Observations on fertile populations of *Lunularia cruciata* (L.) Dumort. ex Lindb. (Marchantiopsida: Lunulariaceae) in Germany

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Abstract

Sporophytes of *Lunularia cruciata* have been recorded in Germany for the first time. All developmental stages were observed outdoors in the botanical garden of the University of Frankfurt am Main; they are illustrated by photographs in this paper. Within a vegetation period, antheridial receptacles developed in early spring, and were followed by archegonial receptacles in spring and finally by sporophytes in late summer. The observed sequence of development is compared to that reported for other regions. The actual distribution of *Lunularia* in Germany, considering fertile populations, is shown and the ecology is briefly described.

Keywords: Distribution, fertile populations, *Lunularia*, sporophytes.

Zusammenfassung

Zum ersten Mal werden Sporophyten von *Lunularia cruciata* in Deutschland nachgewiesen. Alle Entwicklungsstadien wurden im Freiland des Botanischen Gartens der Universität Frankfurt am Main beobachtet und für diese Veröffentlichung fotografisch dokumentiert. Innerhalb einer Vegetationsperiode entwickelten sich die Antheridien im frühen, die Archegonien im späteren Frühjahr, die Sporogone folgten dann im Spätsommer. Diese Phänologie wird mit Daten aus anderen Gebieten verglichen. Unter besonderer Berücksichtigung der fertilen Populationen wird eine Karte der aktuellen Verbreitung von *Lunularia* gezeigt. Die ökologischen Ansprüche werden kurz beschrieben.

Contents

1 Introduction

Lunularia Adans. colonies can be easily identified by the half-moon shaped gemma receptacles. Many records of such colonies are known from Africa, America, Asia, Australasia, and Europe. There has been some debate regarding the number of taxa (species, subspecies, formae) within this genus. Specifically it is debated whether *L. cruciata* (L.) Dumort. ex Lindb. (or one of its respective infraspecific equivalents) is the only taxon, or whether *L. thaxteri* A. Evans & Herzog (or one of its respective infraspecific equivalents) is a taxon of this genus found in the Southern Hemisphere (SCHUSTER 1992). Culture experiments showed that the morphological differences used for segregating *L. thaxteri* as a separate species are not stable and of no taxonomic significance (SRIVASTAVA 1967, BOISSELIER-DUBAYLE et al. 1995 and references given therein). Colonies of different geographic origins (France, Portugal, Spain, South Africa), including a specimen that corresponds morphologically to *L. thaxteri* from Madeira, showed no significant genetic variation with respect to isozymes, and *L. thaxteri* and its respective infraspecific equivalents were all reduced to synonyms of *L. cruciata* (L.) Dumort. ex Lindb. (BOISSELIER-DUBAYLE et al. 1995). Molecular studies in the phylogeny of Marchantiophyta show *Lunularia* as a basal lineage of the complex thalloid liverworts (Marchantiopsida). The unique systematic position of *L. cruciata* led to the proposal of the new monotypic order Lunulariales D. G. Long (LONG 2006).

Though *L. cruciata* is widely distributed and common, records on sexual reproduction and development of sporophytes of this dioecious species are rare and scattered over continents (SAXTON 1930, BOISSELIER-DUBAYLE et al. 1995).

A hypothesis involving the assumed influence of symbiotic fungi in the rare sexual reproduction of *L. cruciata* was refuted after closer examination (NICOLAS 1929, AURET 1930, BENSON-EVANS & HUGHES 1955). Fungi have, nevertheless, the potential to form saprotrophic or symbiotic interactions with *L. cruciata* (Nicolas 1929, Fonseca et al. 2006). The rarity of sporophyte development has been attributed to a disjunctive distribution of archegonial and antheridial clones, which itself is caused by mainly anthropogenic spreading (Goodman 1956).

