THE AUSTRALIAN MYRIOPHYLLUM VERRUCOSUM LINDLEY IN BRITAIN

By J. P. M. Brenan and J. F. G. Chapple.

On 20th July 1946 the B.E.C. Excursion, under the leadership of Dr J. G. Dony, visited a large disused gravel-pit near Eaton Socon, Bedfordshire (v.-c. 30). The excavations from which the gravel had been taken had filled with water and were fairly deep. In one of these a mass of aquatic vegetation grew near the margin which, on examination, proved to consist largely of two species of *Myriophyllum*. One was quickly identified as *M. spicatum* L. in good fruiting condition; the other, mainly in flower and with immature fruits, proved puzzling, and brought forth many suggestions as to its identity; *M. verticillatum* L. var. *pectinatum* DC. being the commonest suggestion. Diligent search was made, without success, for ripe fruits.

On returning to Oxford, the material obtained was examined by one of us (Brenan), and could not be matched with any state of *M. verticillatum* to which, in the field, it appeared to be closest. Reference was then made to A. K. Schindler's (1905) treatment of *Haloragaceae* in *Das Pflanzenreich*, and the plant appeared to key down by this to either *M. verrucosum* Lindl. or *M. elatinoides* Gaudich. Comparison with specimens of *M. elatinoides* in the Fielding Herbarium, Oxford, ruled out the possibility of the Eaton Socon plant being this species, on account of the larger leaves and almost entire floral bracts of the former, but it did show striking similarities to a small piece of a plant with well-developed fruits labelled *M. verrucosum* Lindl. Our Eaton Socon material, with immature fruits, did not show the characteristic tubercles on the mericarps, and it was therefore decided to collect more and riper material at a later date.

Accordingly, the locality was visited again on 11th August in the company of Mr G. M. Ash and Dr J. G. Dony, but the plant in the original pool was found to show very few fruiting spikes. However, only a few yards away on the edge of the same pool, the plant was found in a dwarfed terrestrial state growing on wet gravel and producing an abundance of mature fruits which showed clearly the characteristic tubercles and the whitish line on the back of each mericarp. The plant was also found in a similar terrestrial state on the edge of another pool in the same gravel-pit, and in deep water in a third small pool.

Subsequently Dr J. G. Dony sent us some material of *Myriophyllum* from the Luton Museum Herbarium. Among this were two sheets labelled *M. verticillatum* L. from Eaton Socon, collected in 1944 and 1945, which are unquestionably *M. verrucosum*.

Through the kindness of Dr W. B. Turrill, Keeper of the Herbarium, Royal Botanic Gardens, Kew, a specimen of *M. verrucosum* Lindl. from the

