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# *Vaccinium majuscula* Chassagne *ex* Fridl. *in* French Massif central and its related Scandinavian *Oxycoccus palustris* var *major* Lange

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## Abstract

The south-western limit area distribution of several arctic relict species (cranberries, *Betula nana*) occurs in the French Massif central. Although especially localised in a few relict bogs, *Vaccinium* sect. *Oxycoccus* show an unexpected cytological diversity with diploids (supposedly *V. microcarpum*) in several localities of the Massif central sometimes growing in mixture with tetraploids (putatively *V. oxycoccos*). For the first time in France, we identified hexaploid cranberries. These plants correspond to « *Oxycoccos quadripetala* (Gilib.) var. *majuscula* » Chassagne a large, highly floriferous pioneer taxa of lacustrian mires. *Oxycoccus palustris* var *major* Lange is also a large leaves cranberry but collected in the vicinity of Oslo. Respectively described from Auvergne in 1957 and from Scandinavia in 1883, these two plants have been ignored by all botanists and remained absent from botanical literature, which is why we typify them here. They could correspond to the same species. Then, a new ecological and evolutionary understanding of cranberries is possible. In any case, this underlines the extreme richness and originality of the Auvergne peatlands, which are now home for three species of cranberry among the four known in the world: *V. microcarpum* and *V. oxycoccos* (mostly ombrogenous peatland) and, the apoendemic *V. majuscula* (only in topogenous mire).

***Keywords***
Auvergne France
*Vaccinium* sect. *Oxycoccus*
Hexaploidy
Southern boreal relict species
*Desarmillaria ectypa*
Peatland plant biology

## Résumé

Le Massif central français représente la limite sud-ouest de distribution de plusieurs espèces arctiques relictuelles (*Betula nana*). Bien que particulièrement localisés dans quelques tourbières, les *Vaccinium* sect. *Oxycoccus* y montrent une diversité cytologique inattendue avec des diploïdes (supposément *V. microcarpum*) dans plusieurs localités du Massif central qui poussent parfois en mélange avec des tétraploïdes (supposément *V. oxycoccos*). Pour la première fois en France, nous avons identifié des canneberges hexaploïdes. Elles correspondent à « *Oxycoccos quadripetala* (Gilib.) var. *majuscula* » Chassagne, un taxon très original (inflorescences portant 3-5 fleurs roses, feuilles atteignant souvent 15x7 mm) pionnier des tourbières lacustres minérotrophes. *Oxycoccus palustris* var. *major* Lange est également une canneberge à grandes feuilles mais collectée dans les environs d'Oslo. Respectivement décrites en Auvergne en 1957 et en Scandinavie en 1883, ces deux plantes ont été ignorées par tous les botanistes et ne sont pas citées dans les flores ni les inventaires botaniques ; c'est pourquoi nous les typifions ici. Elles pourraient correspondre à la même espèce ; ces deux hexaploïdies permettent une nouvelle compréhension écologique et biogeographique des canneberges. On soulignera la richesse et l'originalité des tourbières d'Auvergne, qui abritent aujourd'hui trois espèces de canneberges très menacées parmi les quatre connues dans le monde : *V. microcarpum* et *V. oxycoccos* (tourbières ombrogènes) et l'apoendémique *V. majuscula* (tourbières topogènes).

***Mots-clés***
Auvergne France
*Vaccinium* sect. *Oxycoccus*
Hexaploïdie
Espèces boréales sud relictuelles
*Desarmillaria ectypa*
Biologie des plantes de tourbières

## Introduction

For more than two centuries, the taxonomic interpretation of *Vaccinium oxycoccos*, a circumarctic polyploid complex from America and Eurasia, has been controversial. However, numerous cytogenetic, ecological, and morphological studies provide more nuanced and often contradictory results regarding the possible distinction of taxa.

In Canada, diploids and tetraploids often occur in the same localities (Smith *et al.* 2015), but overall, in North America, diploids are more northerly, and the southernmost populations appear to be predominantly or exclusively tetraploids (Darrow *et al.* 1944). As a morphological continuum would be observed and correlation between morphology and cytotypes appears unstable, Vander Kloet (2009) only recognises two cranberries species in the world, all of them present in North America:

- *V. macrocarpon* (Ait.) Pursch, the most vigorous with prostrate stems that reach one meter long, bears lateral flowers at the base of current year shoot. Native from northeastern America, escaped from cultivation in some northwestern states. It was the first species of *Vaccinium* genus to be widely cultivated (before blueberries = *V. corymbosum* s.l. and hybrids). It is the most widely consumed by humans (fruits 1.3-2 cm diameter): it has been intensively cultivated in North America since the beginning of the twentieth century (nowadays ca 380,000 tons per year, on 22 000 ha versus 15 000 ha a century ago). More recently it was also cultivated in Chile and northeastern Europe and in few provisional fields in France. Introduced since the 18th century in Germany (Trochain 1933 a, b, c), it is sometimes sub-spontaneous in some peat bogs as in Switzerland (Aeschiman & Burdet 1994) but considered as invasive in Germany, Great Britain, Lithuania (Weeda 2010; Gudzinskas 2014).
- All other cranberries (smaller in all their parts, terminal flowers) are named *V. oxycoccos* L. by Vander Kloet (2009). Regardless of their origin and taxonomic rank, binomial combinations including epithets *intermedius*, *microcarpum*, *microphyllus*, *ovalifolius*, *palustris*, or *quadripetalus* are considered to be synonyms of *V. oxycoccos*.

In Europe, diploids are similarly dominant in the far north but, further south, particularly in the Alps, they would be rather localised at altitude. Tetraploids are more widespread (Fig. 1) and

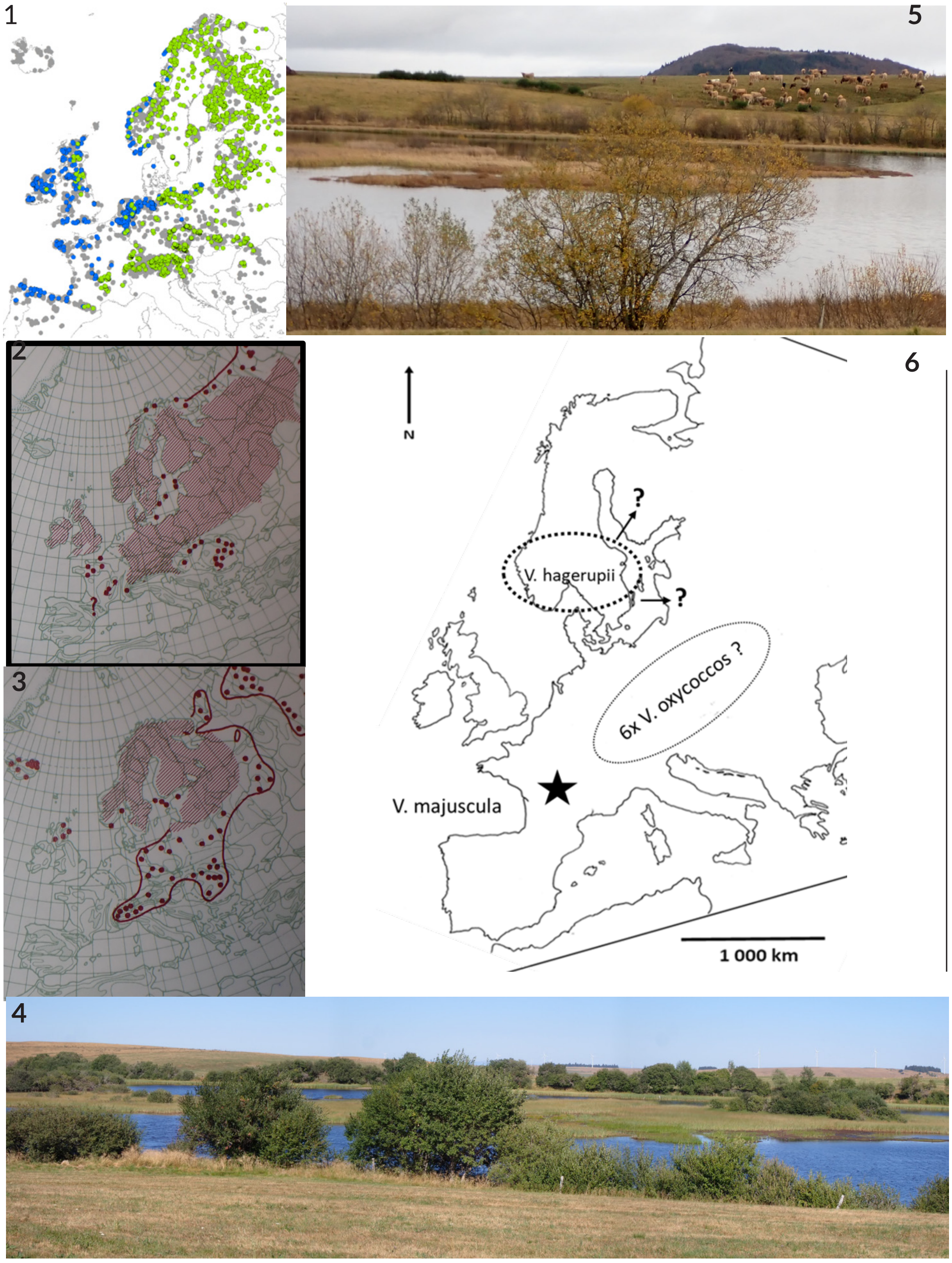

Figure 1 – Distribution of cranberries. **1**: Distribution of the Class *Oxycocco-Sphagnetea*: in blue order *Sphagno-Ericetalia tetralicis* (Atlantic) and in green *Sphagnetalia medii* (Jiroušek *et al.* 2022).

*V. oxycoccos* (**2**) and *V. microcarpum* (**3**) distribution area in Europe. Outside the hatched area, the cranberries occur very sparsely (Hultén & Fries 1986). Note than cranberries are with no doubt absent from the Pyrenees as native species; they have been recently introduced for studies on global warming in some peatland!

**4-5**: Lac des Bordes type locality of *V. majuscula* in early winter and summer.

**6**: Hexaploid cranberries in Europe. Star: *V. majuscula* from Auvergne where we also identified numerous populations of diploids (particularly eccentric, in comparison with map 3) and tetraploids. *V. hagerupii*: hypothetical distribution of Scandinavian species. 6x *V. oxycoccos*: main area where hexaploids morphologically identical to *V. oxycoccos* have been reported.

present throughout the European distribution area of cranberries (Webb 1972; Hultén & Fries 1986; Jacquemart 1997). In central Europe, analysis of hundreds of individuals from numerous localities has shown that diploids and tetraploids often live in mixtures, sometimes with pentaploids and even hexaploids (Von & Wenderoth 1994; Suda & Lysak 2001; Suda 2002). The smaller diploids are fairly homogeneous while the polyploids (4x, 5x, and 6x) are much more polymorphic.

Two cranberries (= sect. *Oxycoccus*) can thus be distinguished in Europe (Fig. 1): diploids with narrow blades (ca. 2-4 mm wide), hairless pedicels, small fruits more or less pyriform (putatively *V. microcarpum* s.l.) and larger polyploids, with 3-6 mm wide blades, hairy pedicels and larger globose fruits (putatively *V. oxycoccos* s.l.). Then, two species, *V. oxycoccos* L. and *V. microcarpum* (Turcz. *ex* Rupr.) Schamalh. are recognised in several recent European floras (Popova 1972; Aeschimann & Burdet 1994; Eggenberg & Möhl 2013; Tison & Foucault 2014). In Eastern Europe and Northern Asia *V. oxycoccos* is generally named *Oxycoccos quadripetalus* Gilib. (Shishkin & Bobrov 1967).