The species is considered native to the Mediterranean region (Frahm 1973, Paton 1999), where sexual reproduction in plants occurs more frequently than in other regions (Sérgio & Viana 1973, Schuster 1992). Sexual reproduction is, therefore, probably triggered by climatic conditions, such as day length (long day conditions) and temperature regimes (rise of temperature after mild winters), but experimental evidence is incomplete (Benson-Evans & Hughes 1955, Perold 1995).

Antheridial and archegonial stages of *L. cruciata* were recorded in the Netherlands where thalli with sporophytes were found in 1873 and 1882 (Gradstein & van Melick 1996). Sporophytes were also recorded in Austria during the second half of the 19th century (Leitgeb 1881). Other records of sporophytes in Europe originated from areas with favourable climatic conditions, e. g. France (Frémy 1925, Nicolas 1929), Italy (Micheli 1729), Spain (Casares-Gil 1919, Schuster 1992), and the south of England and Wales (Goodman 1956, Paton 1999). Outside Europe sporophytes have been found in South Africa (Saxton 1930, Perold 1995), Argentina (Schuster 1992), California (Schuster 1992), India (Naidu 1969), Japan (Shimamura & Deguchi 2002) and New Zealand (Schuster 1992).

L. cruciata was recorded in Germany for the first time in 1828 by Alexander Braun in the botanical garden of Karlsruhe (Frahm 1973). *L. cruciata* was also recorded in 1838 within the botanical garden of Frankfurt am Main (Nees von Esenbeck 1838), which, however, is not situated in the same place today. The liverwort appears to spread from greenhouses and gardens by human activities and is dispersed along flowing water, especially downstream of larger settlements as a result of the influence of sewage and drainage water, and along railways. *L. cruciata* will establish stable populations in shady, moist places without severe winter frosts and competitive vegetation (Frahm 1973, Loos 1991, Tremp & Vulpus 1997). Several authors have stated that only female thalli exist in Germany (Müller 1954, Düll 1980, Frahm & Frey 2004). Nees von Esenbeck (1838) reported a frequent occurrence of archegonial receptacles from Germany, but antheridial ones were only found in the botanical gardens of Bonn. Thalli bearing archegonial receptacles are very rare in Germany (Frahm 2006). Recently (in 2002), however, antheridial receptacles of *L. cruciata* were discovered at the botanical gardens of Tübingen (Schoepe 2005). Until now, sporophytes were absent in this country.

The ecology of *Lunularia* in Central Europe (Tremp & Vulpus 1997, Schoepe 2005) is closely related to that in Great Britain (Paton 1999). The spreading of *Lunularia* outdoors in Germany over the years has been well recorded in distribution maps (Frahm 1973, Düll & Meinunger 1989, Meinunger & Schröder 2007).

Acknowledgements

We thank J.-P. Frahm (Bonn) for helpful discussion of the antheridial stage of *L. cruciata*, the curators A.-M. Lenk and M. Wessel of the botanical garden in Frankfurt am Main for their generosity towards our studies in the garden, M. Preussing (Holzminden) for providing information on locations of fertile *Lunularia*, O. Dürhammer (Regensburg) for generating the distribution map and for kindly providing data, and the referees for their valuable comments and suggestions.

2 Material and Methods

The observed colony of *L. cruciata* covered an area of approximately 1.0 × 0.5 m originally planted with *Mentha* and *Urtica* species at the border of the botanical garden of the Goethe University of Frankfurt am Main. The site was shadowed by trees to the southwest and exposed to light only from the northeast. The soil contained loam and humus in the uppermost layer, becoming loamier in the deeper layers and had not been used for plant cultivation for approximately two years prior to the observation of *L. cruciata* (A.-M. Lenk, pers. comm.). In the spring of 2008, *L. cruciata* was the dominant plant in this area. The colony was observed between 21 February and 8 September 2008.

Fertile specimens of *L. cruciata* have been deposited in the Herbaria of FR and STU.

The nomenclature follows Koperski et al. (2000) in liverworts, Szweykowski et al. (2005) in *Conocephalum* and Hill et al. (2006) in mosses.

The abbreviations (e. g. "4122 SO") in chapter 3 refer to the German ordinance survey maps with a scale of 1 : 25000.

