

***Mannia californica* (Gottsche ex Underw.)
L.C.Wheeler (Aytoniaceae, Marchantiales)
in Ardèche (France), new to Europe**

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Résumé – *Mannia californica* (Gottsche ex Underw.) L.C. Wheeler est signalé pour la première fois en Europe, dans le département de l'Ardèche, France. Les récoltes sont brièvement décrites puis comparées avec les autres espèces européennes du genre *Mannia*, notamment *M. fragrans* et *M. androgyna*. Les populations françaises croissent dans les fissures de parois calcaires au sein de canyons exceptionnellement bien conservés. Les populations sont peu nombreuses dans chacune des localités connues mais produisent des spores en abondance. Bien que les peuplements actuellement recensés ne semblent pas hautement menacés pour l'instant, le site devrait de toute urgence faire l'objet de mesures de protection réglementaire.

Summary – *Mannia californica* (Gottsche ex Underw.) L.C. Wheeler is reported as new to Europe from Ardèche department, France. The French collections are briefly described and compared with other European species of the genus *Mannia*, notably *M. fragrans* and *M. androgyna*. The French populations occur in clefts on calcareous cliffs in well preserved canyons. The plants are scarce at each locality but freely produce spores. The known populations do not seem to be under extreme threat at present but should urgently receive statutory protection.

Liverworts / Marchantiales / *Mannia californica* / Ecology / Phenology / France / Ardèche

INTRODUCTION

During the course of a bryological survey of the vast Paiolive site located in south-eastern France (Ardèche department), the first author had the opportunity on three occasions to find a puzzling taxon that was readily assigned to the genus *Mannia* in the field. With regard to vegetative characteristics, all three gatherings showed a striking structural resemblance to the well known *Mannia androgyna* (L.) A. Evans, but several discrepancies were immediately apparent,

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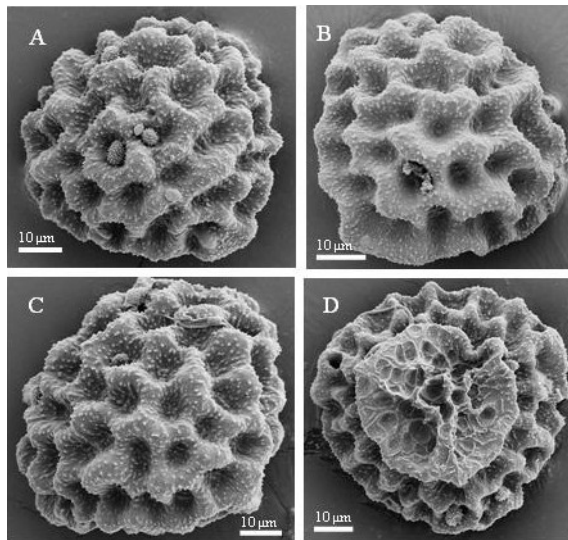


Fig. 1. Spores of *Mannia californica*. **A, B, C**, distal faces. **D**, proximal face. (A, C, D from *VH 664*; B from *VH660*).

notably those concerning sexuality and exine sculpturing. Under certain environmental conditions, spores of *Mannia* are liable to collapse and the possibility that the spores of that troublesome *Mannia* was in fact that of *M. androgyna* with juvenile or aborted collapsed spores was initially considered. Examination of the exine sculpturing under SEM (Fig. 1) at RBGE unambiguously dismissed this possibility as the spores appeared neither juvenile nor collapsed. Evidently the *Mannia* under question was not treated in any European flora so its identification was only made possible through the worldwide revision of the genus *Mannia* by the second author. Through examination of the type and other specimens D.B.S. established the identity of the Ardèche plant as *Mannia californica* (Gottsche ex Underw.) L.C. Wheeler, a species formerly thought to be restricted to the Northern American continent. Taxonomic work in progress suggests that *M. californica* also occurs in other continents (Schill, *in prep.*)

The aims of this paper are to provide a short description of the French material, to describe the ecology, to map the current European distribution and to evaluate the threats that hang over the known localities.

