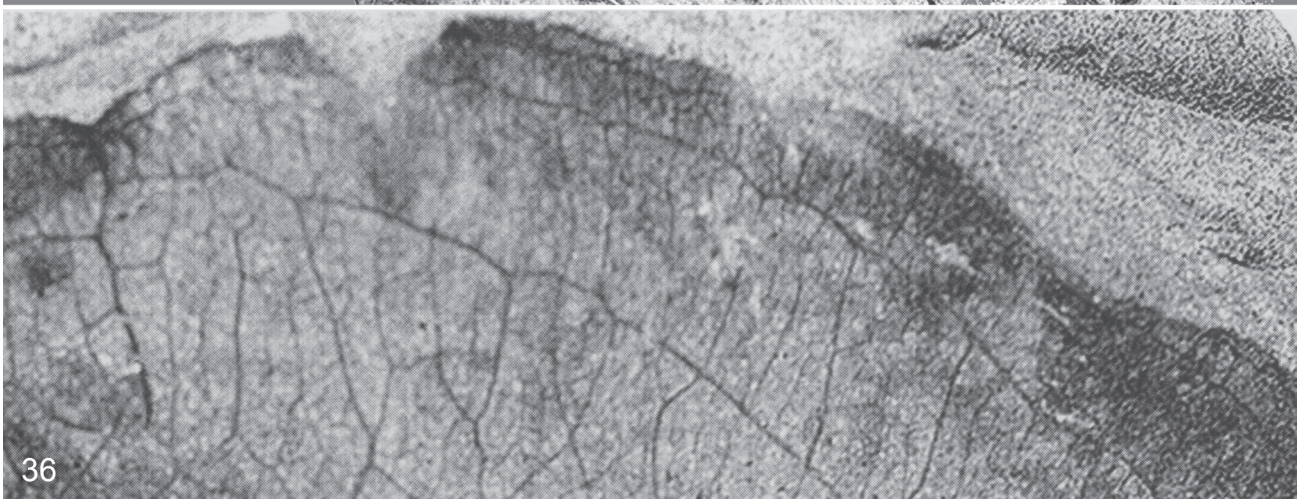
The Lemnoideae contain the smallest flowering plants in the genus *Wolffia*. *Wolffia arrhiza* (L.) Horkel ex Wimmer (Fig. 25) is often said to be the smallest flowering plant, but this is not the case (Strasburger 2008). There are much smaller species in this genus, with the following frond dimensions (length/width/thickness): *W. globosa* (Roxb.) Hartog & Plas has fronds with dimensions 0.8/0.6/0.7 mm and *W. angusta* Landolt has fronds with 0.8/0.4/1.0 mm (Landolt 1998), while in *W. arrhiza* they are up to 1.5 mm long and 1.2 mm wide.

8. Conclusions

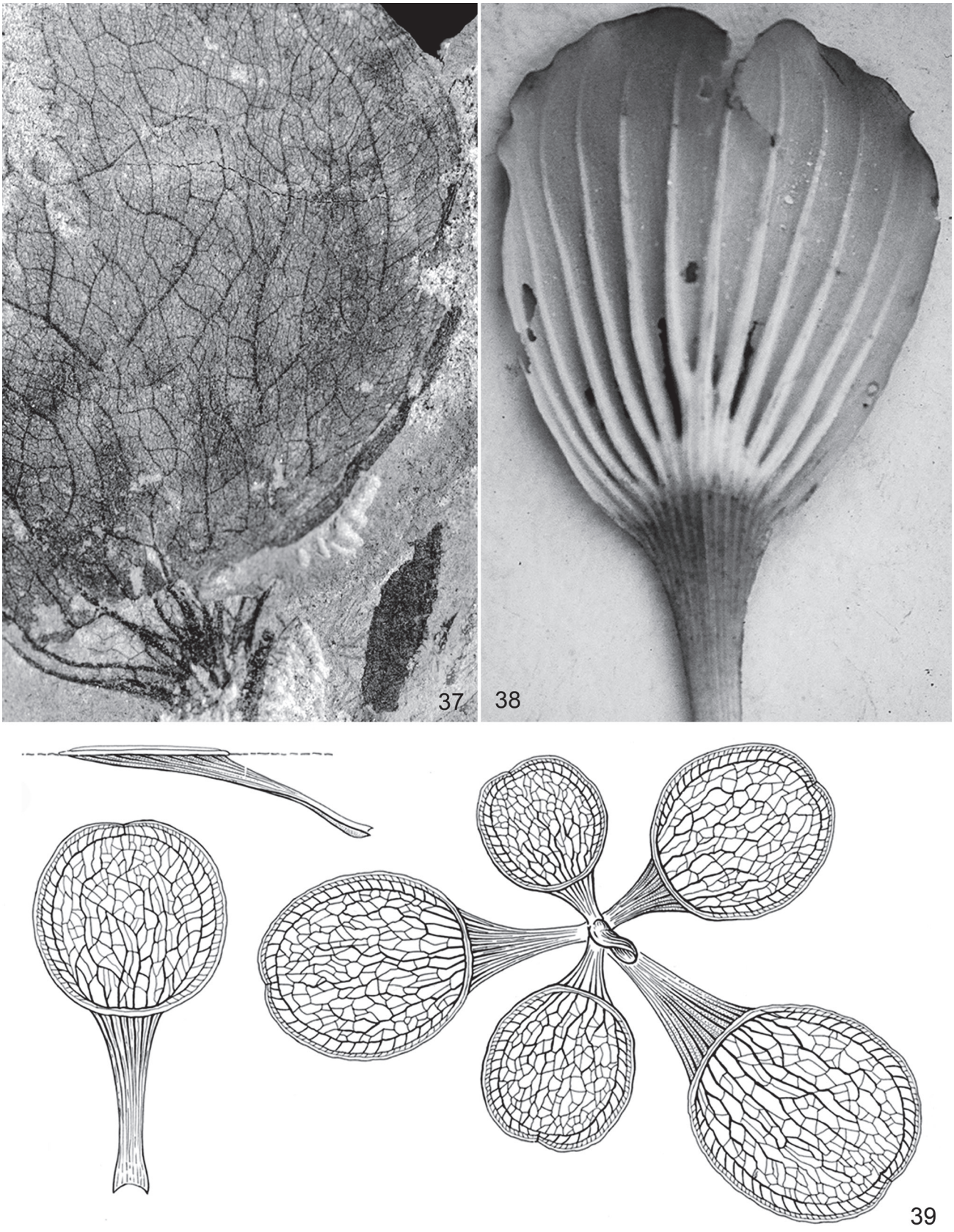
The systematic position of the Lemnoideae is as a near-basal clade within the bisexual-flowered Araceae, well supported by