Then, in France, the two European cranberry species have been reported in the north-east of the country for about a century. *V. microcarpum* is only reported from the most acid *Sphagnum* bogs of Savoie and Massif central by C. Sauvage (1982). But these two taxa are not recognised on the other side of the French border (Lambinon *et al.* 2005) and not mentioned in several floras (Coste 1901; Fournier 1947). Their distribution in France and Switzerland remains unclear due to numerous confusions (Aeschimann *et al.* 2014; Tison & Foucault 2014).

The Massif central represents the south-western limit of the European range of the sect. *Oxycoccus* (ca 44°N, between 900 and 1300 [1600] m). The destruction of the fen land and peat bogs (peat exploitation, drainage to enlarge pastures) has been massive during the last ten centuries: most of them have been transformed into meadows and wetlands, often eutrophic, or into coniferous forests. In this remote refuge, one might expect to find only the most common and resistant tetraploid plant. However, *V. microcarpum* was discovered there recently, first in the Limousin mire (Brunerye 1975, 1977). However, the cooccurrence of putative *V. microcarpum* with *V. oxycoccos* in the French Massif central has been controversial for 50 years. Tison *et al* (2014) assume that at the edge of its range, *V. oxycoccos* L. s.l. would better correspond to an introgressive taxon. As identification from the available literature is uncertain and nomenclature remains confused, unsurprisingly information on the ecology or distribution of cranberries remains approximate. Some inventories for conservation purpose (ZNIEFF 2021) even often report the “ three species ” *V. oxycoccos* + *V. microcarpum* + *Oxycoccus quadripetalus* in the same peatland! Indeed, from rapid observation several species can be identified from the different parts (isolated axis) of the same individual (see § The different axes and their growth and § Leaves).

We have measured ploidy level, observed the flowering, fruiting, and development of cranberries in several populations of the Massif central (mainly, Puy-de-Dôme, Cantal, Lozère, Haute-Loire and Limousin).

Against all expectations (cranberries being in a refuge situation, cf. above), we identified diploid in peat bogs all over French Massif central sometimes mixed with tetraploid (these observations will be detailed later). But, even more surprisingly, for the first time in France we have identified hexaploids, downstream of the Godivelle peatland complex (Compains-Bordes, Cézallier). These plants from the eastern Massif Sancy differ significantly from all other populations, as Maurice Chassagne (1957) had pointed out by proposing a variety (“ *Oxycoccos quadripetala* Gilib. var. *majuscula* ” Chassagne) which has never been taken into consideration by botanists, and whose name was not validly published as it lacks a latin description or diagnosis. However, the morphological, ecological and cytological originality of this cranberry undoubtedly makes it a distinct species. On the other hand, it clearly resembles the description of *Oxycoccus palustris* var *major* by Lange (1883) “ in Christiania ”; however, this name has not been retained by botanists either. The purpose of this note is therefore to describe these two taxa and typify these names, which could correspond to the same species and describe the biology of the French endemic cranberry *V. majuscula*.

## *Vaccinium majuscula* Chassagne *ex* Fridl., *sp. nov.*

**Syn.:** « *Oxycoccos quadripetala* Gilib. var. *majuscula* » Chassagne, Fl. Auvergne II : 235 (1957), *nom. inval. sine descr. lat.*

**Loc Type** : « Puy de Dôme : bords vaseux et herbeux des lacs des Bordes près Brion et de Chambedaze à 1150 m ».

**Diag.**: Stems, leaves and flowers larger than *V. oxycoccos* and *V. microcarpum*. Leaves white below; leaves of plagiotropic axes 13-14 [16] mm long and 4-7 mm width. Inflorescences of 3-6 flowers with hairy pedicels, ciliated sepals and pink petals. Plants hexaploid (Fig. 2 & 3).

*Typus*: « *Oxycoccos palustris* var *majuscula nobis*, Lac des Bordes (Cantal) », s.d., leg. Dr. Chassagne. Holo- : CLF289819!, Fig. 4.

**Habitat and distribution**: *V. majuscula* was probably first “ discovered ” by Charles D’Alleizette in 1933 (CLF174703) at Chambedaze lake and latter collected by Maurice Chassagne on August 7, 1936 on Chambedaze lake banks (few stems of “ *Oxycoccus* cf. *microcarpa* in mixture with var. *majuscula* ”, CLF289818!). Then Typus from Brion has probably been collected the same year. Chassagne distinguished its sample by the short description « Robuste. Feuilles grandes atteignant sept mm » and cites two localities.

*V. majuscula* has only been collected in floating *Sphagnum* carpets from three Auvergne lakes (Bordes, Chambedaze and l’Esclauze [leg. Lamotte 1846 - CLF005920]), all located in the south of the Puy-de-Dôme department.

**Other specimens in CLF**: « *O. palustris* var *majuscula* », Puy-de-Dôme, Lac de Chambedaze, forme à feuilles larges, 1 août 1963, legit R. Deschâtres CLF393811!; « *V. oxycoccos* L. var. *majuscula* Chassagne », Lac des Bordes (Compains, 63), 2-7-2012, legit Bernard, CLF104081!; Brion, Tourbières des îlots du lac de Bordes, 1200 m, A. Fridlender, novembre, 2019, ibid. fruits juillet 2021, ibid. fleurs mai 2022; Lac de l’Esclauze, A. Fridlender, mai 2023.

**Note:** plants from Bordes and other localities are cited as *V. oxycoccos auct*. in various local and French national inventories.

Figure 2 – *Vaccinium majuscula* blooming and fruiting. The surface of the sphagnum moss is covered by a carpet of large pink flowers often grouped in dense clusters consisting of 2 or 3 inflorescences each bearing 3-6 flowers (**1, 3, 4**: flowers seen in profile, and from above -4). The flowers have bright pink petals, red filaments are covered with light-coloured hairs giving them a fluffy appearance (**3**). The fruits are also grouped in tight clusters (**6**) or arranged in stars around inflorescence axis (**2**: a 6-fruit infructescence!).

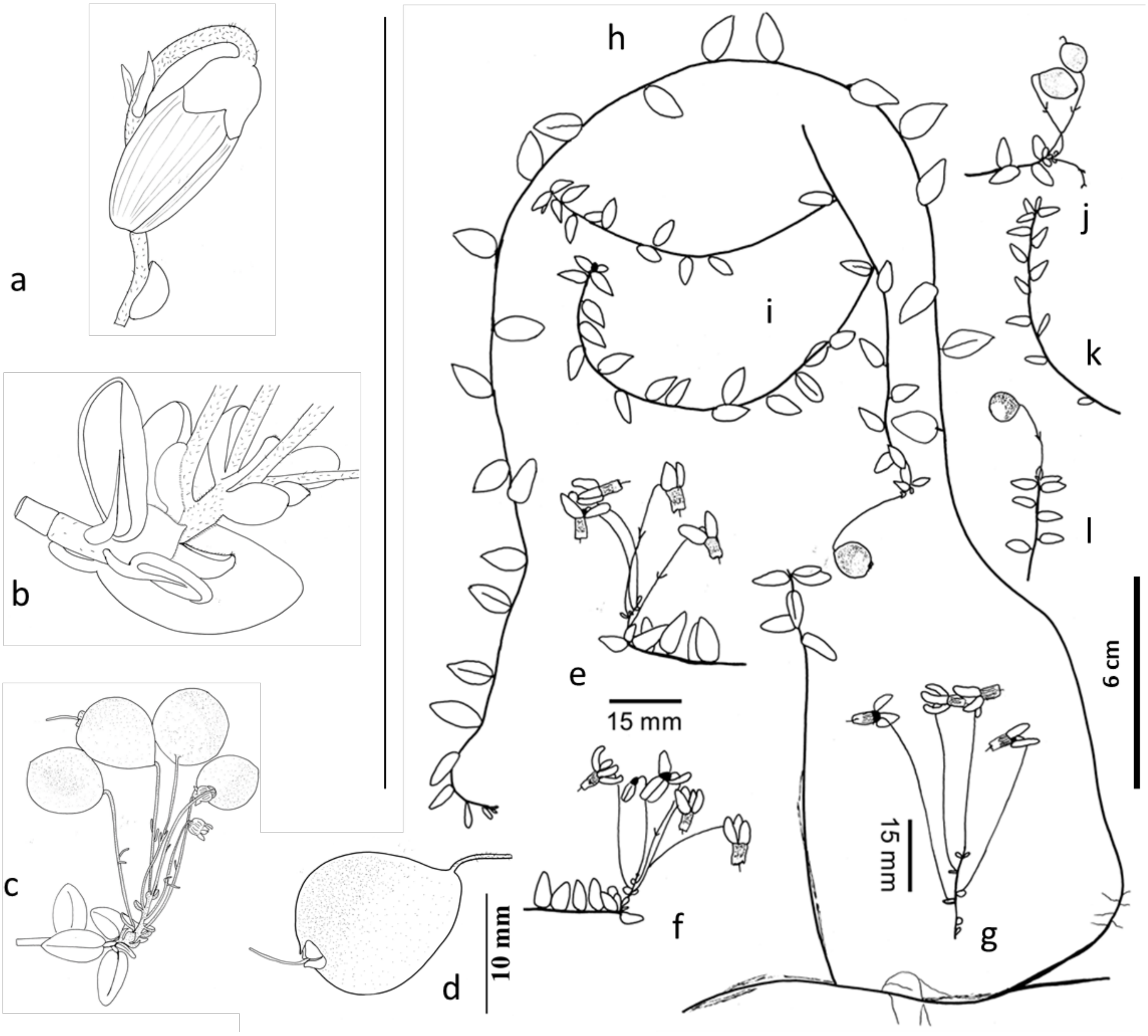

Figure 3 – *Vaccinium majuscula* stems and inflorescence.
(**a**) Flower bud, pedicel puberulent, bearing 2 bracts of 2-2.5 mm.
(**b**) The 4 terminal leaves of the previous year's axis form a rosette topped by the scales of the floral bud. A small shell-shaped bract axils each of the four floral pedicels.
(**c**) Infructescence in July with 2 aborted flowers and 4 fruits in formation.
(**d**) Pyriform fruit in early September.
(**e, f, g** - scale bar = 15 mm) The internodes of the inflorescences are more or less elongated depending on the environment, if buried or not in the mosses.
(**h**) A three-month plagiotropic axis of exploration still growing at the end of summer. Notice adventitious roots at its base; and the rhytidome desquamation.
(**i**) Short plagiotropic axis from the previous spring (n-1) bearing only one fruit (flowering year n) and two plagiotropic shoots, the most apical one end in a floral bud.
The largest leaves (ca 14-16 x 5-7 mm) are those of the plagiotropic axis of exploration (**h**).
**h, i, j, k, l**: scale bar = 6 cm.