**DESCRIPTION OF FRENCH MATERIAL
OF *MANNIA CALIFORNICA* (GOTTSCHKE EX UNDERW.)
L.C.WHEELER**

Thalli mostly 1-2.3 mm wide and 10-12 mm long, generally forming dense mats of interwoven segments, margins strongly incurved when dry, thalli then appearing as a mass of vermicular lobes. Upper surface dark green with a narrow

marginal strip of purple, minutely undulate-lobulate; lower surface almost completely hidden by shining imbricate dark purplish scales. Ventral scales 0.3-0.5 mm wide and 0.8-1.2 mm long, lunate, deep black-purple, not forming a dense apical brush but often extending over thallus margin, inconspicuously inflexed over the apex, and slightly projecting; appendages (1)-2, narrowly triangular, purplish. Older parts of thallus with a slight tendency to rupturing, grey-pinkish. Branching latero-ventral and (apparently less frequently) dichotomous. Branches lunate in cross section, broadly rounded beneath and not keeled, tapering to very narrow wings. Aerenchyma very compact, almost fully occupied with chlorophyllose divided free filaments, with scattered oil cells. Ventral tissue occupying 0.5-0.7 of thallus height with many scattered, very obscure blackish to occasionally dark grey-brownish oil bodies. Dorsal epidermis with thin-walled but distinctly collenchymatous cells 12-21 μm in diameter, with scattered oil cells; air pores simple and elevated, surrounded by 2 concentric rows of 8-9 cells without evident thickening.

Autoïcous, frequently fertile, but gynoecia vanishing after spore release. Androecia borne over the main thallus, not forming a cushion but a poorly defined median group of 6-23 antheridial chambers, strongly persisting along the axis and not limiting the growth of the leading thallus. Female receptacle restricted to short latero-ventral branches (*ca* 1.5 mm long), cordiform from a narrow base, serially arranged (up to 6) along the main axis. Peduncle sulcate, 0.8 cm long, yellowish, surrounded by a small inconspicuous brush of purple scales at base, these persisting after disappearance of stalk. Carpocephala *ca* 2 mm diameter, with 2-4 campanulate lobes beneath. Sporophyte blackish; spores dark violet-brown, 54-60 μm , with dissimilar sculpturing on distal and proximal surface, distal face deeply ornamented with irregular areolae, 5-7 across the diameter, occasionally alveolate and ridged, exine minutely verruculose; proximal face similarly sculptured but with an indistinct trilete mark. Elaters purplish, long attenuate, 250 μm long and 4-15 μm wide, 3-spiral.

Specimens studied:

Europe. FRANCE. Ardèche, Labeaume, Peyroche, 150 m, Jurassic calcareous pavements, 18 avril 2004, *V. Hugonnot* VH657 (private herbarium of VH), VH661 (private herbarium of VH), VH664 (E and private herbarium of VH); Ardèche, Chandolas, Fontgraze, 130 m, Jurassic calcareous pavements, 12 novembre 2004, *V. Hugonnot* VH662 (private herbarium of VH), VH663 (private herbarium of VH); Ardèche, Banne, Granzon, 155 m, Jurassic calcareous pavements, 21 mars 2005, *V. Hugonnot* VH658 and VH659 (private herbarium of VH), VH660 (E and private herbarium of VH).

Our material falls within the variability of the species. The stalks of the carpocephala appear very short (*ca* 8 mm) but this has also been reported for stalks of specimens from Utah (2-5 mm) (Flowers, 1961).

COMPARISON WITH SIMILAR SPECIES

In Europe, five species of the genus *Mannia* have previously been found. Aside from the arctic-alpine *M. pilosa* (Hornem.) Frye & L. Clark and *M. sibirica* (Müll. Frib.) Frye & L. Clark, the three species *Mannia fragrans* (Balb.) Frye & L. Clark, *M. androgyna* (L.) A. Evans and *M. triandra* (Scop.) Grolle are much more widespread.

Mannia triandra differs from *M. californica* and *M. androgyna* by the rather delicate thallus, loose assimilatory layer and the position of the antheridia.

It is described at length in many classic manuals and keys (Müller, 1954; Schuster, 1953, 1992b; Schumacker & Váňa, 2000). A revised key to the European species of *Mannia* (including *M. californica*) will be published in the near future (Schumacker & Váňa, 2005).

Mannia fragrans is generally easy to distinguish from *M. californica* by the usually present strong smell (cedar oil), and apical brush of tufted appendages of ventral scales conspicuously projecting, notably at the apex of female branches. Sterile specimens can be troublesome to identify, especially in the field, as thalli may confusingly resemble those of *M. androgyna* or *M. californica*. The sexuality is almost always distinctive; the androecium is a slightly prominent disc in *Mannia fragrans* and a diffuse group of antheridial chambers in *M. californica* and *M. androgyna*. In *Mannia fragrans* the gynoecia are located on the leading thallus and more or less elongated and isolated ventral branches of determinate growth. In contrast to this, the female branches of *M. californica* originate in a ventral series of much abbreviated ones. Schuster (1953, 1974, 1992a & b) insists on the fact that the archegoniophores can occasionally be on abbreviated ventral branches in *Mannia fragrans* and discusses at length the high polymorphism of sexuality (of female and male parts) in that species.