Acronyms of depositories

FR Herbarium Senckenbergianum, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany

STU Herbarium Staatliches Museum für Naturkunde, Stuttgart, Germany

3 Distribution of *Lunularia cruciata* in Germany

Sterile plants (Fig. 1)

Lunularia cruciata is widespread in Germany. Centres of distribution are the city states of Berlin, Hamburg and Bremen. In Schleswig Holstein, the species occurs mainly in the eastern parts along the Baltic Sea; in Niedersachsen in the southern parts; in Nordrhein-Westfalen in the western parts and along the river Rhein; in Hessen in the southern and north-eastern parts; in Baden-Württemberg in the northern parts, mainly along the river Neckar; in Rheinland-Pfalz, Saarland and Sachsen it is scattered over the whole area; and in Bayern, it is found only in the north-central region.

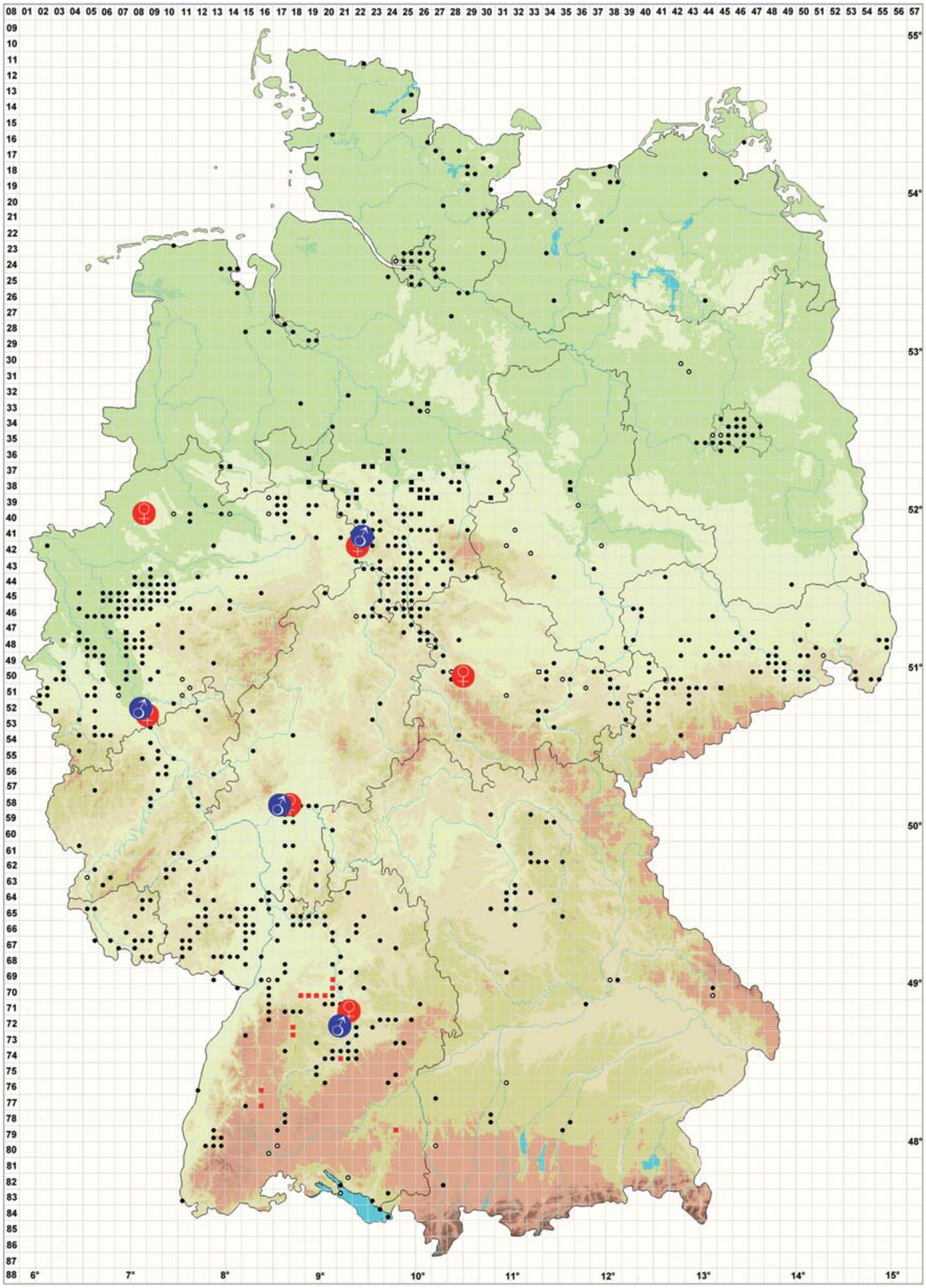
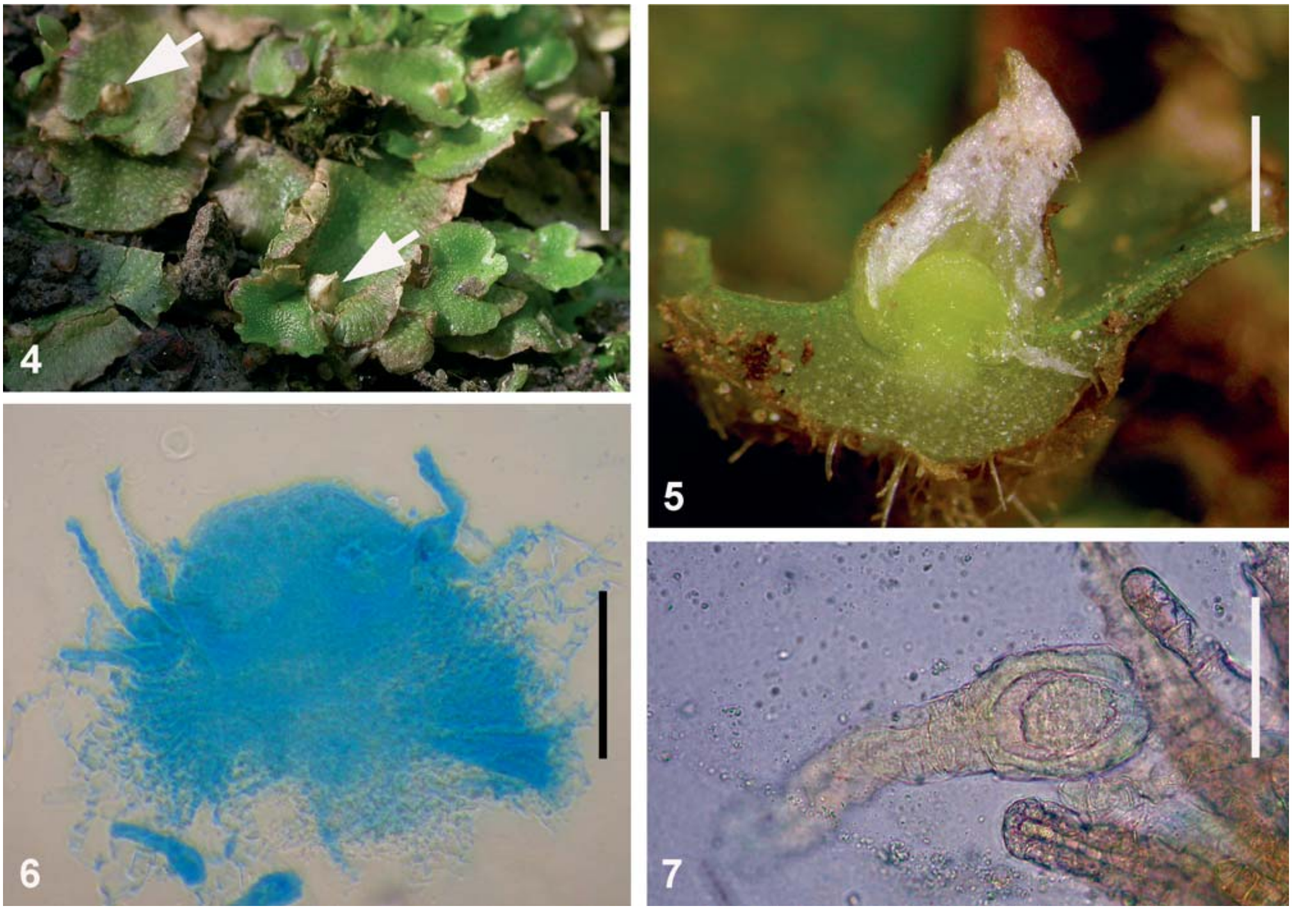


