MONTIA FONTANA L.

By S. M. Walters

Botany School, Cambridge University.

The Linnean species *Montia fontana* has long been recognised as very variable, and many attempts have been made to subdivide the aggregate into smaller taxonomic units. The earliest attempts were rather naturally based on the more obvious type of variation in habit which was closely correlated with differences of habitat; thus Gmelin (1805) recognised two species, *M. minor* and *M. rivularis*, the former a small terrestrial plant with erect stems, the latter a more or less submerged or floating aquatic plant with long trailing stems. The less striking variation shown by the ripe seed was first recorded by Chamisso (1831), whose *Montia lamprosperma* of N. Temperate and Arctic Eurasia was distinguished by the possession of a smooth, shining seed, in contrast to the dull, tuberculate seed type common in Central and Southern Europe. In most later work, the seed-coat differences have been used in attempts to define the species within the aggregate, usually in association with the habit characters. Thus Ascherson & Graebner (1919) give three species in the aggregate : *M. minor*, annual, with dull, tuberculate seed; *M. lamprosperma*, annual, but with looser growth, and shining seeds with very brittle coat; and *M. rivularis*, perennial, with shining, finely tuberculate seeds. Koch's *Synopsis* (1892) gives the same three species, but with slightly different diagnoses. The French and other W. European floras have generally adopted *M. minor*, the erect land form with dull tuberculate seeds, and *M. rivularis*, more or less aquatic, with more shining, finely punctate or tuberculate seeds. Lindberg (1901), in a general review of the problem, gave as his opinion that any attempt to use characters of habit or vegetative structure to define the taxonomic units within the aggregate was useless, and that the characters of the ripe seed provided the only satisfactory basis. He agreed fundamentally with Chamisso's division into two main types, for which he adopted the names *M. fontana* subsp. *lamprosperma* and subsp. *minor*; the *M. rivularis* of Continental authors he considered to be merely an aquatic form of *M. minor* and described, as var. *boreo-rivularis*, analogous aquatic forms of subsp. *lamprosperma*. Samuelsson (1922) considered the Scandinavian types within the aggregate, and gave a good review of previous treatments by Scandinavian workers; he agreed with Lindberg in distinguishing two forms on seed characters, and in rejecting any characters other than those of the ripe seed, though differing from him in his interpretation of *M. rivularis*.

In Britain, the division into two types – the northern shining-seeded and the southern dull, tuberculate-seeded types – had been generally accepted, until Beeby (1909) pointed out that British material was more satisfactorily divisible into three, not two, seed-types. These he called : subsp. *lamprosperma* (the northern type), subsp. *minor* var. *chondrosperma* Fenzl (the southern type), and his new subsp. *minor* var. *intermedia*. Each of these could exist in ' land and water states ' which were ' merely temporary conditions directly induced by the environment, and not varieties.' Druce (1920) gave some details of the British distribution of var. *intermedia*, and stated that he had seen material referable to this from Belgium and Spain, and that it was ' doubtless elsewhere.' The existence of this third seed-type, intermediate between the other two, has undoubtedly contributed to the difficulties of British botanists attempting to apply continental work to the British material, and the distinctness of the three types has not generally been realised (cf. however Salmon (1931), who was obviously familiar with three types in the field).

A note by Hylander (1945) has done a great deal to clear the way to a solution of the taxonomic problem; in this the author points out that Beeby's var. *intermedia* is (as interpreted by Druce) at least in part identical with *M. lusitanica* Sampaio and refers material from Cork with certainty to this species.

Sampaio's *Montia lusitanica* is adequately described and discussed by the author (1912) who points out that the whole of the *Montia* material of Portugal is referable to this single species, and that previous references to *M. minor* and *M. rivularis* in Portugal were merely to habit-forms of extreme habitats (see below). He distinguishes his species from '*M. minor, rivularis* and *lamprosperma*' basically on seed size and characters of the seed-coat; and although the difference in size is certainly by no means so great or so constant as he suggests (see below), the seed-coat character 'dense et acute tuberculatis' is clearly stated. Apparently no type material was quoted, but I have seen material determined by Sampaio (in Herb. Inst. G. Sampaio, Porto, by courtesy of the Director), and there is no doubt as to the identity of this plant with var. *intermedia* Beeby.