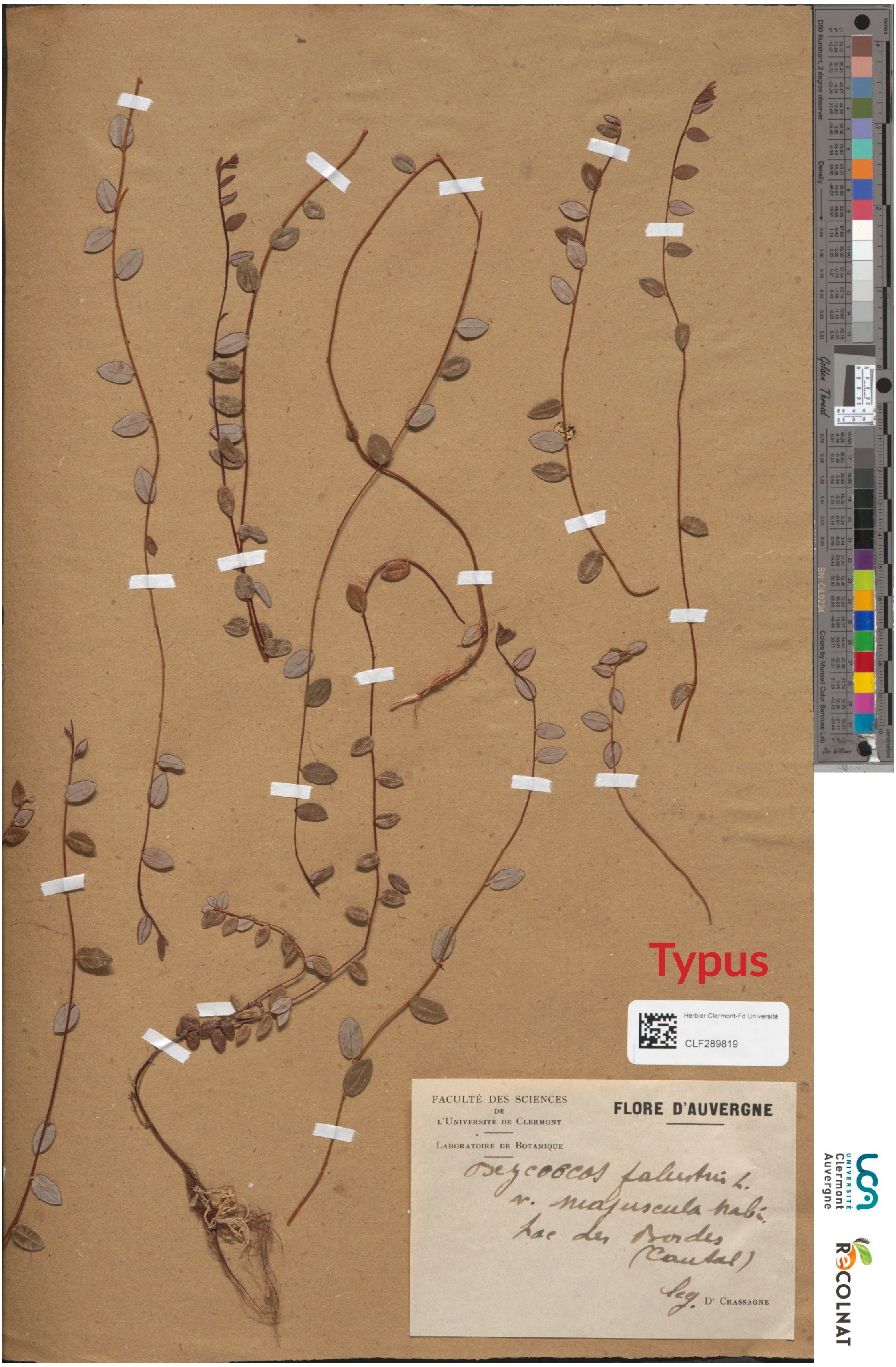

Figure 4 – *Vaccinium majuscula* Chassagne *ex* Fridl. Type specimen CLF289819. *O. palustris* var *majuscula nobis* Lac des Bordes (Cantal), leg. Dr. Chassagne.

### *The different axes and their growth*

Cranberries are dwarf shrubs with prostrate stems, early rooting. The main stems are underground and only the lateral branches and twigs are exposed as in many other *Vaccinium* (Camp 1942). Quickly, sometimes even before the end of their growth, some stems are buried under the *Sphagnum*. Indeed, the mosses grow almost all year round, gradually burying all plants in the bog, as illustrated by the *Drosera* observed in spring (Fig. 5.1). In early spring, the 2-5 cm stem bears 2-5 leaves (some of them almost white, without chlorophyll) and is compressed between the moss. The depth to which the dead leaves of the previous year's *Drosera* summer rosette is found, in relation to the present spring bog surface, allows us to estimate the length of growth of the bryophytes since the previous autumn.

Stem moss elongation during winter is therefore important (some centimeters here), but it largely depends on the microhabitat. In northern Europe, up to 10 percent of the elongation of *Sphagnum* axes takes place during winter (Küttim 2020). Also, in some places, some cranberry spring stems are sometimes buried under the moss before the end of summer, while in other (more xeric) places stems older than one year are still lying on top of the mosses (Fig. 5).

In various peatlands, we observed than basitonic axes are emitted twice a year, at the beginning of spring and then at the end of summer in various *Ericaceae* like *Vaccinium uliginosum* or *Andromeda polifolia*, probably to resist the permanent burial by the *Sphagnum*.

The plagiotropic axes are lying on the peaty substratum or partially covering the other plants. At the end of their growth their internodes shorten. Some of them (spring short plagiotropic axes) end in a rosette of a few leaves in the middle of which the flower bud of the next year's terminal inflorescence is already pre-formed in the end of July (Fig. 6). Sylleptic branches that give rise to other plagiotropic axes are scarce. In spring after autumn-winter burying, they emit some orthotropic axes that can branch out more or less (Fig. 7).

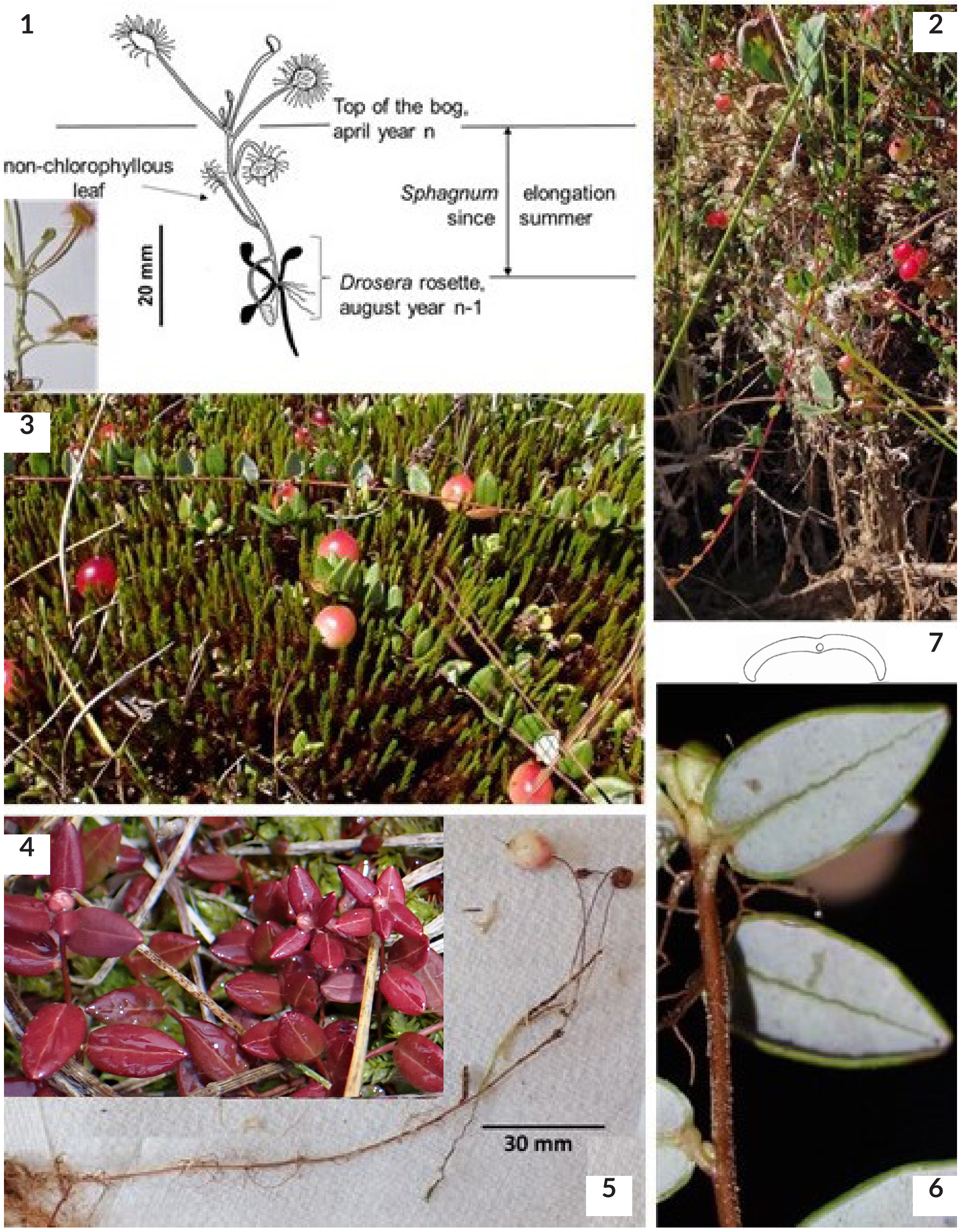

Figure 5 – *Vaccinium majuscula* biology and growing pattern to avoid burial by *Sphagnum*.
**1**: Spring stem elongation of *Drosera* sp. from previous dead summer rosette year n-1 (in black).
**2**: Plagiotropic exploring axis which in a few months can cover moss tussock, pass over *Andromeda* or *Menyanthes* leaves.
**3**: A long plagiotropic axis of exploration (P-ex). Previous year stems are no longer visible, only the fruits and the tips of some leaves are not yet buried by the bryophytes. Note that mosses' elongation speed is not the same on the whole peatland nor according to the species of mosses.
**4**: During the winter some leaves remain green, others turn red but remain alive.
**5**: year n-1 stem of *V. majuscula* has been buried during winter, in spring only the flowers were emerging, in August the fruits are buried in the moss and all the leaves are already decomposed (note the two aborted flowers).
**6**: White below wax that protect the stomata, hairs on the stem still visible in November.
**7**: Transverse section of a leaf blade: flat, only slightly recurved at the margins.