Fig. 1. Distribution of *Lunularia cruciata* in Germany, sterile [small black squares (herbarium specimens) and circles 1980 and later, open black squares (herbarium specimens) and circles before 1980, small red squares in addition to MEINUNGER & SCHRÖDER 2007], fertile male (large blue dots) and fertile female (large red dots) populations. – Base map by H. BLATT (Friedberg); map composition: Zentralstelle Deutschland (www.moose-deutschland.de).

Figs. 2–3. Antheridial receptacles of *Lunularia cruciata*. – **2**. Male thalli with antheridial receptacles and half-moon shaped gemma receptacles. **3**. Two antheridial receptacles, the epidermis of the left one lifted in order to expose the ellipsoidal antheridia filled with white masses of spermatozoids. – Scales: 10 mm (2), 1 mm (3).



Figs. 4–7. Archegonial receptacles of *Lunularia cruciata*. – **4**. Female thalli with archegonial receptacles (arrows). **5**. Longitudinal cross-section through an archegonial receptacle. **6**. Archegonial receptacle with mature basilateral archegonia (stained with cotton blue) seen with the light microscope. **7**. Mature archegonium. – Scales: 5 mm (4), 1 mm (5), 200 µm (6), 50 µm (7).

Since the publication of the first distribution maps by Frahm (1973) and Düll & Meinunger (1989), *L. cruciata* has obviously spread. Whereas, in the past, most of the populations occurred in the western area, the species can now also be found regularly in the eastern parts of Germany. *L. cruciata* prefers lower elevations, the valleys of large rivers and urban areas. Above 500 m altitude, it becomes rare. In the south of Germany, it reaches 630 m altitude in the Neckar valley east of Dauchingen (Schoepe 2005).

The mapping of the distribution of sterile plants is mainly based on data from Meinunger & Schröder (2007).

Records of male plants
(Fig. 1)

4122 SO: Holzminden, Stadtpark, Thomaskirchweg, lehmige Erdböschung [= loamy soil-slope], 120 m, 25.III.2009, M. Preussing (STU).

5208 SO: Bonn, Poppelsdorf, Botanischer Garten [= botanical garden], Nees von Esenbeck (1838).

5817 SO: Frankfurt, Botanischer Garten [= botanical garden], 21.II.2008, R. Kirschner (FR, STU).

7421 SW: Tübingen, Botanischer Garten [= botanical garden], Farntälchen, 430 m, X.2002 and 12.I.2005, M. Nebel, M. Preussing (STU).

Records of female plants
(Fig. 1)

4008 NO: Sierksfeld 3 km NE Coesfeld, end of March/beginning of April 1957–1966, Neu (1967).

4222 NW: Höxter, Corbiestraße 5, Mauer am [= along a wall] Grube-Bach, Spritzwasserbereich [= spray zone], 100 m, 5.III.2009, M. Preussing (STU).

5208 SO: Bonn, Poppelsdorf, Botanischer Garten [= botanical garden], Gewächshaus [greenhouse], 2005, Frahm (2006).

5817 SO: Frankfurt, Botanischer Garten [= botanical garden], 2.V.2008, R. Kirschner (FR, STU).

7121 SO: Waiblingen, Remsaue [= floodplain of the river Rems], Steinschüttung am Ufer [= rock fill along a riverbank], 220 m, 12.IV.2009, M. Nebel (STU).