Decker (1927) described as a new species, *M. limosa*, a plant which he collected in Brandenburg, Germany and was unable to refer either to *M. minor* or to '*M. rivularis*.' There can be no doubt from his description that this new species is *M. lusitanica*; thus he recognised it as distinct from the common *M. minor* of the district by the appearance of its seeds under a lens – 'ihre scharf gekörnelten, wenig glänzenden Samen.' Decker suggests that Ascherson and Graebner's '*M. rivularis*,' particularly records from the N. German plain, is in large part his *M. limosa*. Compare also Lindberg's comments (1901) on material determined as *M. rivularis* from C. Europe, from which it is clear that he was aware of the somewhat intermediate nature of the seed type of Continental '*M. rivularis*,' although he considered the differences – a rather shiny seed with smaller tubercles – not sufficient to justify its separation from *M. minor*, and seemed to think that even these seed differences are attributable to environmental modification.

Comparison of herbarium material with ripe seeds soon confirms the view that throughout N., W. and C. Europe the aggregate *M. fontana* is largely divisible into three plants distinguished on seed type, and that over a considerable area, including parts of England and much of N.W. Europe, two or all three types may occur together, yet remain distinct. In total range, moreover, the three types show striking differences; one (*M. lamprosperma* Cham.) is N. Temperate-Arctic and Alpine; one (*M. minor* auct.) is Temperate European; and the third, *M. lusitanica*, is W. European.

If the morphological separation on seed type were more or less complete, it might be taxonomically justifiable to treat the three as separate species. In fact, however, in parts of northern England, and elsewhere in N.W. Europe, there occur plants whose ripe seeds have small and somewhat variably developed tubercles, intermediate between *M. lusitanica* and *M. lamprosperma*. Between *M. verna* and the other two, there are in Britain and N.W. Europe as a whole apparently very few intermediate types, but such seed types undoubtedly occur more frequently in the Mediterranean region. It would seem best therefore to treat the aggregate as a single species, *M. fontana* L., with geographical subspecies, viz.:–

(1) subsp. *fontana* (*M. lamprosperma* Cham., the plant of the Linnean Herbarium).

*(2) subsp. *chondrosperma* (Fenzl) comb. nov. (*M. fontana* var. *chondrosperma* Fenzl (1843) in Ledebour, *Fl. Ross.*, **2**, 152).

(3) subsp. *intermedia* (Beeby) comb. nov. (*M. fontana* var. *intermedia* Beeby, *M. lusitanica* Samp. *M. limosa* Decker).

Plants with seed type between that of (1) and (2) could be treated as the expected

* I have followed Mr. J. E. Dandy's advice in the matter of nomenclature of this subspecies. Neither *M. verna* Neck. nor *M. minor* Gmel. is legitimate, both being renamings of *M. fontana* L.

intermediates between geographical subspecies if they were only very local or rare; but the occurrence of this type over a considerable area where, locally, the other subspecies may be almost absent (as seems to be the case, for example, in the Isle of Man), suggests that, whether the plant is of hybrid origin or not, it requires recognition as a widespread population type of similar status to the others. It is moreover fairly clear that many European records for '*M. rivularis*,' based on seed type, refer to such plants with seeds with small low tubercles near to ssp. *fontana* (cf. remarks by Hylander, 1945, 143-5). The most reasonable taxonomic treatment would here seem to be to treat such types as constituting a fourth subspecies (see below for description). It is interesting that Mansfeld (1940), following Decker, gives *four* species under the aggregate *M. fontana* in Germany, which seem to correspond with the four subspecies here proposed.

It is impossible to determine what Gmelin's *M. rivularis* was – the Gmelin Herbarium was destroyed in Karlsruhe during the last war – and a great deal of confusion surrounds the use of the name. This is partly due to the fact that there is a general habitat and correlated habit difference between ssp. *chondrosperma* and the other subspecies, by virtue of which it is often possible to distinguish roughly in the field between two types of plant. For example, in areas such as the Channel Isles, N.W. France and N. Italy where subsp. *chondrosperma* and subsp. *intermedia* are almost the only subspecies present, a classification on habit into '*M. minor*' and '*M. rivularis*' will very largely separate these two subspecies. Material distributed as *M. rivularis* from N. Italy in Fiori, Béguinot & Pampanini, Flora Italiana Exsiccata (no. 789) – which is typical subsp. *intermedia* – has the following note on the label :– ' species rather similar to the preceding (i.e. *M. minor*) . . . characterized by its submerged, not erect, habit, by the position of the flowering branches, and by the structure of the seed surface . . . Grows only in water poor in minerals . . .'. Decker (1927) makes similar remarks on his *M. limosa*. In areas where all four subspecies may be found, as in England and parts of Germany, '*M. minor*' will generally be subsp. *chondrosperma*, whilst '*M. rivularis*' will include aquatic or subaquatic forms of all four subspecies – though such forms of subsp. *chondrosperma* are not common. Lastly, in areas where there is apparently only one subspecies, as in Portugal, the attempt to apply the habit characters will give '*M. minor*' and '*M. rivularis*' which are, as Sampaio rightly recognized, merely modifications of the one type – here subsp. *intermedia* – to terrestrial or aquatic habitats.