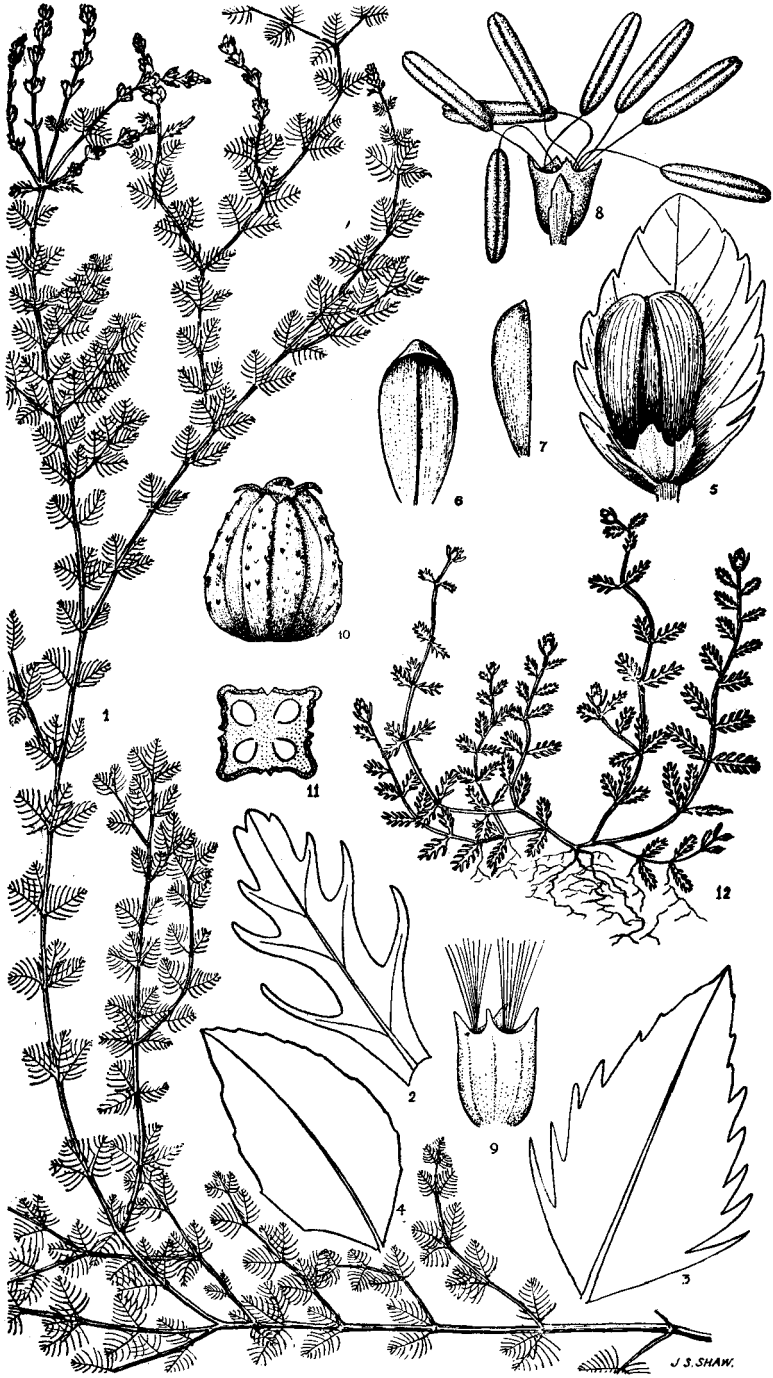

Fig. 1, upper portion of submerged plant, habit, *half natural size*; 2, 3, 4, bracts from different positions on spike from below upwards, ×9; 5, bract and unopened flower, viewed from axial side, ×8; 6, single petal, ventral view, ×8; 7, single petal, side view, ×8; 8, flower, early stage, petals removed, showing stamens, calyx and bracteoles, ×8; 9, flower, late stage, stamens fallen, showing elongate stigmatic hairs, ×9; 10, fruit, ×7½; 11, fruit, diagram of transverse section; 12, terrestrial plant, habit, *half natural size*.

type collection ("Sub-Tropical New Holland," *Lt.-Col. Sir T. L. Mitchell*, 1846; Herb. Bentham) was obtained on loan. Comparison of the Eaton Socon plant with this left no doubt of their identity, and showed that *M. verrucosum* Lindl. had been found in Britain and for the first time in the Northern Hemisphere. A good many other Australian specimens of *M. verrucosum* were subsequently seen, including several representing an apparently terrestrial condition similar to that seen at Eaton Socon.

M. verrucosum was first published by J. Lindley in Mitchell (1848), from specimens collected by Lt.-Col. Sir T. L. Mitchell in Queensland. It was described as follows:—

> "Foliis submersis capillaceo-multifidis, emersis ternatim verticillatis ovatis pinnatifidis, floribus octandris, fructibus tuberculatis."

M. verrucosum has, apparently, only been figured once before, by Williamson (1928), fig. 5 on p. 327. As this figure is small, sketchy, and without dissections we feel that a further figure of *M. verrucosum* will be useful, and we are grateful to Mr J. S. Shaw for preparing the plate of the Eaton Socon plant reproduced here.

We have drawn up the following description entirely from British material, indicating, where necessary, the few discrepancies with Schindler's excellent description.

MYRIOPHYLLUM VERRUCOSUM Lindl. An *aquatic herb*, submerged except for the inflorescences, or ± entirely emersed when growing on exposed mud or gravel close to water. *Stems* of the submerged plants caespitose at base (at least sometimes), moderately robust, up to about 50-60 cm. long in the British plants (up to 1 m. long, *teste* Schindler), about 1-2 mm. in diameter, often ± slightly swollen between the nodes, suberect, rooting at the lowermost nodes, branched from the base upwards and especially in the upper part, lateral branches arising singly or in pairs; stems often blackish and ± defoliated below, whitish-green above, terete or nearly so in section, glabrous, often with numerous, scattered, very minute, brown dots even on the younger parts (apparently due to disease); stems of the emersed plants short, up to 10 cm. long, decumbent (a few cm. high), slender, rooting freely from the lower nodes, profusely branched especially below, pale green or ± tinged with bright red-purple. *Leaves* on submerged plants in whorls of 3 (3-5 *teste* Schindler), crowded and longer than the internodes on the barren shoots, less crowded and shorter than internodes on flowering shoots and on lower parts of stem, up to c. 9 mm. long × 10-13 mm. wide (up to 4 cm. long, *teste* Schindler), deep green to olive, glabrous, sessile, rigid, ± upcurved, short, very broadly triangular in outline, smaller towards bases of shoots and somewhat so towards apices, pinnatipartite; rhachis linear, with about 4-9 linear-subulate, slightly forward-curved, acute segments arising alternately or opposite one another on each side of the rhachis, the lowermost segments up to 7.5 mm. long, the upper ones rapidly but regularly decreasing in length, the upper-