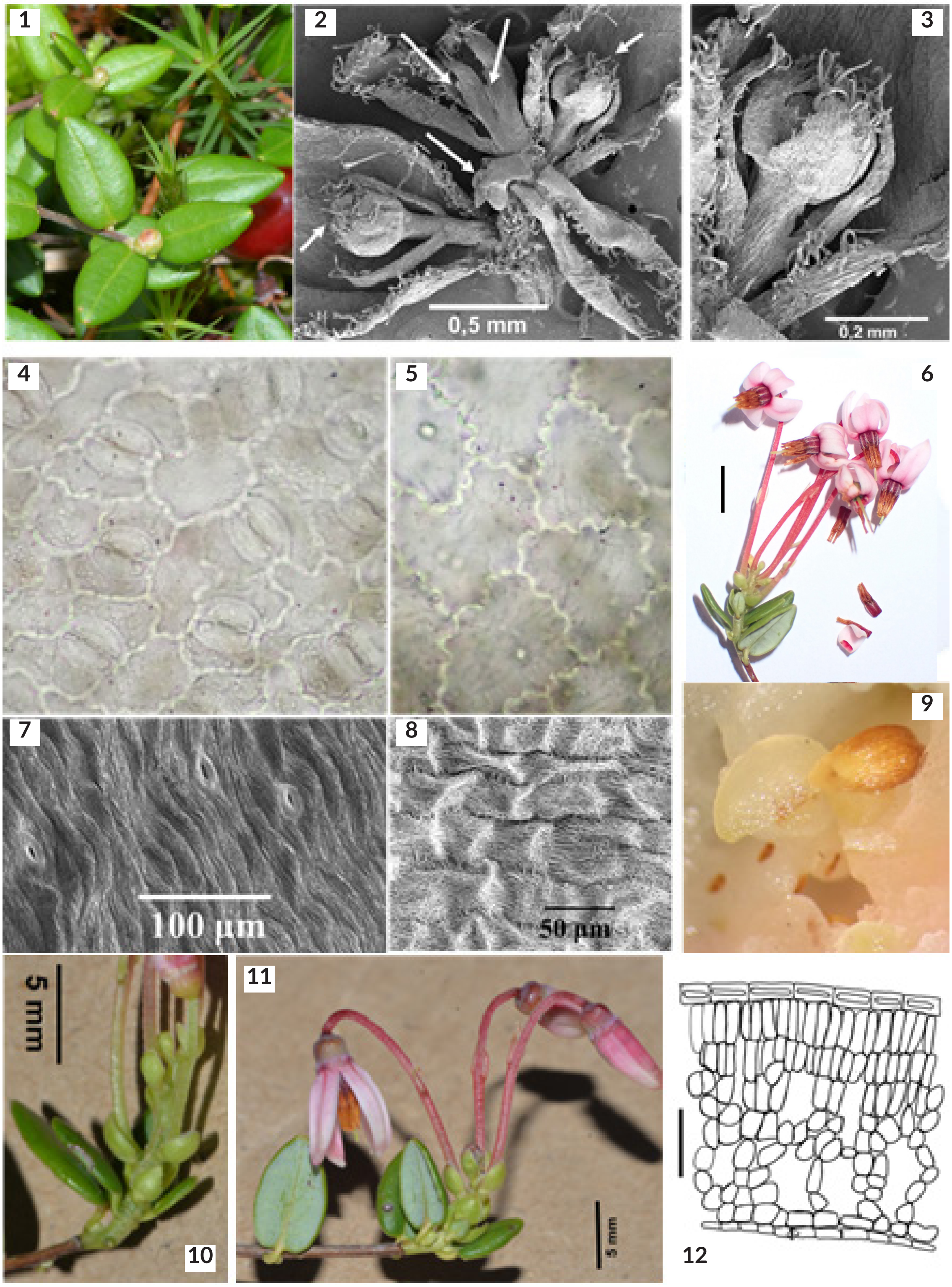

Figure 6 – *Vaccinium majuscula* biology and phenology.

**1, 2, 3, 6**: The short plagiotropic axis ends by a flower bud (see also Fig .7); its dissection (end July) shows that the 5 flowers (8-2, white arrows) are already fully preformed 10 months before flowering. Aspect of such a 5-flowered inflorescence in May (6). Note the ciliated calyx sepals (3).

**4, 5**: Leaf epidermis: the stomata are only present and abundant on the abaxial side (4), the adaxial side is formed by undulated outline cells and a thick pleated surface cuticle (5).

**7, 8:** Petal epidermis observed by SEM. Only the abaxial side (7) of the petal has stomata; folds of the petal upper surface (8).

**9:** Open fruit in August: seeds in various stages of ripening (white, brown) and many small aborted ovules, the ornamentation is clearly visible (see 4-3).

**10, 11:** The axis of the year ends in a flower bud, but its apical few millimetres remain green with a diameter greater than the totally lignified part (brown); in the following spring, after the bud has opened, it could be thought that the flowers bloom on the green stem of the year (whereas they were formed the previous year at the tip of the n-1 stem) which has led to various confusions between *V. oxycoccos* s.l. and *V. macrocarpon* (flowers on the year's shoot).

**12:** Cross section of a leaf. Aerial parenchyma developed, stomata on the adaxial side, two / three layers of photosynthetic cells, parenchyma in palisade. *V. majuscula* has anatomical characters of aquatic plants (abundance of stomata, developed air pith) but also xeric (waxy layers...). Scale bar = 100 µm.

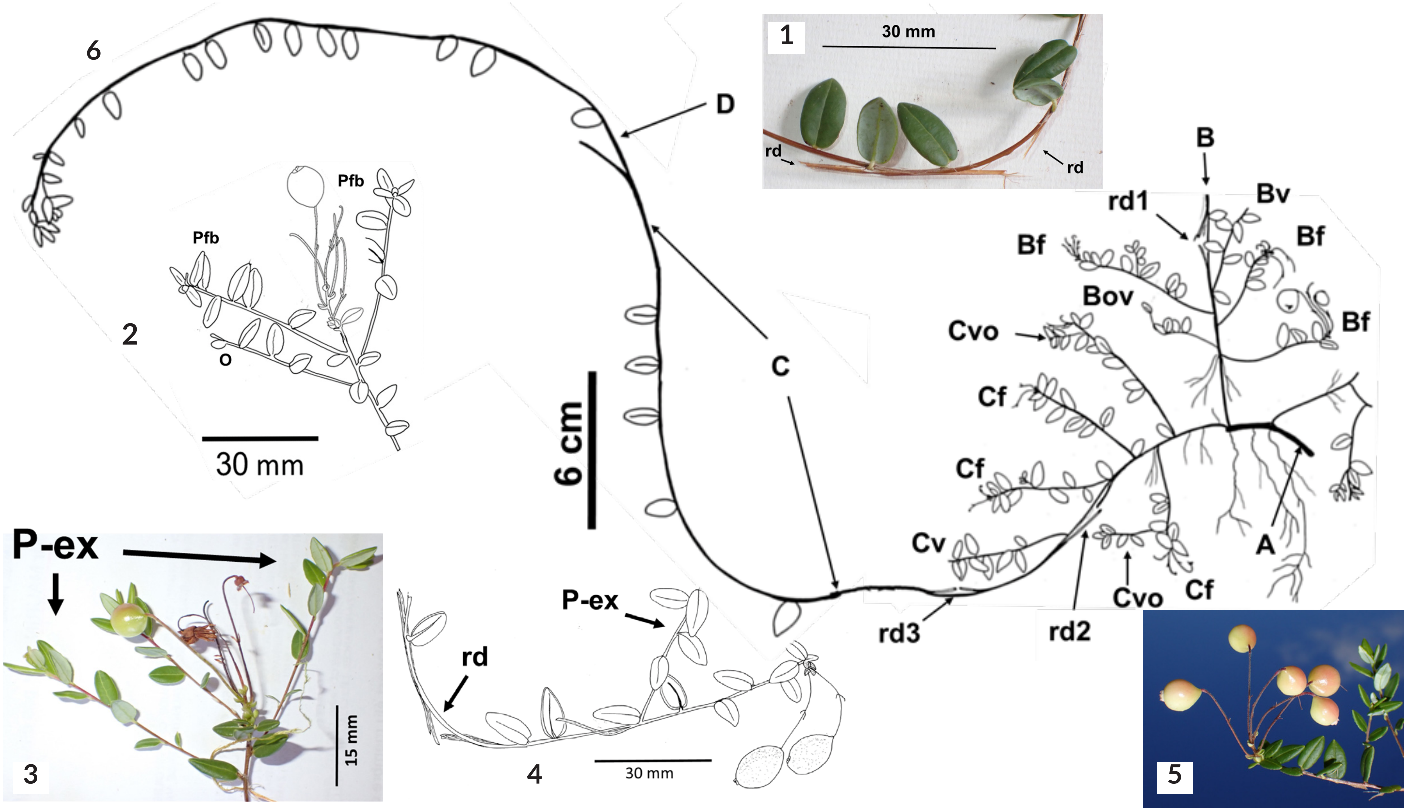

Figure 7 – *Vaccinium majuscula* biology and growing pattern.

**1**: Aspect of the desquamation of the rhytidome (rd rhytidome desquamation) on a plagiotropic axis a few months old.

**2**: The short plagiotropic axis of the year n-1 end by an infructescence (only one fruit drawn out of the 5 fertile ones). Two sympodial axes developed in early spring when the inflorescence exerted a strong apical dominance: they are short and terminate in a flower bud (Pfb). The third axis, more distant, from inflorescence remains vegetative but has stopped growing in summer.

**3**: The subterminal buds of an axis similar to (2) but with only one terminal fruit (the other flowers have aborted), have not developed in the spring when flowering. They begin their development in the summer, when they are free from apical sexual dominance, and then they produce plagiotropic axes of exploration (vegetative P-ex).

**4**: The plagiotropic exploration axis is emitted in early summer (arrow) on a one-year old axis which starts to separate physiologically from the other parts of the individual (rd).

**5**: The orthotropic axes are short, their leaves sometimes being almost as large as those of the short flowering plagiotropic axis, note the five-fruit infructescence (common in *V. majuscula*, unknown in other cytotypes).

**6**: The individual carried by axis A (n-2) has emitted a long plagiotropic axis B rooted and widely branched at its base and whose distal part has been physiologically separated from the rest (rd1 - rhytidome desquamation). All emitted axes are short (plagiotropic and floriferous -Bf- or orthotropic -Bov- and vegetative -Bv-). The C-axis (from A) is a plagiotropic summer exploration axis (P-ex) which bears short floriferous axes (Cf) at its base and near the floral parts of B. The only vegetative axes are very small orthotropic ultimate branches (Cvo) or larger for Cv axis which is beyond rd2 (desquamation marks the loss of correlation between axis). Not surprisingly the long plagiotropic part of C is still isolated by rd3 and has a new plagiotropic sympodial axis of exploration (D). The leaves on C and D are clearly larger than those of the branch part with short axes (most of them floriferous).

Then, the spring plagiotropic axes are generally shorter (5-10 cm and often bear a terminal flower bud) than the summer plagiotropic axes, which stop growing in early autumn and bear much larger leaves. These long, late plagiotropic shoots rapidly elongate by several decimetres: they explore the space and quickly colonise the mire surface, forming a carpet of bright green leaves (Fig. 5).

The density of long summer plagiotropic axes is higher on the mire margins where they may intertwine with the *Menyanthes trifoliata* L. and *Comarum palustre* L. in floating *Sphagnum* carpet, and along the banks of *Scheuchzeria palustris* hollows (Fig. 8).

From the second year, the rhytidome of the half-buried stems in *Sphagnum* hummocks desquamates, but it may occur on stems a few months old (so that the terminal part of the axis separates quite rapidly from its base); this “ abscission ” of the terminal parts of the axes differs from that of the leaves since it is the oldest part that usually disappears first.

It is therefore difficult to follow the architecture of this subterranean ligneous, which axes separate from each other sometimes from their first year and completely in their second or third year.