Record of sporophytes
(Figs. 8–13)

5817 SO: Frankfurt, Botanischer Garten [= botanical garden], 23.VII.2008, T. BUTTERFASS (FR).

4 Ecology of *Lunularia cruciata*

L. cruciata is a nutrient indicator found in moist to wet (sometimes flooded), alkaline, eutrophic to highly eutrophic, shaded habitats that are often disturbed. It is frost sensitive.

The species is distributed mainly on banks along rivers with little fluctuation of water level; on loam, alluvial loam and alluvial loam-covered stones, boulders and concrete; on steep loamy slopes, on exposed tree roots and soil-covered logs. As well as being found alongside flowing freshwater it appears as a horticultural weed in and around glasshouses, in gardens and parks, in churchyards, sometimes also on railway stations (LOOS 1991) growing on moist soil in the shadow of walls and in gaps between sidewalk flagstones. It is usually associated with the following liverworts and mosses: *Marchantia polymorpha* ssp. *ruderalis*, *M. polymorpha* ssp. *polymorpha*, *Pellia endiviifolia*, *Conocephalum conicum*, *C. salebrosum*, *Platyhypnidium riparioides*, *Cratoneuron filicinum*, *Brachythecium rutabulum*, *B. rivulare* and *Oxyrrhynchium hians.*

In Central Europe *L. cruciata* grows under ecological conditions that are close to those described for the British Isles (PATON 1999). In Germany, it was originally only found in greenhouses and botanical gardens, but it since has established itself primarily on banks of nutrient rich rivers in locations with mild winters. Most populations are located in a small belt near the water, because a great amount of the gemmae are washed ashore here. The frost decreasing effect of water spray in this habitat is also important. Even after frosty periods with ground temperatures from –20 °C, vital thalli can be found here. TREMP & VULPUS (1997) observed prospering populations of *L. cruciata* on riverbanks downstream from or below sewage works.

5 Observations on fertile populations of *Lunularia cruciata*

Boat-shaped, purplish antheridial receptacles (Fig. 2) were discovered on 21 February 2008. After detaching the covering epidermis of antheridial receptacles, ellipsoidal white antheridia arranged in two rows (Fig. 3) could be detected. In the light microscope, the antheridia were found to be immersed in the receptacles containing densely packed masses of spermatozoids. On 2 May, many thalli with conspicuous white, scaly, nipple-shaped archegonial receptacles (Figs. 4, 5) were intermingled with antheridial thalli. Mature archegonia developed laterally at the base of a stout column covered by white imbricate scales (Figs. 6, 7). During summer, herbaceous plants developed between the thalli and became dominant. In the first week of July, no sporophytes were observed, but on 23 July and during August, sporophytes at all stages of development occurred along with archegonial receptacles that apparently had ceased to develop, probably because of ineffective development of archegonia or lack of fertilisation by spermatozoids. The column enclosed by the imbricate scales of the archegonial receptacle elongated considerably, exposing its apex, which became campanulate (Fig. 8). Eventually after maturation, 1–3 sporophytes became apically exposed from each of the four finger-like involucral arms (Figs. 9–11). The sporophyte was composed of a seta and a capsule that opened with four valves, and exposed spores and bispiral elaters (Figs. 12, 13). Sporophytes were not found on 8 September 2008.

In another, smaller population of *L. cruciata* in the botanical garden of Frankfurt, represented by a few thalli covering only few square centimetres shaded by a mugo pine in the alpine garden, only gemma receptacles were found during the whole observation period.