most about 1 mm. long; leaves on the emersed plants ternate to paired and opposite or even alternate, usually pale green or ± purple-tinged, and usually with a broader rhachis and shorter, broader, and often fewer segments. *Inflorescences* (of submerged plants) terminal, elongating, up to c. 18 cm. long (but usually shorter), nodes crowded towards apex, more spaced below; bracts normally ternate, occasionally opposite, 2-8 × 1.25-3 mm., broadly ovate to elliptic or obovate-elliptic, obtuse at apex, densely but microscopically papillose with projecting epidermal cells, the lower bracts pale glaucous-green, incise-serrate with the undivided portion ovate to oblong, the median and upper bracts pale glaucous-pink with green points to the teeth or a narrow green margin, ± serrate, the uppermost subentire; flowering nodes usually separated from the normal submerged sterile nodes by a few to several nodes bearing intermediate leaves with broader rhachides than the normal submerged leaves; emersed plants without any clear division into flowering and sterile parts, the flowers extending down to near the base of the plants. *Flowers* all apparently hermaphrodite, solitary in each bract axil, 1-3 per node, subsessile. *Bracteoles* 2, c. 0.75-1 mm. long × c. 0.3 mm. wide, whitish, narrowly ovate to oblong, ± serrate, subacute at apex. *Calyx* lobes 4, c. 0.3 mm. long, minute, whitish, oblong or ± triangular, ± serrate. *Petals* 4, entire, pinkish-green, 2.75 mm. × 1.4 mm., obovate, with a single central nerve almost reaching the rounded, hooded apex, papillose on back (like the bracts). *Stamens* 8; filaments filiform, c. 0.75 mm. long; anthers 1.3-2 mm. × c. 0.3-0.7 mm., yellow. Styles 4, c. 0.2-0.3 mm. long, ± bluntly conical, connivent, at first (when stamens are dehiscing) almost smooth, later (when stamens have withered) densely clothed with elongate hair-like stigmatic papillae towards apex. *Ovary* inferior, cup-shaped, 4-sulcate, sulci opposite the sepals, c. 0.5 mm. long and 1 mm. wide at apex. *Fruit* up to 1.5 mm. long and 1.75 mm. wide, with persistent bracteoles at base, broadly ovate-truncate, bluntly four-lobed at apex with the persistent styles; tetragonal in cross-section, ultimately separating into four one-seeded mericarps; mericarps prominently, bluntly and longitudinally ridged on back, ridge becoming acute, narrower and more evident when dry, and with a less prominent ridge along the commissure, minutely and bluntly tubercled on the outer faces, purplish-red on faces and cream to grey on ridges.

V.-c. 30, Beds.; gravel-pit, Eaton Socon, 30th August 1944, *J. G. Dony*; same locality, 3rd August 1945, *E. Milne-Redhead* and *J. G. Dony*, both in Herb. Luton Museum as *M. verticillatum* L.: large pools in gravel-pit near Eaton Socon, 20th July 1946, *J. P. M. Brenan* No. 7343, and *J. F. G. Chapple* No. 467205 (and others—B.E.C. Excursion); 11th August 1946, *J. P. M. Brenan* No. 7343A and *J. F. G. Chapple* No. 468119; specimens of both gatherings are in Herb. Oxford, and in Herb. Brenan.

M. verrucosum appears to be confined to Australia where, according to Schindler (1905) it occurs in all the states except Central Australia.

Black (1926) says that it is found throughout South Australia and extends to the far North. Ewart (1930) says that it is widely spread in North-east Victoria. Williamson (1928) gives a similar distribution for this state. Bailey (1900) for Queensland cites specimens from Mount Elliott, Balonne River at St George's Bridge, and Moreton Bay, but says that it is common.