Careful observation of many plants in situ shows (Fig. 3, 5 & 7) that the axis correlations of cranberries resemble those of other fruit shrubs and tree fruits (Champagnat 1965a, b). The short axe are flowering stems and the apical dominance decreases on the most distant buds (and 2/3 months after flowering), which will allow the long plagiotropic axes of exploration development. The loss of apical dominance is evidenced by the desquamation

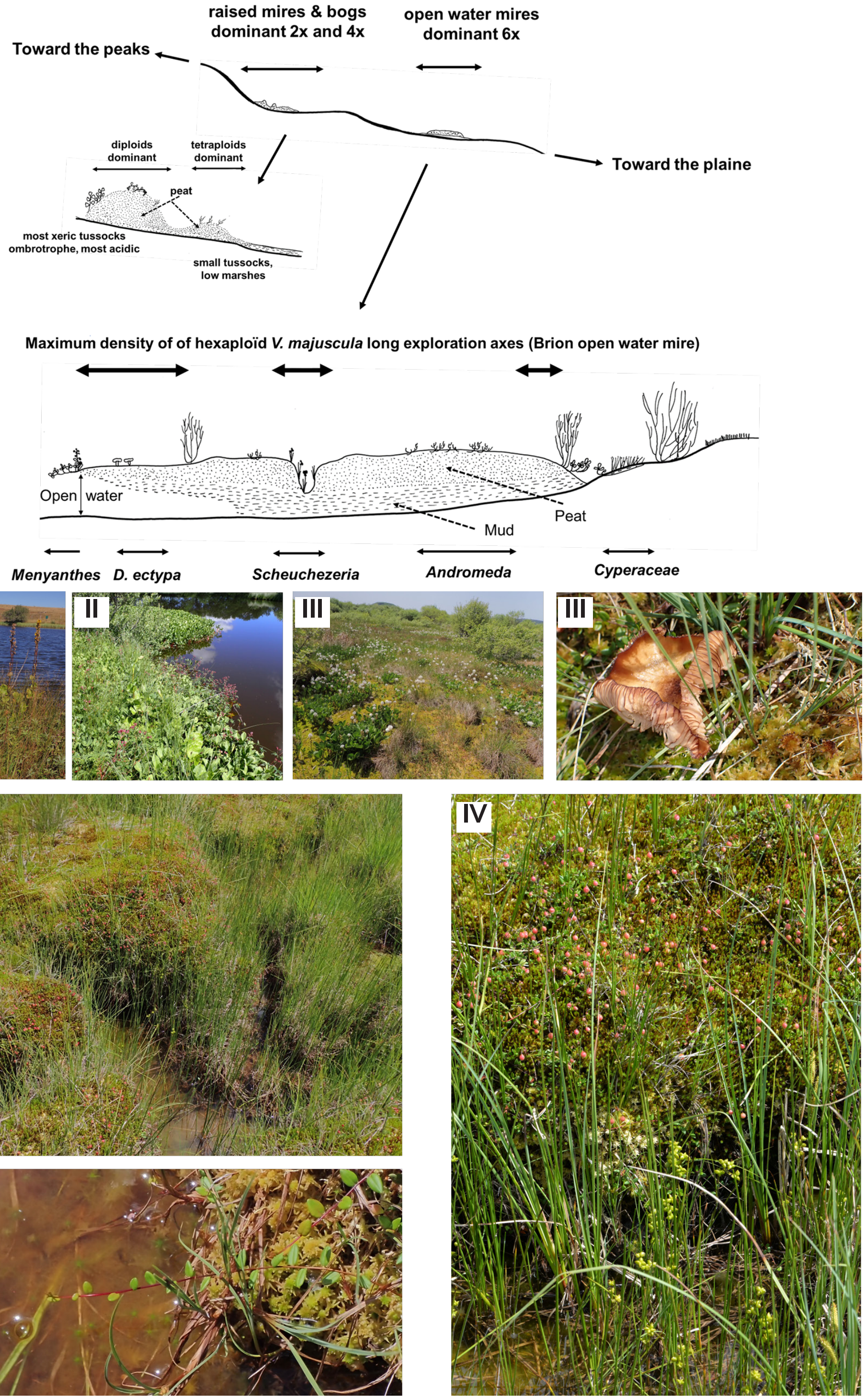

Figure 8 – Schematic comparison of ecology of sect. *Oxycoccus* three cytotypes in Auvergne.

In ombrotrophic peatland (maximum physiological dryness, high acidity) the diploid (2x) is dominant on the highest tussocks (dried or active hummocks), tetraploids (4x) are also present on ombro-minerotrophic mires but are predominantly found in wet stages of fens. Hexaploids (6x) are found in topogenous minerotrophic peatlands (lacustrian mires). Note that tetraploids (4x) generally occupy an intermediate position between 2x and 6x.

In the transversal profile of lac des Bordes lacustrine mire, the 6x *V. majuscula* is present everywhere, but shoot density is the highest in some parts (arrows above the diagram). Exploration and colonisation plagiotropic axes density is maximum in those microhabitats closest to, or in contact with, phreatic waters (I to IV).

**I-II**: ***Menyanthes***: young floating rafts with *Menyanthes trifoliata*, *Comarum palustre* and rare relict *Ligularia sibirica* (II).

**III**: ***D. ectypa***: location of *Desarmilaria ectypa* carpophores discovered in August 2022, among the abundant stems of *V. majuscula* and numerous *Eriophorum* on great floating sphagnum carpets.

**IV**: ***Scheuchzeria***: in *Scheuchzeria palustris* (other rare and relict species) hollows, *V. majuscula* plagiotropic exploration stems often protrude above the water like the pioneer species (*i.e. Menyanthes*) that make the floating rafts.

**V: *Andromeda***: drier or active hummocks where *A. polifolia* dominates (*Polytrichum* more abundant than *Sphagnum*).

**VI**: ***Cyperaceae***: sedge and large helophyte belt. The main peatland colonising shrubs are *Betula*, *Salix* and some young pines. Some *Picea abies* (introduced invasive species in Auvergne) are also beginning to germinate there.

of the rhytidome (Fig. 7) which precedes the abscission and sometimes possible reversals of the nature of future axes. The sympodial axes produced in spring are sexually dominated: they are short and in July their growth is completed by the formation of a terminal flower bud. The sympodial axes emitted in summer escape this domination and can grow until the end of autumn; they produce the plagiotropic exploration axes (Fig. 7.3).

The hierarchy of axes appears strong as soon as they are emitted: plagiotropic flowering axes, plagiotropic exploration axes, orthotropic axes with secondary orthotropic branches that have smaller blades than their underground plagiotropic bearing axis. Finally, the secondary orthotropic axes are even smaller.

The individual is then composed of “ central ” sexual parts with short, more or less branched axes (production of seeds likely to be disseminated) while “ peripheric ” vegetative ones (long plagiotropic axes), are free from sexuality and explore the peatland which they can rapidly colonise.

The detached parts of the axes reconstitute “ new individuals ”. The cranberries in a bog thus correspond to a few potentially immortal clones.

## *Leaves*

The leaf blade is bright green above, white below with a midrib clearly visible. The underside is covered with a waxy layer which protects stomata (abundant on the underside but absent on the adaxial side). The leaves are very slightly recurved on the margins in contrast to the ones of other cytotypes which are strongly curved and sometimes almost folded (Fig. 5 & 6).

The leaves overwinter without visible damage and remain green and alive for about 10-15 months on the aerial stems but many of them are buried after only a few months by the growth of the bryophytes so that they turn red and then brown and quickly disappear, probably decomposed by fungi, since in the following spring very few are seen in the young peat.

The bud correlation that exists during axis formation (cf. supra) is also visible in the heteroblastic development of the leaves: those of the plagiotropic exploration axes have twice as large blades as those of the orthotropic axes (Fig. 3, 7 & 9).

Only meticulous observation of plants in nature makes it possible to follow the links between the different axes: if they are pulled, they break easily so that the individual (Fig. 7) is divided into various parts, each of which will be made up of a single type of axis (long plagiotropic, short orthotropic branched...). When these parts, particularly leaves on these axes, are observed separately (*i.e.* in herbarium specimen), the same individual can be interpreted as different species or, on the contrary, as evidence of a continuum. In fact, some consider that there is a leaf continuum with no real relation between leaf dimension and ploidy level (Vander Kloet 1983; Ravenko 1990). On the other hand, if we compare leaves from same axis types and from the same place along the stem (on a given plagiotropic or orthotropic axis, the terminal leaves become progressively smaller), then the differences between the Auvergne cytotypes are clear (Fig. 9). Blade width and length are reliable taxonomic characters as long as the position of the leaves is specified.! But as heteroblasty is generally not considered in cranberries description, it is illusory to compare the dimensions provided in the literature to distinguish species.

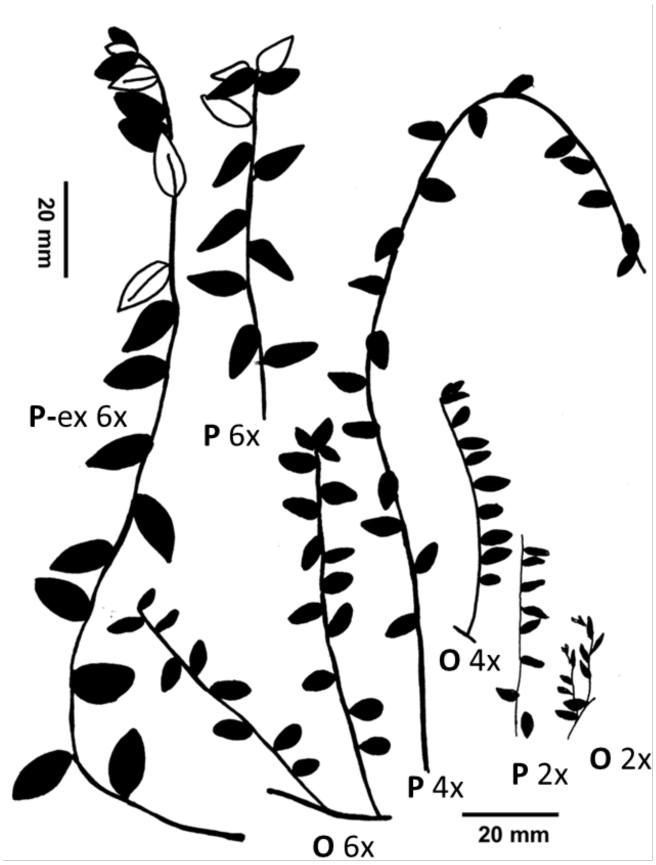

Figure 9 – Apparent continuum of leaf dimension amongst various cranberriy individuals from Massif central. All the leaves are represented at the same scale from individuals whose ploidy has been previously measured by flow cytometry. Leaf blade size varies along the stem and apparently from one stem to another within the same clump. But in fact, the length and width of the median leaves of a stem correspond to the nature of the axis (orthotropic versus plagiotropic) and the ploidy level of the individual. **O**: orthotropic axis. **P**: short plagiotropic axis often floriferous. **P-ex** plagiotropic axis of exploration (vegetative). **2x, 4x, 6x**: di-, tetra-, and hexaploid individual.

In *V. majuscula*, the middle leaves of the plagiotropic axes measure 10-11 x 5-6 mm on the “ short ” spring axes (most of which will become flowering the next year) but 13-14[16] x 6-7 mm on the long exploratory plagiotropic axes (mainly emitted in summer and growing until the beginning of winter). The median leaves of orthotropic axes have much smaller blades (6-8 x 3-4 mm). The terminal leaves of the axes (and those of the apical rosettes) are always much smaller.

## Flowers

When *V. majuscula* blooms the mosses are then covered by a spectacular dense carpet of large flowers clustered in 3-5, with four light pink revolute petals (Fig. 2). Pedicels are red and puberulent mostly long of (15) 20-35 (40) mm (sometimes very short or much longer if the terminal rosette of the axis has been buried under sphagnum moss) with two linear bracteoles 1.5-2 (2.5) mm long. While 70-80% of the inflorescences of di- and tetraploid individuals (*i.e. V. microcarpum* and *V. oxycoccos*) from Auvergne are uniflorous (Fig. 10.9), 80% of the inflorescences of *V. majuscula* have 3 to 5 flowers (35.2% to 4 flowers). The sepals are slightly ciliated (Fig. 6.3). Revolute part of petals 5-6(7) x 2-3 (4) mm, pink (sometimes pinkish red but not red as in other cytotypes).