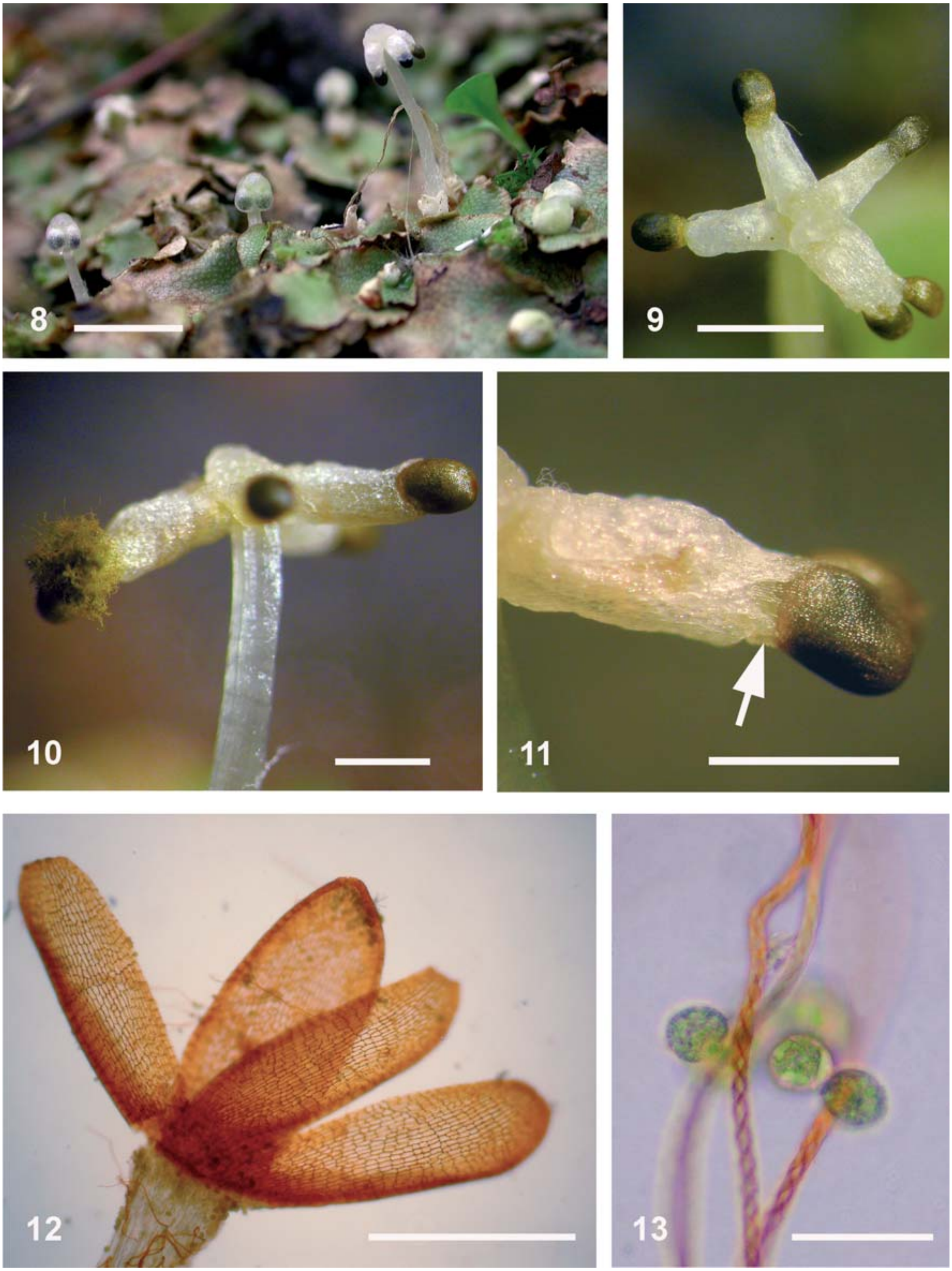
6 Discussion

Morphology

The studied morphology confirms the results of previous contributions. Cellular details of antheridial and archegonial receptacles were illustrated by SAXTON (1930), BENSON-EVANS & HUGHES (1955) and PATON (1999). Sporophytes were first described and illustrated by MICHELI (1729). Cellular details of sporophytes were illustrated as seen with the light microscope by SAXTON (1930), by transmission electron microscopy by SHIMAMURA & DEGUCHI (2002), and by scanning electron microscopy of spores and elaters by PEROLD (1995). Colour photos of all developmental stages (Figs. 2–13) are provided for the first time in this paper.