Schindler (1905) divides the genus *Myriophyllum* into three subgenera. *M. verrucosum* comes under the subgenus *Eumyriophyllum* Schindler, characterised by hermaphrodite (or, by reduction, unisexual) flowers, 4 or 8 stamens with broadly linear, not elliptic, anthers, and a 4-partite fruit; the other two subgenera have unisexual flowers, 2 or 4 stamens with elliptic anthers not more than thrice as long as broad, the leaves never whorled and the fruit 2- to 4-partite. Under *Eumyriophyllum* there are two sections, *Pentapteris* DC. emend. O. Kuntze, and *Tessaronia* Schindler, characterised by having eight and four stamens respectively. *Pentapteris*, to which *M. verrucosum* belongs, is divided into four subsections, based principally on the arrangement of the leaves, and also on the shape, surface, and persistence of the mericarps. Of these our plant belongs to the subsection *Spondylophyllum* Torrey & Gray on account of its normally verticillate leaves and flowers, and on the prolonged coherence of its mericarps, which are neither cylindrical nor smooth. A further division is made into two series, of which *M. verrucosum* belongs to the second series *Anisophylleae* Schindler on account of the well-developed laminae of nearly all the bracts, and its position is further limited by the marked distinction between the bracts and the submerged leaves, also by the former being sessile with the lower ones pinnatifid.

The species most closely related to *M. verrucosum*, and with which it might easily be confused, is *M. elatinoides* Gaudich., which is widely distributed in the southern Hemisphere (except Africa), extending north to Mexico and Oregon (Fernald (1919)). The principal character distinguishing *M. elatinoides* is the smooth, rounded, not tubercular or ridged, back to each mericarp. In addition, the bracts are larger and mostly subentire, and the plant as a whole is more robust. Williamson (1928) says that *M. verrucosum* " resembles *M. elatinoides* in miniature, with finer submerged leaves." The leaves of all the material that we have seen of *M. verrucosum* are considerably shorter (up to 8 mm.) than those of *M. elatinoides* (10-15 mm.), although Schindler (1905) describes the leaves of the former as being up to 40 mm. long; no material, however, that we have seen of *M. verrucosum* even approaches this length. If Schindler's synonymy is correct, the name *M. elatinoides* Gaudich. must be replaced by the earlier *M. quitense* H.B.K.; 1823: *Nov. Gen. et Sp. Pl.*, *6*, 89, which was based on a sterile specimen from the district of Guancabamba (i.e., Huancabamba, which, although described as on the Quitonian Andes, is now in northern Peru: see Sandwith (1926)). It seems unwise to adopt this name until its identity has been confirmed, since the original description is so indefinite.

M. verrucosum is less closely related to any of the British species, but it may be useful to mention the main points of difference. The closest relative among these is *M. spicatum* L., which differs in the much larger submerged leaves (up to 35 mm. long), mostly in fours, in the entire bracts, which are shorter than the, normally hermaphrodite, flowers, and in the larger fruits, not ridged on the back of the mericarps. *M. verticillatum* L. differs from *M. verrucosum* very obviously in its simple or slightly branched stem, much more robust habit, with longer, 4-5-nate leaves, and in the bracts often being similar in size and cutting to the submerged leaves, or, if reduced, then with the rhachis at most narrowly triangular and not dilated into an ovate lamina; the fruits of *M. verticillatum* are subglobose, with the mericarps rounded on the back and not ridged. *M. alterniflorum* DC. is most distinct in the reduced inflorescence and unisexual flowers, with only the lower (female) verticillate, and the flowers equalling, or slightly exceeded by, the bracts. *M. alterniflorum* var. *americanum* Pugsl. somewhat resembles *M. verrucosum* in habit and size of submerged leaves, but in no other significant characters. The recently found alien, *M. heterophyllum* Michx., differs in its sparse branching; much longer, 4-6-nate leaves; very different bracts; flowers with only 4 stamens; and mericarps ± rounded on the back. Fuller descriptions of, and a key to the three native British species will be found in a paper by Pearsall (1934). Pearsall implies that the flowers of all the British species are normally unisexual. This certainly seems to be true of *M. spicatum* and *M. alterniflorum*, but we have seen some specimens of *M. verticillatum* with predominantly hermaphrodite flowers and others which seem almost entirely female.