The stamens are about 4 mm long (Fig. 11), larger and not as well-proportioned as those of other cranberries, and the anthers are covered with warts (small mamelon-like folds). The filaments are purplish and have white hairs on them which give them a nice slightly fluffy appearance (Fig. 2).

Plants of the type population of Bordes, apparently flower only once in early spring (in May, but 2 flowers in CLF104081!, collected in July 2), whereas the other species often have a second flowering in late summer (even if it concerns few individuals).

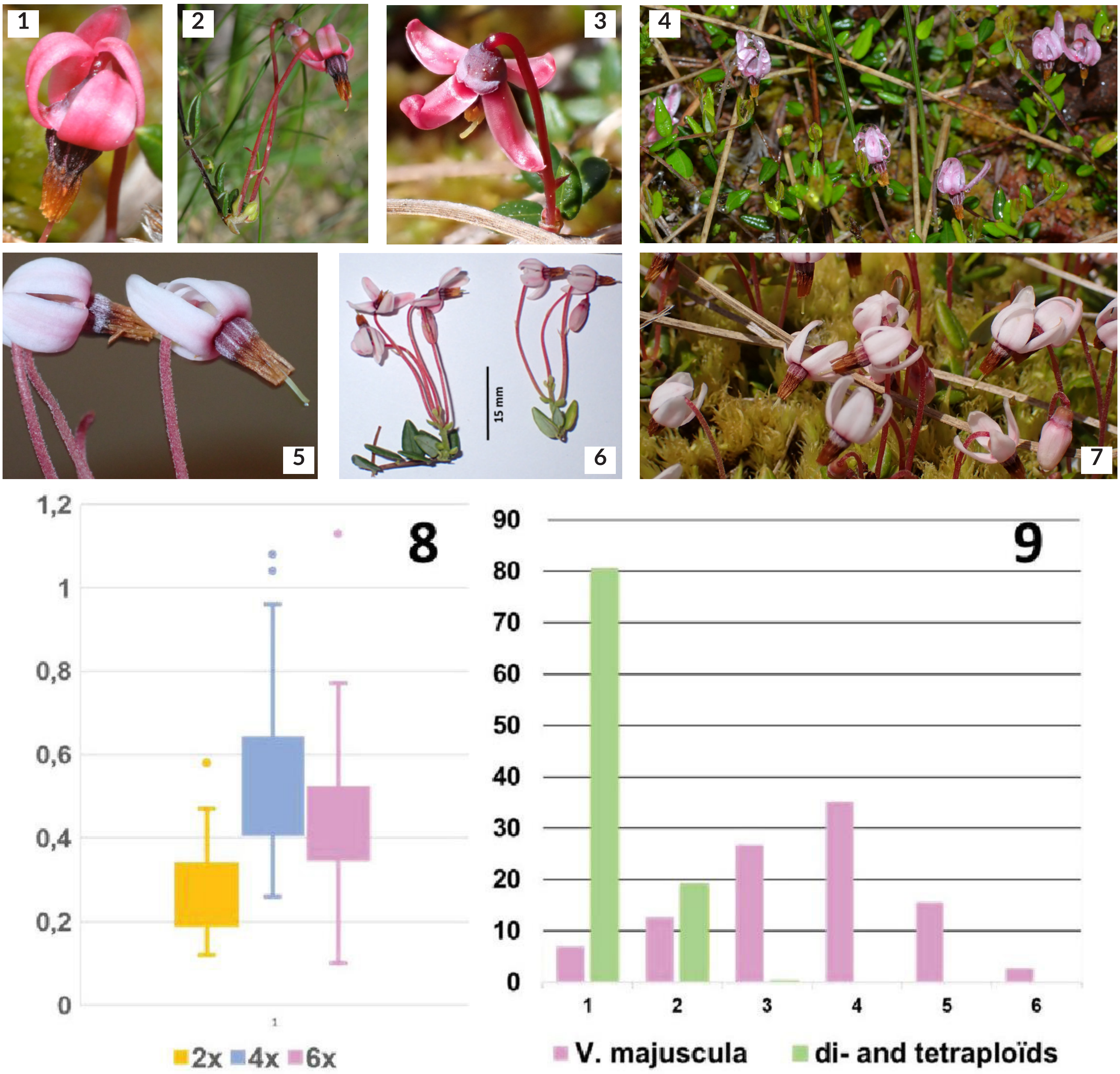

Figure 10 – Comparison of cranberry inflorescences and flowers from Auvergne.
**1 to 3**: Diploid cranberries have hairless pedicels, flowers with red petals, inflorescences with one or two flowers.
**4**: Flowers of di- and tetraploid cranberries are isolated on the mosses.
**5 to 7**: *V. majuscula* has hairy pedicels, pink petals, and inflorescences of 3-5[6] flowers which form a dense carpet on top of the mosses.
**8**: Fruit mass (in grams) by ploidy level. *V. microcarpum* fruits (2x) are smaller than polyploids ones. (n = 28, 75 and 197 fruits, for respectively 2x, 4x and 6x). Fruits collected in September 2021 & 2022, two dry years (and very warm for 2022).
**9**: Proportion of inflorescences (percentage) with 1, 2, 3, 4, 5 or 6 flowers. Hexaploids are distinguished by their 3 to 5 flowered inflorescences (3 flowers= 26.8%, 4 flowers 35.2% and 5 flowers =15.5%), while 80 % of the inflorescences of di- and tetraploids have only one flower. (n=40 inflorescences for *V. majuscula* and n = 65 for the two other cytotypes, from several populations in May 2022).

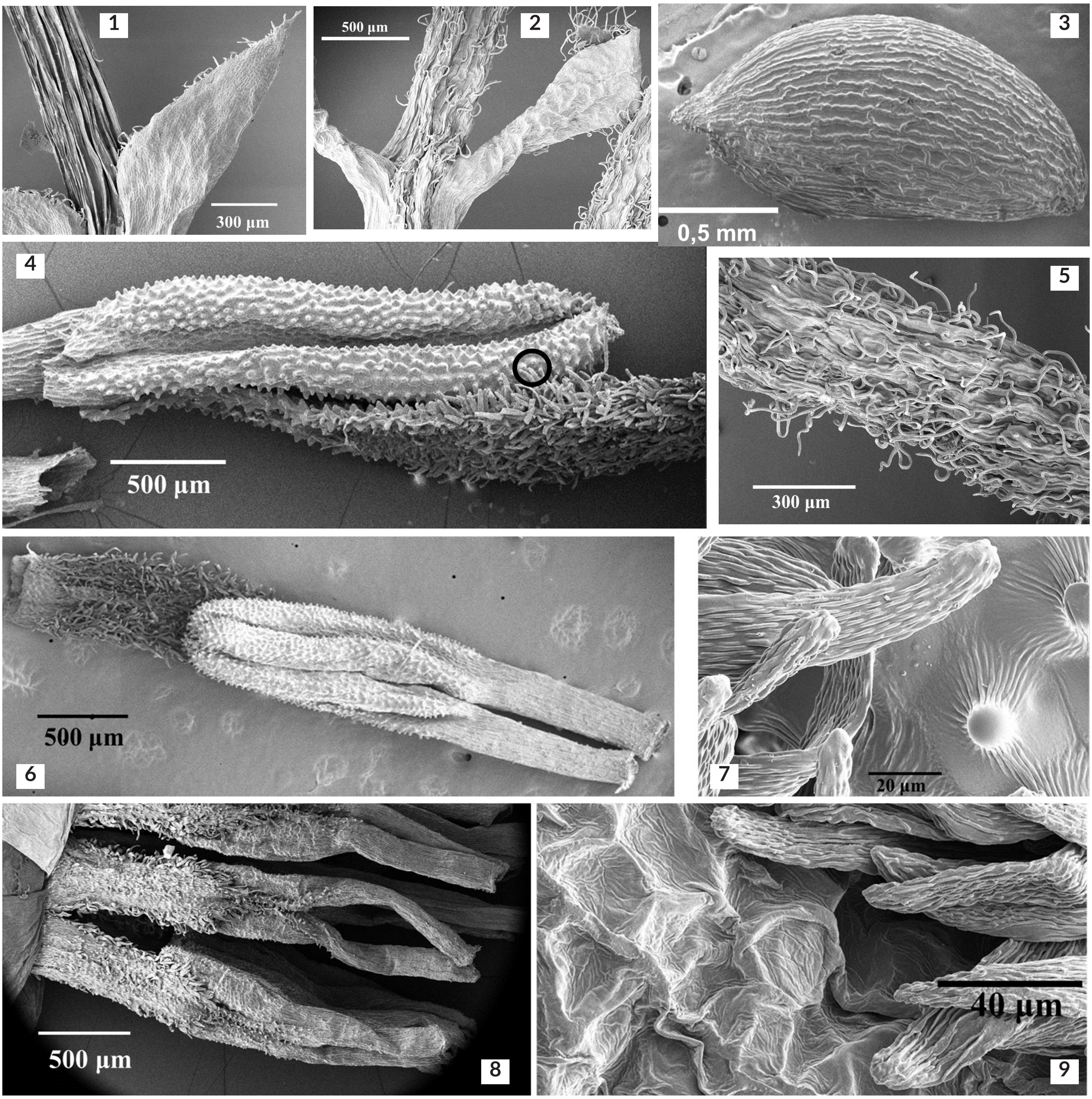

Figure 11 – Comparison of stamens and pedicels.

**1, 2 & 5**: Pedicel with their two bracteoles: glabrous in diploids (1) and hairy in *V. majuscula* (2 & 5).

**3**: Ornementation of *V. majuscula* seed.

**4**: *V. majuscula* which anthers are warty on surface (the black circle represents the enlarged area in 7 and 9).

**7 & 9**: enlargement of the edges of the anthers and filaments: the warts are only present in *V. majuscula* (7). The filament hairs have a pleated surface.

**6 & 8**: Stamens at the same scale, those of *V. majuscula* are longer with slightly different proportions.

**2 to 7**: *V. majuscula*. 1, 8 & 9: diploid cranberries from Massif central.

### *Fruits and seeds*

The globose fruits, grouped by 3 to 6 (Fig. 2 & 5), are quite variable in shape, even on the same infructescence. They are sometimes clearly pyriform (Fig. 3d) and do not differ from those of *V. oxycoccos*. The same is true for their mass (Fig. 10.8); these characters, as well as the quantity of aborted flowers, depend strongly on environmental conditions. They sometimes mature buried in mosses and old fruits can be found intact under several centimetres of peat (Fig. 5). The red colour only appearing progressively during August.

Ovules are numerous but as in other *Vaccinium*, few of them (3-5) give seeds. The mature fruits contain a rather variable number of well-developed seeds which we have not tested for fertility; they are mixed with small seeds and aborted or unfertilised ovules (Fig. 6).

The seed size (1.4-2.3 mm x 0.7-1.2 mm), seed colour (light brown to reddish – maybe due to staining by fruit juice), and crested ornamentation (laying ridge, Fig. 11) seem quite similar to other cytotypes.

Their dissemination, such as plant regeneration by seeding, is still to be explored (if it exists at all).