It is not possible to decide how valid is the ecological separation of the subspecies (particularly of ssp. *chondrosperma* from the others) and to what extent the correlated habit characters are purely phenotypic, without extensive study of the plants in the field and in cultivation; but there is little doubt that differences in ecological preference do exist, and that it is therefore possible to use a variety of habit and habitat characters with some degree of success. If we consider the characters, other than those of the seed, which have been used in attempts to define the different types, this will be clearer.

1. The habitat of subsp. *chondrosperma* is generally described as wet, or at least seasonally wet, sandy places. In such a habitat the habit of the plant is more or less tufted, with short erect flowering branches. The aquatic or semi-aquatic habitats favoured by the other subspecies would naturally call for a loose submerged or floating habit.

2. Annual or perennial habit may be expected to show a similar correlation. The typical subsp. *chondrosperma* of sandy soil is, as Necker's name *M. verna* suggests, a spring-flowering annual, whilst aquatic plants would naturally flower later and may normally remain green throughout the winter. This is presumably the basis of the colour differences referred to by some authors – '*M. minor*' is described as yellow-green, whilst '*M. rivularis*' is pure green.

3. The difference between ' terminal ' and ' lateral ' inflorescences is often mentioned. The short, erect branches of typical ssp. *chondrosperma* terminate in cymes of flowers. The so-called ' lateral ' cymes of ' *M. rivularis* ' arise by the continued vegetative growth of a lateral bud below the inflorescence; this is clearly a reflection of the general vegetative vigour of an aquatic or semi-aquatic plant, and is in no way a fundamental difference.

4. Connate leaf-bases, it is sometimes claimed (? following Gmelin's original description of *M. minor*), distinguish subsp. *chondrosperma*. Again this character seems to be merely an expression of difference in vegetative vigour – the comparatively short, slender stems normally show the opposite leaf-bases in contact, as opposed to the separated leaf-bases of the more vigorous aquatic shoots of ' *M. rivularis*.' Quite apart from the difficulty of using such a character, it is very doubtful whether it has any basis other than the obvious modificatory one.

Given this different habitat preference, these vegetative characters, even if shown to be purely phenotypic, would normally serve to distinguish subsp. *chondrosperma* from the other subspecies. Yet herbarium identification relying on habit characters alone may be completely unreliable – aquatic forms of subsp. *chondrosperma*, for example, undoubtedly occur, in Britain and elsewhere.

The comparative descriptions of the subspecies which follow are based on personal observations, and on the descriptions of the seeds given by Lindberg (1901) and Beeby (1909). The details of the cellular structure of the seed-coat, and the shape, size and distribution of the tubercles on it, can be seen either directly under the binocular microscope or, as Lindberg stated, by removing a portion of the coat (easily detachable in subsp. *fontana*, less easily in the others) and studying under low power of the microscope. The vice-comital distribution is given for Britain and is based only on material personally examined. It is clearly very far from complete, but is useful as indicating the difference in British distribution. Records from Ireland are as yet too inadequate to justify publication, and Irish material needs much further study.

(1) subsp. FONTANA

M. fontana L. (1753), *Sp. Pl.*, 87, *sensu stricto.*
M. lamprosperma Chamisso (1831), *Linnaea*, **6**, 564.
M. rivularis auct., ? C. C. Gmelin.