The status of *M. verrucosum* at Eaton Socon is clearly closely bound up with that of the numerous other adventive species, more especially the various remarkable Australian rushes, that have been found there. It seems reasonable to suspect that at least all the Australian species found there have a common origin. Direct evidence on this is lacking, but a good deal of circumstantial evidence points to these plants, whose intentional introduction seems almost out of the question, having arrived in this country with Australian wool. It is known that wool-shoddy has been, and is, extensively used in the neighbourhood by market-gardeners and farmers as a manure and water-retaining agent. A florula, seen growing from actual wool-shoddy at Flitwick station, Beds., duplicated several of the more unusual alien species seen at Eaton Socon (see the account of the B.E.C. Excursion to Bedford in *B.E.C. 1946-7 Report* (1948)). The vast majority of the alien species at Eaton Socon have been previously recorded as wool-aliens on Tweedside (Hayward and Druce; 1919), and, although many are native of the Mediterranean region, almost all these are recorded as common established aliens in Australia. Several of these are dealt with by Milthorpe (1943), who discusses their presence in New South Wales wool and their dispersal mechanisms, with illustrations; he makes no mention, however, of any

Myriophyllum. It seems perfectly feasible that mud containing the fruits of this plant, or even portions of the plant bearing fruits, should become attached to the fleece of sheep going to drink. It is significant, in this connection, that such a typical mud-plant as *Limosella* has been recorded as a wool-alien by the Tweed.

As will be seen from the specimens cited, *M. verrucosum* has been collected at Eaton Socon in three successive years and when we saw it it had every appearance of being well-established* in several places in this gravel-pit. It was in good quantity and fruiting well, and it seems quite likely that it may spread from here by natural means (birds, etc.) to other suitable water in the neighbourhood, and it should be looked out for. A considerable number of water-fowl frequent these pools, and may well be agents for its dispersal.

As yet little is known of the biology of this species. When first seen in July at Eaton Socon it was in flower and young fruit. Early in August it was still flowering but with a number of apparently mature fruits. The flowers appear to be markedly protandrous, the anthers dehiscing while the petals are still attached, or at least soon after they fall, and while the stigmas are still immature. Only later, after the petals have fallen and the stamens withered, do the stigmas apparently become receptive by developing the characteristic crown of hairs referred to in our description.

Plants from Eaton Socon have been cultivated by one of us (Chapple) and at the time of writing (January 1947) are still green and living, and show no signs of "dying back" although kept in an exposed tank where the temperature has at times fallen to 20° Fahrenheit or even lower.†

With the existence of Schindler's (1905) admirable monograph of the genus, it seems time that the species of *Myriophyllum* recorded from Britain were arranged in accordance with it, and we propose the following order to replace in the next edition of the *British Plant List* that of Druce (1928):—

216 MYRIOPHYLLUM L.
1. **verticillatum** L.
2. **spicatum** L.
3. *verrucosum* Lindl. Australia.
4. **alterniflorum** DC.
   b. **americanum** Pugsl.
5. *heterophyllum* Michx. N. Am.

*It should be noted that since this paper was written visits have been made to Eaton Socon in 1947 and 1948, and *M. verrucosum* was not seen on these occasions. The unusually severe winter of 1946-7 may have been too much for it.

†The history of these plants may now be completed. They appeared to live through the cold winter of 1946-7, but did not produce new shoots in 1947 and gradually decomposed. The plants produced fruits, which were found in the bottom of the tank, but they did not germinate in 1947 or 1948.

It will be noticed that *M. verticillatum* L. var. *pectinatum* is not mentioned. It appears to us to be no more than an inconstant state produced by terrestrial growth, or by changes in water-level during development. In a pond at Kennington, Berks., v.-c. 22, abundant *M. verticillatum* in deep water showed innumerable gradations between spikes with bracts similar to the submerged leaves and those of " var. *pectinatum*." Pearsall's (1934) contention that it is due to shallow-water conditions thus does not seem to be always the explanation. Those who retain var. *pectinatum* should note that its attribution to De Candolle is incorrect. The epithet first appears as a species, *M. pectinatum* DC.; 1815: *Fl. Fr., 6,* 529, with *Millefolium aquaticum pennatum spicatum* Magn. *Bot.* 178 as a synonym. It seems first to have been used in varietal rank by Wallroth; 1822: *Sched. Crit., 1,* 489; but he only cited the previous names of De Candolle and Magnol as doubtful synonyms of his var. *pectinatum*. It was left to Koch; 1843: *Syn. Fl. Germ., ed. 2, 1,* 270, to lump Wallroth's variety and De Candolle's species. The correct citation is, then, *M. verticillatum* L. var. *pectinatum* Wallr.

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