### *Ploidy*

Chromosome count of cranberries needs a difficult process (cultivation for root tip). But fortunately, the relationship between chromosome number and the amount of 2C-DNA (genome size) has been widely documented in *Vaccinium*. So, we evaluated ploidy level by flow cytometry according to classical methods (Costich *et al.* 1983; Suda 2002; Suda & Travnicek 2006) which allows us to obtain a larger sample without growing or destroying individuals.

**Method of genome size obtention**: The total nuclear DNA amount was assessed by flow cytometry according to Fridlender *et al.* (2014). Dried leaves of sect. *Oxycoccus* and the internal standard (*Hordeum vulgare* cv 'Sultan', 2C = 9.81 pg) were chopped with 600 µl of modified Galbraith nucleus-isolation buffer; the nuclei were stained with 75 µg/ml propidium iodide. The total 2C DNA value was calculated by using the linear relationship between the fluorescent signals from stained nuclei of the cranberries and the internal standard.

The analysis of numerous cranberry individuals from various peatlands allows us to recognise without difficulty the three main levels of ploidy. The 2C DNA values of diploids (2x) from Auvergne vary between 1.2 and 1.5 pg, tetraploids (4x) 2.6 to 2.8, and hexaploids (6x) between 3.6 and 4.4 pg DNA.

Of all the cranberries analysed in several Massif central populations, only *V. majuscula* was hexaploid.

## *Vaccinium hagerupii* (Á.Löve & D.Löve) Rothm.

**Publ. place :** Feddes Repert. Spec. Nov. Regni Veg. 67: 8, 1963

**Bas.**: *Oxycoccus hagerupii* Á.Löve & D.Löve, Bot. Not. 114(1): 40, 1961.

**Syn.**:

- *Oxycoccus palustris* var. *major* Lange Fl. Dan. 51:MMMXIX (3019), 1883.
- *Oxycoccus palustris* subsp. *hagerupii* (Á.Löve & D.Löve) A.P.Khokhr. & Mazurenko, Sosud. Rast. Sovet. Dal'nego Vostoka 5: 156, 1991.

**Isonym**: *Vaccinium hagerupii* (Á.Löve & D.Löve) Ahokas, Ann. Bot. Fennici 8 : 255, 1971 (comb. inval ; in Hereditas 68 : 134, 1971, basionym not stated).

**Description**: « ramis brevioribus minusque diffusis, foliis majoribus, subtus eximie glaucis, obsolete venosis, pedunculo puberulo, floribus majoribus quam in forma vulgari, calycis laciniis ciliatis. »

**Loc type**: « Specimen depictum ad Christianiam ».

***Typus***: Plate 51:MMMXIX of Lange (1883) is very accurate and corresponds perfectly to the protologue. In the Lange herbarium there are several herbarium sheets with several cranberries' samples. The sample at the bottom left of the herbarium sheet Museum Botanicum Hauniense - C10021825 is obviously the one that was used to draw and describe the plant. This flowering specimen from Christiana is therefore the one we choose here as *LECTOTYPUS* (Fig. 12a).

Lange's *Oxycoccus palustris* var. *major* samples are too few to allow a " definitive " comparison with *V. majuscula*. The dry blades of the long stems measure 8-10 x 3-4.5 mm while those of the orthotropic axes are somewhat smaller 6-9 x 2.5-4 mm. These plants have significantly larger leaves (and flowers) than the other samples (sub. *Oxycoccos palustris microcarpa* (Turcz.) Rupr) collected in Oslo. Lange described a ciliate calyx as in *V. majuscula*. From the limited herbaria data available, the difference of leaf size between *V. majuscula* and *V. oxycoccos* from Auvergne is of the same order as that between the *Oxycoccus palustris* var. *major* and *V. oxycoccos* samples from Norway. The leaves seem to be slightly smaller than those of *V. majuscula* (but we do not have sample of exploration plagiotropic axes which have larger blades) and the samples do not show inflorescences with numerous flowers (only two and not 3-6). Finally, we lack information on chromosome number for plants from Oslo.

NB: A cranberry is also described in the Flora Danica G.V. Oeder edition of 1763 (vol. 2: LXXX [80]), the illustration of *V. oxycoccos* L. is not very realistic (Fig. 12b) and no information is given on the polymorphism of the species: then we realise the rigor and precision brought to us by Johan Lange a century later.

A comparative study on living plants from south Scandinavia will have to be carried out before we can make a statement on the conspecificity of *V. majuscula* and *V. hagerupii*.

It should be noted that several plants that seem to correspond to Lange description are mentioned on herbarium samples from Russia, Finland and the Baltic States under the following names:

- *O. palustris* Persoon (1805) which refer to Fl. Dan. Tab.80 (Fig. 12b).
- *Oxycoccus quadripetala* Gilibert (Fl. Lit., 1781, Unipetalae Fasc. 1, Pl. lignosae :5) invalid name based on *V. oxycoccos* L., Gilibert's description is not very precise but would not correspond

(“ Flores pauci terminantes. ”) to the hexaploids which have many flowers.

## Discovery of *Desarmillaria ectypa* in *V. majuscula* lacustrian mire, main ecological characteristics of different cytotypes

### Ecology of *V. majuscula* in Lac des Bordes type locality: *Compains, Puy-de-Dôme, alt. 1200m; 45°24'N, 2°55'E (Fig. 8)*

*V. majuscula* is found throughout the lacustrian mire.

Cranberry individuals usually present short fruiting branches with few plagiotropic axes of exploration and are often moribund in the driest bog parts (largely colonised by *Andromeda polifolia* L. and *Polytrichum strictum*). On the other hand, long vegetative plagiotropic axis massively colonises sphagnum carpets in the most open areas where water is outcropping. On the edge of *Menyanthes trifoliata* and *Comarum palustre* floating rafts in formation, a profusion of long plagiotropic axes of exploration are intermingled. At the edge of the *Scheuchzeria palustris* hollows, stems of *V. majuscula* go forward on the water as *Menyanthes* do (Fig. 5.2 & 8).

We found only one non-flowering stem with small leaves that appeared to belong to *V. oxycoccos* in Lac des Bordes peatland, an identification confirmed by cytometry (tetraploid based on genome size).

*V. majuscula* had been observed by Chassagne in a mixture with *V. oxycoccos* in the Chambedaze lake in 1936: the cohabitation of these two species remains to be studied. *V. majuscula* produces much more vigorous and faster-growing axes than the other cytotypes, which may have been eliminated by competition in minerotrophic mire. Furthermore, the surface of the peat bogs is generally colder than the surrounding soils and the negative impact of freeze and thaw cycles has been shown on the growth of *Sphagnum* (Küttim 2020). It can be assumed that hexaploids also have a better physiological resistance to submersion (low oxygenation) and late winter temperature variations and therefore dominate in the wetter parts where the surface is more exposed to the freeze and submersion alternation.

The flora associated with *V. majuscula* is remarkable as illustrated by other northern species both rare in France and Europe (*Scheuchzeria palustris* L., *Carex limosa* L., *Drosera rotundifolia*, *Andromeda polifolia)*, and occasionally approaches the more mesotrophic *Ligularia sibirica* (L.) Cass. habitats. We also discovered a population of *Desarmillaria ectypa* (Fr.) Koch & Aime in a dense *V. majuscula* area (Fig. 8-III). This boreal fungus grows amongst *Sphagnum* on moorland, active raised bogs, and also alkaline fens. *D. ectypa* is extremely rare in Europe as a whole (Britain, Sweden, Denmark, Finland, discovered in Ireland in 2002), apparently extinct in Switzerland and Poland and even unknown in Norway (Wright 2007; Stasinka 2015; Kibby 2021). It is a saprotroph, and probably a *Carex* or *Salix* symbiote. It has been discovered in 1929 in vegetation flushed with fresh water and peat bogs in Auvergne (species southernmost distribution), less than ten localities are known (Zolciak *et al.* 1997; Jalla pers. com.), almost all of them in the Godivelle sector (Cézallier) and precisely in the two peat bogs with *V. majuscula* of Bordes and Chambedaze lakes. Like many other species, it is an indicator of a relatively preserved peatland (Ohenoja 2006), as evidenced also by the otter (*Lutra lutra* L.) prints we observed there.

Lac des Bordes lacustrine mire is presently isolated among pastures and develop in a small dam putatively built in the 17th century. But no water is shown around “ Briou ” on the Cassini map (Carte Générale de la France, N°53-89 Brioude, 1769) but a lake is visible on 19th century maps (Cartes de l'état-major, 1820-1866). Then, most of actual *V. majuscula* habitat is therefore only a few centuries old.

Up to now, *V. majuscula* has been collected (CLF!) only in other lakes, especially in the southern part of Puy-de-Dôme between monts Dore and Cézallier. Then *V. majuscula* grows (exclusively?) in more humid and minerotrophic habitats (lacustrian mire) than *V. oxycoccos* s.l. (more xeric, predominantly ombrogenous bog).

### *Dynamics in space and time and cytotypes distribution*

The three main cytotypes (and then three taxa) of sect. *Oxycoccus* are present in the Massif central at the southern limit of their distribution range, as in Scandinavia where cranberries are much more abundant. In southern France, central Europe and probably southern Scandinavia, shoots from various ploidy levels may intertwine. However, we observe a ploidy gradient based on the availability of water for the plants from diploids (= physiological dryness at the top of the tussock, ombrogenous most acidic environment) to hexaploids (= phreatic water generally richer in minerals and accessible even in summer as in floating raft margins).

Thus, in a bog-fen complex where the microhabitats are progressively evolving, each cytotype would have an optimum growth rate, which would allow the cranberries to remain on the peatlands for a long time. Depending on the peatland dynamics, one or other of the cryptic taxa could be favoured (or locally eliminated). In this hypothesis, the lacustrian mire of Lac des Bordes with *V. majuscula* should normally evolve towards an ombrogenous bog with *V. microcarpum* as dominant cranberry species (Fig. 8: 6x in young lacustrian mire ↔ intermediate stage with 4x *V. oxycoccos* ↔ 2x dominant on drier tussock top). The observation of a tetraploid stem in Bordes probably reflects the beginning of this transitional process. The connections of the vast network of streams, wetlands, fenlands and bogs of the Sancy-Cézallier allowed each species to migrate and find a favourable ecological niche. This mosaic has been fragmented by drainage and pastoral pressure. Presently peatlands (Godivelle, Chambedaze, Bordes, Esclauze…) are completely isolated from each other. Then the arctic relicts cannot migrate anymore; cytotypes and/or species only may disappear one after another.

The cytological exploration that we are carrying out on numerous individuals from several peat bogs in the Massif central will allow us to define better these dynamics at various scales (Fig. 8).