Mannia californica appears to be more closely related to *M. androgyna* and it is with that species that confusion is more likely to happen. The dark-blackish oil bodies of *Mannia californica* are very different from those of *M. androgyna*, in which they appear distinctly pale greyish. In *Mannia androgyna* the female receptacle occurs most frequently on the leading thallus and rarely on ventral branches. Massalongo (1915-1916) described and illustrated *Mannia androgyna* in some detail and his account is still useful.

Much controversy arose in the past from the conflicting interpretations of the anatomical structure of the assimilatory layer in the genus *Mannia*. Evans (1918) pointed out the discrepancies that are found in the works of earlier authors and established that the assimilatory layer is composed of chambers subdivided by secondary dentate plates, the chambers totally lacking free filaments. The troublesome account of Preston (1939), stating that the chambers of *Mannia californica* are undivided and filled with free photosynthetic filaments, is unfortunately based on a misidentification of her material, which was in fact *Targionia hypophylla* L., as later corrected by Schuster (1992b) and as is apparent from her figures. No useful differentiation regarding the anatomical structure of the assimilatory layer of *M. californica* and *M. androgyna* could be found. The two taxa have a comparable internal structure.

Finally, it is worth pointing out that Schuster (1992) keyed and described at length three deviant phases of *Mannia californica* from North America. Such a polymorphism seems to be virtually absent from the French populations under study. Furthermore, our collections seem to randomly combine certain of the characteristics of the phases described by Schuster.

DISTRIBUTION

Mannia californica was initially considered to be endemic to California but was later demonstrated to be much more widespread in several parts of Northern America with a Mediterranean climate. It is mentioned by Schuster (1992b) in California, Arizona, Texas, North Carolina, Arkansas and Tennessee



Fig. 2. Distribution of *Mannia californica* (Gottsche. ex Underw.) L.C. Wheeler in Europe.

and by Flowers (1961) in Utah. Its discovery in France is a major extension of range to Europe (Fig. 2). Although no other European collections have been made, a number of specimens from Africa and Asia probably belong to this taxon but are still under revision and will be published later.

ECOLOGY

The Païolive site is a pivot between the mountainous metamorphic Cévennes and the Mediterranean region. It shows typically a submediterranean climate with two humid seasons (spring and autumn) and a relatively dry period (summer). Storms and violent rainfall are most frequent in autumn and often

cause flooding and destructive soil run-off. The vast karstic system of Païolive never holds water superficially, so vegetation is typically xerophytic.

In the three known localities the geological substratum is composed of massive Jurassic calcareous pavements. The populations of *Mannia californica* are developed on the small cliffs of canyons running alongside temporary rivulets or permanent rivers. The joints of the calcareous strata are externally made of a fine accumulated mostly argillaceous material that strongly positively reacts with HCl.

The bryoflora of these calcareous cliffs is variably rich or poor depending on microclimatic characteristics such as insolation, allied vascular plant cover and microtopography. Typical saxicolous communities are developed directly over the rock (or over a very fine layer of substrata) and are dominated by *Grimmia dissimulata* E. Maier, *Grimmia tergestina* Tomm. ex Bruch & Schimp., *Orthotrichum anomalum* Hedw., *Pleurochaete squarrosa* (Brid.) Lindb. and *Syntrichia montana* Nees. The earthy joints are able to retain a certain amount of humidity, mostly at the base of the cliff, where *Lunularia cruciata* (L.) Dumort. ex Lindb. together with *Mannia triandra* rarely thrive. Higher along the cliff, the joints are subject to far greater desiccation and are colonized by *Targionia hypophylla* L., *Reboulia hemisphaerica* (L.) Raddi, *Scorpiurium circinatum* (Brid.) M. Fleisch. & Loeske and *Mannia californica*. Nevertheless, *Mannia californica* is most often observed without any close associate and tends to form dense thallus crusts of several square centimetres. Under dehydration these small plates tend to lift on the margins and to lose their adherence. It is rather easy to visualize the fall of these unsteady crusts under adverse climatic conditions (notably heavy rains or occasional frost).

The vascular herbaceous cover of the cracks more or less in direct contact with *Mannia californica* is very sparse with only several small tufts of *Sedum dasyphyllum* L., *S. album* L., *S. sediforme* (Jacq.) Pau, *Asplenium ceterach* L., *Petrorhagia prolifera* (L.) P.W. Ball & Heywood, *Stachys recta* L., etc. The allied vascular vegetation of the surroundings is the characteristic sub-Mediterranean open *Buxus sempervirens* garrigue with *Juniperus oxycedrus* L., *Buxus sempervirens* L., *Pistacia terebinthus* L., *Rhamnus alaternus* L., *Phillyrea latifolia* L. in the shrub layer and scattered individuals of the white oak, *Quercus humilis* Miller.