Ripe seed 1·1 to 1·35 mm., smooth and shining seen under lens; under higher magnification, individual cells of seed-coat easily seen as a reticulate pattern, rather elongated, irregular in size and shape, with slightly convex outer walls; those in rows by keel elongated along row; seed-coat thin, brittle, often, in dried material, broken open. Plant variable in habit, usually looser than subsp. *chondrosperma*, often submerged (var. *boreo-rivularis* Lindb. f.), green or yellow-green. *Habitat* : trickles of water or very wet places, on acid soil or rock only.

Distribution : Circumpolar Arctic and N. Temperate; also in the S. Hemisphere into the Antarctic. Common in Scotland and N. England. V.c.'s : 45, 46, 49, 50, 58, 61, 64, 65, 68, 69, 70, 72, 73, 77, 78, 80, 83, 85-90, 92, 93, 96-98, 100, 104, 105, 107-112.

(2) subsp. **chondrosperma** (Fenzl) comb. nov.

M. fontana var. *chondrosperma* Fenzl (1843), in Ledebour, *Fl. Ross.*, **2**, 152.
M. verna Necker (1768), *Delic. Fl. Gallo-Belg.*, **1**, 78, nomen illeg., quoad descr.
M. minor C. C. Gmelin (1805), *Fl. Bad.*, **1**, 301, nomen illeg., quoad descr.

Ripe seed 1·0 to 1·2 mm., dull and entirely covered with rather coarse tubercles as

seen under lens; under high magnification cells of surface more or less hexagonal, each with a broad, blunt tubercle occupying most of the outer wall of cell (cells in centre of plano-convex surfaces of seed rather larger and somewhat elongated); tubercles finely papillose under microscope (high power). Plant usually tufted, yellowish-green, not submerged, with short erect branches terminating in cymes. *Habitat* : light acid soils, usually sandy or gravelly, with high water table at least in spring; only rarely more or less submerged in water, and then much modified in habit.
Distribution : Central and southern Europe; also Australia (see p. 6). The common, and in some areas the only, subsp. in southern England; rarer in N. England and Scotland. V.c.'s: S, 1-3, 7, 9-12, 14-21, 26-30, 33, 34, 36-38, 40-43, 45, 46, 49, 52, 58, 61-63, 66, 69, 71, 77, 83-85, 95, 105.

(3) subsp. **intermedia** (Beeby) comb. nov.
M. fontana subsp. *minor* var. *intermedia* Beeby (1909), *Ann. Scot. Nat. Hist.*, 104.
M. lusitanica Sampaio (1912), *Ann. Sc. Acad. Polyt. Porto*, **7**, (1) 52.
M. limosa Decker (1927), *Verh. Bot. Vereins. Brandenburg*, **69**, 57.
M. rivularis, auct. mult., ? C.C. Gmelin.

Ripe seed rather smaller than in the preceding sspp., 0·85 to 1·1 mm., finely tuberculate at edge and rather shiny under lens, under higher magnification seen to have (2-) 3-4 (-5) rows of cells on each side of keel bearing small but relatively narrow and high tubercles, one in centre of each cell; tubercles finely papillose under high power of microscope; cell-walls quite obvious, cells rather elongated. Plant usually loose in habit, often more or less aquatic, with long bright green trailing branches bearing apparently axillary cymes only. *Habitat* : as for subsp. *fontana*.
Distribution : W., C. and S. Europe; also Australia (see p. 6). Common in W. England and Wales; rare in Scotland. V.c.'s: S, 1-6, 8-11, 13, 14, 16-22, 24, 27, 30, 35-37, 39-49, 52, 54, 55, 57, 58, 60, 62-64, 66, 69-71, 88, 100.

(4) subsp. **variabilis** subsp. nov.
M. rivularis auct. mult., ? C. C. Gmel.

A subsp. *fontana* differt : semine maturo 0·9—1·1 mm. magis minusve plano minus nitido quam in subsp. *fontana*, oculo valde armato tuberculis minimis varie evolutis saepe humillimis circa carinam praedito, seminibus maturis plantarum simul lectarum saepe conspicue inter se dissimilibus.

Typus in Herb. Univ. Cantab. : v.c. 45, Pembrokeshire; just north of Tedion Mt., at edge of outlet from shallow pool, Martletwy, 22 June 1952, *E. Milne-Redhead*.