These hypotheses are consistent with other observations on the ecology of cryptic taxa in the sect *Oxycoccus*. For example,

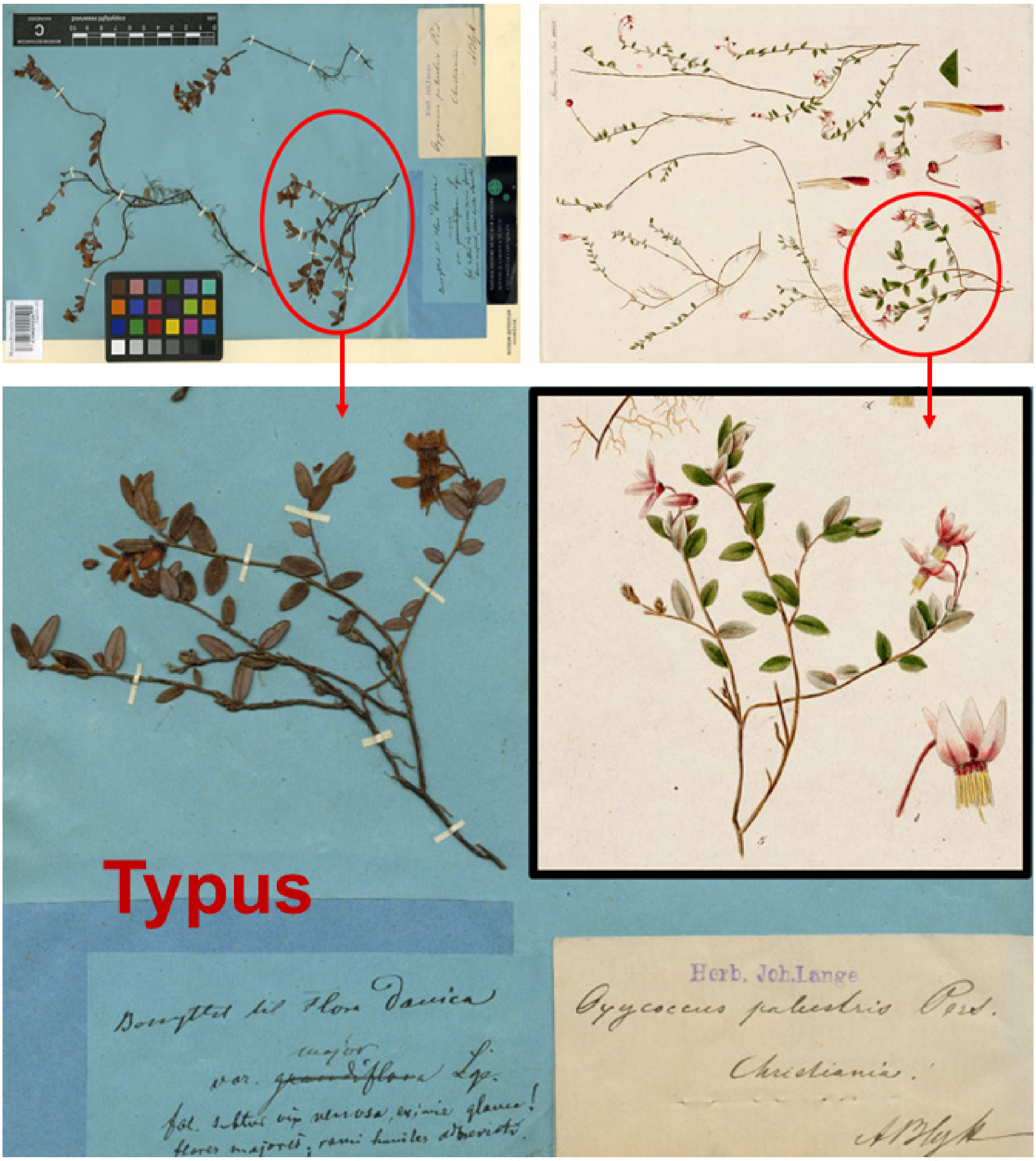

Figure 12a – *Oxycoccos palustris* var. *major* Lange type specimen.**Top left.**: Sample (herb. Joh. Lange) with handwritten of the type locality « Christiana » (Herbarium Lange, Museum Botanicum Hauniense - C10021825). **Top right**: Fl. Dan. 51 plate MMMXIX (3019), 1883. Below - enlargements of the selected parts in red on specimen C10021825 and on plate MMMXIX which represent the specimen we select as the lectotype specimen. Reproduced with the permission of Natural History Museum of Denmark - University of Copenhagen.

Figure 12b – First illustration of *V. oxycoccos* L., in Flora Danica LXXX (80) - 1763 edition.

Ahokas (1996) considers that there are no tetraploid cranberries but only hexaploid individuals in southern Finland: some of these hexaploids are fertile and seem to be rapid pioneers of newly created human wetland habitats. In Lithuania, *V. oxycoccos* seems quite polymorphic in various habitats but *V. microcarpum* is a rapidly declining species from a few large raised bogs (Z. Gudzinskas, pers. com.). Unfortunately, in those Nordic regions tetraploids are generally much larger than in Auvergne, which makes comparison on herbarium samples difficult. In Japan, Asada (2001) also observed that *V. microcarpum* preferentially colonise habitats where the depth to ground water is more important than do *V. oxycoccos* which is therefore found closer to ground water and at higher pH. A quiet similar pattern occurs in eastern America in a different species and cytological context: the vigorous southern *V. macrocarpon* habitats are open bogs, swamps, mires, and wet shores (pH 4.8-6.1) whereas the northern smaller *V. oxycoccos* s.l. grows half buried in oligotrophic *Sphagnum* hummocks (pH 2.9-3.8) (Vander Kloet 1988). In contrast, there are no ecological differences between the cytotypes in central Europe (Suda 2002). This remains to be explored as it seems to us that according to their data tables, hexaploids are more frequent at low altitudes and diploids more frequent at high altitudes.

## Discussion taxonomy and biogeography

### Taxonomy

Hexaploids are thus currently attested in the territories bordering the Baltic Sea (Denmark, southern Norway and Sweden, southern Finland, some Baltic States, Poland), in central Europe (Czechia, Austria and southern Germania) and finally in the French Massif central (Fig. 1). Although at the southern limit of the distribution of sect. *Oxycoccus*, three cytotypes are found in Auvergne: diploids seem as abundant as tetraploids but hexaploids are very localised.

The hexaploids clearly do not all have the same origin: in central Europe they are morphologically identical to the tetraploid *V. oxycoccos* (Suda & Lysak 2001; Suda 2002) whereas it is a completely distinct species (*V. majuscula*) in Auvergne. This apoendemic is apparently almost identical to *V. hagerupii* from the territories bordering the Baltic Sea where numerous hexaploids have been identified but we do not have sufficient data to know their exact relationships, especially concerning plants from the vicinity of Oslo.

### *Biogeography*

In the Massif central, *V. majuscula* is only known on lacustrian mire, some stems even growing in direct contact with water. In northern Europe, it seems that diploids (*V. microcarpum*) predominantly grow on drier parts of *Sphagnum* tussocks (*Sphagnum fuscum* tufts), that tetraploids occur in wetter habitats and that hexaploids (*V. hagerupii ?*) live in the wet lowlands of southern Scandinavia. Polyploids spread rapidly in the most humid habitats, pushing the other cytotypes back to the tussock's tops, which are more xeric: a pioneer colonising new wet environments and, also mineralized habitats where competition between plants is more important.

We could therefore reconsider the evolution of sect. *Oxycoccus*, whose diversification could also have taken place in southwestern Europe and not necessarily only in the Arctic zone. During glacial episodes, diploids probably maintained themselves in various Scandinavian ice-free (Andersen *et al.* 2012), xeric microhabitats, “ nunatak refuges ” and, of course on snow-cleared sectors of the Alps and the Massif central (slopes, ridges). Isolated by the recurrence of Pleistocene glacial episodes, these *V. microcarpum* stands slowly diverged and would have given rise on several occasions to various tetraploids resembling to the diploids but capable of colonising wetter environments whose extension has been favoured by post-glacial warming. In central Europe, penta- and hexaploids (almost identical to each other) have also been formed perhaps during the recurrent glace age of the Quaternary. In the Massif central, however, a completely different hexaploid has emerged, whose origin probably goes back to the tertiary period. The vigorous *V. majuscula* was able to compete better with other species in humid environments. This hexaploid could then have taken advantage of the ice melt to colonise the newly created habitats: wetlands mainly located at the base of mounts from where it could have followed the streams, the numerous glacial lakes and valleys that descended into the plains. This pioneer would have taken advantage of (inter-)post-glacial break-ups (when heaths and mires expanded) to colonise immense new wet habitats on the Atlantic side of Europe (from which it would have disappeared) and spread northwards to the soggy regions bordering the Baltic sea where lake, mires, and bogs abound. Some of which actually contain related 6x *V. hagerupii*!

This scenario would explain the concordance between our observations on the morphology and ecology of the three cytotypes from central France and those from Denmark (Hagerup 1940) which would correspond, in part, to “ abysmal ” populations. Far from any Atlantic influences, the cranberries of central Europe probably have a different natural history! Furthermore, the taxonomic originality of the hexaploids of Western Europe (Massif central - Norway) versus those of Central Europe is to be compared with the Atlantic distribution of the order *Sphagno-Ericetalia tetralicis* (Atlantic) versus *Sphagnetalia medii* order (in Classe of the *Oxycocco-Sphagnetea*, Jiroušek *et al.* 2022, Fig. 1.1).

North American tetraploids (*V. oxycoccos*) have some alleles characteristic of the East American endemic *V. macrocarpon* (Mahy *et al.* 2000). American cranberries are therefore unlikely to have the same history as European plants and probably represent another cryptic species to be described. Similarly, tetraploid cranberries from Auvergne, which are less vigorous than those of the north-eastern Europe, do not correspond exactly to the same taxon (*V. oxycoccos* s.l.). Polytopic origin, recurrent formation of polyploids and the polyphyletic origin of most species in arctic plants (Stebbins 1984; Soltis & Soltis 1999; Marhold & Lihova 2006) is a challenge to name them (Soltis *et al.* 2007). But it is not because nomenclature or our taxonomic concepts (Linnaean species, biological species) are partially inoperative in the face of this reticulated evolution that singular populations do not exist; however, we cannot name them all at specific rank. We are therefore condemned to navigate in this in-between situation so frequent in natural history.

If the Massif central is without contest a remarkable refuge (the southernmost) for numerous presently arctic-alpine and circumboreal species like *Betula nana*, the two species of *Empetrum*, and numerous *Sphagnum* species (*Sphagnum balticum*, *S. majus*, *S. fuscum*, *S. obtusum*), it could also have been a centre of speciation of this flora within which we recognise three cranberry species: *V. microcarpum*, *V. oxycoccos* and the apoendemic *V. majuscula* which are, if not identical, at least morphologically and ecologically close to the three Scandinavian taxa. Finally, we can question about these famous subarctic species which would have swept through southern Europe during the Pleistocene glaciations. The " alpine " flora of the Massif central is more probably partially derived from an ancient local flora that lived on the high peaks of the Auvergne and not recent glacial colonisation from subarctic areas (Braun Blanquet 1931). Recent studies (Faure 2021) confirm the 19th century hypothese that described the Massif central as a " Himalayan massif " whose peaks reached an altitude of 3,000-4,000 m during the Pliocene.

This study has obvious implications for the protection of peatlands, the dynamics of which seem to be stagnating, which is not surprising given that their number and surface area are decreasing and that they no longer communicate with each other. The lacustrian mire type locality is colonised on its margins by *Salix atrocinerea* and invasive *Picea* (mineralisation processes). Observation of experimental plots showed a decrease in the density of *V. majuscula* over the last ten years (Thébaud *et al.* 2022). According to the few historical data available and current observations, *V. majuscula* appears to be in decline.

For general inventory or conservation purposes, it is not shocking to consider that *V. oxycoccos* L. is one rare polymorphic species that should be protected throughout France. On the other hand, we must obviously consider the different cytotypes if we want to understand in depth the mire plant dynamics at different scales (tussocks, bogs, peatland complexes, mountain massif) and maintain all the ecological and evolutive potentialities offered by this cryptical diversity.

In any case, we must be respectful of the diversity of these cranberries, and we can only admire the beauty of this profusion of species linked to microhabitats that total just represent a few hectares in the 26 000 square kilometres of Auvergne, each one resulting to long history largely escaping our understanding.

## Acknowledgements

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