All the three cliffs are of south, south-western or western exposure and the three canyons with populations of *Mannia californica* are at around 130-155 m above sea level.

It is quite noticeable that the two other members of the genus *Mannia* that are to be found in the same Païolive site do not exhibit the same ecological requirements at all: *Mannia triandra*, as we have already mentioned, inhabits the more or less dripping cracks protected from direct sunlight (together with *Eucladium verticillatum* (Brid.) Bruch & Schimp., *Gymnostomum calcareum* Nees & Hornsch., etc.) (Hugonnot & Offerhaus, 2005) and *Mannia fragrans* colonizes carbonate free "terra rossa" in the clearings of xerophilous sub-steppic grasslands (together with *Riccia ciliata* Hoffm., *Oxymitra incrassata* (Brot.) Sérgio & Sim-Sim, *Corsinia coriandrina* (Spreng.) Lindb., *Cheilothela chloropus* (Brid.) Lindb., etc.).

The habitats described in Schuster (1992b) are reasonably comparable to that observed in France. The typical xerothermophilous habitats, notably soil-filled crevices with at least two common recorded liverwort associates (*Reboulia hemisphaerica* and *Targionia hypophylla*) fits with the structure and the composition of the community in France. Nevertheless it should be noted that Schuster (1992b) mostly reports the species on acid metamorphic rocks or quartzite with only one occurrence over limestone in North America contrasting with the wholly calcareous nature of the Ardèche sites.

Frye & Clark (1937) mentioned *Mannia californica* “on wet rocks” but this is considered erroneous by Schuster (1992) on the basis of the supposed strongly xeromorphic structure of the plant. Still at variance with Schuster’s opinion, Flowers (1961), for Utah, also indicates “damp or wet soils” and “overhanging rocks where intermittent water trickles”.

DISCUSSION

In Ardèche, *Mannia californica* occurs in less than ten distinct stands in each locality. These stands are generally small (from a few cm² to approximately 160 cm²) and very elongated because of the linear structure of the supporting joints.

Obviously, in Ardèche, *Mannia californica* appears to be in active vegetative growth in the winter months. The violent winds and insolation rapidly cause the thallus to dehydrate so that it becomes involute with its flanks totally hiding the dorsal thallus surface and leading to a supposed complete halt of growth. Occasional summer rainfalls generally do not allow the thallus to restart active growth for a significant period.

The reproductive phenology of the populations has not been accurately assessed but it seems that, at least locally, carpocephala begin their development late in the winter and shed their spores by May. The spores are very abundantly produced and they are rather easy to locate among the old thalli even after disappearance of the sporophytes. Dissemination from one crack to the other is not easy to visualize, because of relative scarcity of suitable cracks and presumably inescapable falling down (under gravity effects and rainfall) of the great majority of the spores. Further studies of the reproductive strategies of hepaticae such as *Mannia californica* could usefully be undertaken.

From a phytosociological point of view, the *Mannia californica* community seems to be near the *Mannion androgynae* Ros & Guerra 1987 (in the *Barbuletea unguiculatae* Mohan 1978 Class and the *Barbuletales unguiculatae* v. Hübschm. 1960 Order). This alliance has been described by Ros & Guerra (1987) to incorporate basophilous communities dominated by thallose hepaticae and is the Mediterranean vicariant of the *Grimaldion fragrantis* Smarda & Hadac 1944. Although three associations belonging to this alliance have previously been mentioned in France (Bardat & Hauguel, 2002), a more precise description should ideally await a bryosociological study of the Païolive site.

The possibility that *Mannia californica* is not native in France has to be dismissed because the three localities under question fail to show any trace of disturbance and are precisely located in habitats (vertical cliffs) that have escaped all forms of human remodelling (Bischler, 2004). The occurrence in Païolive of at least three distinct populations and the fact that all three are located in the less visited sites confirm this view. As the herbarium examination of European collectors failed to reveal other localities of *Mannia californica*, it seems more likely that this species has not been confused with other members of the genus but that it is genuinely a rare element of the European bryoflora.

Nowadays the major threat is certainly the considerable tourist pressure on all of southern Ardèche. All of the Païolive site merits statutory protection that is fully justified by the occurrence there of many Red List taxa such as *Mannia*

triandra, *Riccia crustata* Trab., *Orthotrichum philibertii* Vent. or *O. sprucei* Mont. (ECCB, 1995) in addition to other rare or endangered taxa.

Management should be carried out by minimal intervention as vegetational succession is notably very low if not absent on such subvertical calcareous cliffs.

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