Figures 33–34. 33: Carpet of free-floating plants of *Pistia stratiotes* L. (behind), *Limnobium laevigatum* (Willdenow) Heine and *Salvinia auriculata* Aublet in a natural habitat in Peru, 0.1 x; **33:** Reconstruction of an Early Miocene aquatic vegetation (fresh water lake) in Bohemia: 1 = *Salvinia reussii* Ettingshausen, 2 = *Azolla* sp., 3 = *Lemna cestmirii* Kvaček, 4 = *Limnobiophyllum expansum* (Heer) Kvaček, 5 = *Elephantosotis dvorakii* Kvaček, 6 = *Hydrochariphyllum buzekii* Kvaček, 7 = unidentified monocot, 8 = *Salix haidingeri* Ettingshausen, 9 = *Pistia sibirica* Dorofeev, 10 = *Stratiotes* sp. Photograph 33 by Ch. Kasselmann, 34 reconstruction by Z. Kvaček.





Figures 35–36: *Cobbania corrugata* (Lesquereux) Stockey, Rothwell & K. R. Johnson, **34:** whole plants connected by a stolon, note also the branched roots, 1,4 x; **36:** part of a leaf blade, note the reticulate venation and three collective veins along the margin, 6 x. Photographs by R. A. Stockey.



Figures 37–39. 37: *Cobbania corrugata* (Lesquereux) Stockey, Rothwell & K. R. Johnson, leaf blade, note the reticulate venation, lacking a midrib (midvein), 2.5; **38:** *Pistia stratiotes* L. leaf from the abaxial side, note the subparallel primary veins, 1 x; **39:** *Cobbania corrugata*, reconstruction: right whole plant seen from above, left single leaf, note the petiole with a sheath at its base and above left one leaf in the position as it is floating at the water surface, ca. 0.8 x. Photographs 37 and 38 by R. A. Stockey, 39 reconstruction by R. A. Stockey.

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Figures 40–41. 40: *Cobbania corrugata* (Lesquereux) Stockey, Rothwell & K. R. Johnson, reconstruction: two plants connected by a stolon and with branched roots as they are floating at the water surface, 0.8 x; **41:** *Cobbania corrugata*, floating plants inspected by an *Ornithomimus* dinosaur. The quarry in the Dinosaur Provincial Park, Alberta (Canada), produced numerous whole plants and the most complete skeleton of this dinosaur. 40 reconstruction by R. A. Stockey, 41 image by Marjorie Leggin.

molecular analyses. The ancestors of the Lemnoideae (with the genus *Limnobiophyllum*) go back to the Late Cretaceous. The Lemnoideae living today are highly reduced plants that are best interpreted as partly neotenous and as highly adapted to their aquatic habitat (Fig. 34). The inflorescence is here interpreted as one bisexual flower in the Wolffieae and as one bisexual flower (with a single stamen) and one male flower (with a single stamen) in the Lemneae. *Limnobiophyllum* has an inflorescence with a few bisexual flowers, each with six stamens.

The genus *Pistia* belongs to the advanced Aroideae s. l. which have unisexual flowers and is not closely related to the Lemnoideae, having originated from a different evolutionary line which otherwise did not include free-floating plants. There is very probably a third evolutionary line of Araceae which evolved into free-floating plants with *Cobbania corrugata* (Figs 35, 39–41). It appeared in the Late Cretaceous and died out before the Cretaceous/Tertiary boundary. Reproductive organs are not yet known with certainty.

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