Ripe seed 0·9 to 1·1 mm., more or less smooth (under lens) but not so shining as subsp. *fontana*; under higher magnification showing variable development of small usually very low tubercles around keel, the variation often obvious between different ripe seeds of same gathering. Plant usually loose in habit, resembling commonest forms of subsp. *intermedia*, and found in similar habitats.
Distribution : West and Central Europe ; elsewhere ? Locally common in N. England and Wales, and occurring throughout the area where both subsp. *fontana* and subsp. *intermedia* occur, but in certain districts (e.g. Isle of Man) the common and perhaps the only subspecies. V.c.'s : 1-6, 9, 17, 30, 32, 35, 38-52, 55, 57, 59, 62, 64-66, 69-73, 75-77, 79, 83, 86, 88, 90, 91, 98-100, 108, 110.

The seed sizes given in these descriptions are in each case the range of measurements of ' largest diameter ' made on three ripe seeds from each of four British gatherings. The

size differences shown, though insufficient to use as a taxonomic character, are nevertheless consistently, in my experience, to be found; and, so far as subsp. *intermedia* is concerned, support Sampaio's description of the seeds of his *M. lusitanica* as smaller than those of the other species of *Montia* he knew. It would, however, seem that Sampaio's material was somewhat atypical; for it can hardly be claimed, as he did, that the other subspecies have seeds $1\frac{1}{2}$ to 2 times as large as subsp. *intermedia*. Measurements made on seeds in material determined by Sampaio as *M. lusitanica* gave a size range virtually identical with that found for the British material.

Note on Australian Material

Whilst the common *M. fontana* of the S. Hemisphere is undoubtedly subsp. *fontana*, it is interesting that in Australia both subsp. *chondrosperma* and subsp. *intermedia* seed-types also occur. Of 11 sheets with ripe seed, lent by the National Herbarium, Botanic Gardens, Sydney, no fewer than seven were referable to subsp. *chondrosperma*, and three to subsp. *intermedia*. The remaining gathering, a Tasmanian one, was the expected subsp. *fontana*. This situation is very interesting, and would repay further investigation. Several possibilities suggest themselves; for example, the seed-coat character, so clearly correlated with distributional differences in Europe, may occur more or less sporadically in the Australian populations; or both subsp. *chondrosperma* and *intermedia* may be aliens in the Australian flora.

I am indebted to Mr. D. E. Allen and Mr. J. E. Dandy for help with nomenclature, to Dr. N. Hylander of the University of Uppsala, who originally suggested the investigation to me and has contributed much to it, to Mr. R. Anderson, Curator of the National Herbarium, Sydney and Mr. E. J. McBarron for information and the loan of Australian material, and to Miss C. Lambert for the seed drawings.

SUMMARY

The Linnean species *Montia fontana* is divisible in north-west Europe into four taxa which it is suggested should be given subspecific rank, viz. :—

(1) subsp. *fontana*, northern in European distribution;
(2) subsp. *chondrosperma* (Fenzl) comb. nov., southern in European distribution;
(3) subsp. *intermedia* (Beeby) comb. nov., western in European distribution;
(4) subsp. *variabilis* subsp. nov., intermediate in seed-coat marking and distribution type between 1 and 3.

The value of characters other than those of the seed-coat is discussed. Vice-comital distribution of the four subspecies in Britain is given, and also some indication of the distribution in Europe, and a note on their occurrence in Australia.

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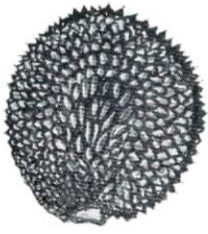
PLATE 1.

1



2

3

4

5

Seeds of Montia fontana (x 25).

1. subsp. *chondrosperma*, Odiham Common, N. Hants., v.c. 12, C. E. Palmer, 1902, Herb. Univ. Oxon.

2. subsp. *intermedia*, rill below County Gate, N. Devon, v.c. 4, W. C. Barton, 1917 (Wats. B. E. C. Distr.) Herb. Univ. Cantab.

3. subsp. *variabilis* (with obvious tubercles by keel), Umberley Brook, Brampton East Moor, Chatsworth, Derby, v.c. 57, P. S. Green, 1950, Herb. Univ. Cantab.

4. subsp. *variabilis* (with very low tubercles by keel), stream, Yewdale, Coniston, N. Lancs., v.c. 69, J. Comber, 1911, Herb. Univ. Cantab.

5. subsp. *fontana*, Loch Tay, Mid Perth, v.c. 88, G. C. Druce, Herb. Univ. Oxon.