Phenology

The periods of antheridial and sporophyte development in February and July–August, respectively, correspond to the periods recorded from France (NICOLAS 1929), Portugal (SÉRGIO & VIANA 1973), and South Wales (BENSON-EVANS & HUGHES 1955). NEES VON ESENBECK (1838) recorded antheridia for a German specimen collected in March. These periods do not agree with the season of sporophyte development given as January to March in Spain by SCHUSTER (1992), who assumed a genetic basis for such phenological differences. SÉRGIO & VIANA (1973), however, who investigated 8–46 populations of *L. cruciata* in each of the four seasons in Portugal, found that antheridial, archegonial and



Figs. 8–13. Sporophytes of *Lunularia cruciata*. – **8**. Thalli with sporophytes at different stages of development. **9**. Sporophytes extending from four involucral arms seen from above. **10**. Sporophytes extending from involucral arms in lateral view, with the capsule at the left opened and exposing elaters and spores. **11**. A single sporophyte with spore capsule and apex of seta (arrow) separated from the involucral arm in lateral view. **12**. Valves of an opened, emptied spore capsule (mounted in 5 % aqueous KOH solution) seen with the light microscope. **13**. Elaters and spores seen with the light microscope (5 % KOH). – Scales: 5 mm (8), 2 mm (9), 1 mm (10), 500 µm (11, 12), 50 µm (13).

sporophytic stages can be formed in every season of the year, but with antheridial stages being predominant in winter (January to March), archegonial stages in spring (April to June) and sporophytes in summer (July to September). The sequence of development of antheridia (in February) and archegonia (in May) leading to the development of sporophytes in July–August indicates that different climatic conditions are possibly required for the optimal development of each stage, including initially low temperatures and short day lengths which gradually rise over several months (Benson-Evans & Hughes 1955). In our observations, we found antheridia in mature stages in early spring. According to Benson-Evans & Hughes (1955), the development of antheridial receptacles is initiated in late summer and finishes in the spring of the subsequent year, whereas archegonial receptacles complete their development within a single vegetation period. In contrast to the development of archegonial receptacles that could be induced in the laboratory, antheridial receptacles were not observed in laboratory culture (Benson-Evans & Hughes 1955).

Initiation and maturation of antheridial receptacles apparently require a complex sequence of different environmental conditions. These specific requirements in addition to the distribution of male and female thalli explain the general rarity of sporophyte development outside areas with Mediterranean conditions. We assume that male thalli have not recently immigrated into Central Europe, but were present and unrecognised over the time, which is indicated by the historical records of not only archegonial receptacles, but also antheridial receptacles and/or sporophytes from Austria and Germany (Leitgeb 1881, Nees von Esenbeck 1838). Leitgeb (1881) did not explicitly state the origin of the sporophytes which he described, but wrote that the species was common in "our gardens" (i. e. in Austria, probably in Graz). Nees von Esenbeck (1838) expressly based his detailed description of antheridial and archegonial receptacles on material from Germany (botanical garden of Bonn) and the description of sporophytes on Italian material (J. Raddi's collection), because sporophytes did not develop in Germany. The note about the presence of male and female thalli in the botanical garden of Bonn by Müller (1906–1911) presumably originated from the observation by Nees von Esenbeck (1838), but afterwards became obscure to Müller himself and was omitted from his later publications (Müller 1954).

The recent observations of antheridial receptacles in Tübingen and Frankfurt, and sporophyte development in Frankfurt, might indicate the influence of climatic changes in Germany on phenology. This change could be characterised as tending towards a "Mediterranean-type" as indicated by other records of sporophytes. This observation agrees with the general poleward range-shifting of geographic distribution and phenological changes in plants and animals as a result of climate change (Parmesan et al. 1999, Thomas & Lennon 1999, Walther et al. 2002).

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