THE IMPORTANCE OF POLYPLOIDY IN *MECONOPSIS* WITH PARTICULAR REFERENCE TO THE BIG PERENNIAL BLUE POPPIES

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ABSTRACT

A comparison is made between evolution of the genus *Meconopsis* through natural selection, which takes a long time, and rapid evolution through polyploidy. The possible formation of the tetraploid *Meconopsis grandis* from the diploid *M. baileyi* is considered in detail. The possibility of an extended diploid to hexaploid chromosome series in the 'Big Blue Poppies' is discussed. Each component of the series is described. The formation of *Meconopsis* 'Lingholm' as an example of a probable new hexaploid species with its evolution through somatic chromosome doubling is considered in detail. The possibility of pentaploids, a new ploidy level or cytotype in the proposed series is discussed with putative examples. A glossary of the terms used is provided.

INTRODUCTION

Polyploidy has been described as 'the presence of three or more sets of chromosomes in an organism' (Grant, 1971). The very first polyploid plant was discovered in 1907. Its chromosomes were counted using a microscope technique newly developed at that time; this method of investigation was later to become a branch of cytology. Polyploids are known to occur more frequently in angiosperms, the flowering plants, than in other groups such as gymnosperms. Not all genera contain polyploid forms; in some they have never been detected, in others they occur infrequently. In a number of genera polyploids are frequent and may be a special feature of that particular genus, and this is the case with *Meconopsis*. One of three subgenera, loosely called the 'Big Perennial Blue Poppies', is found to have a range of particularly high chromosome numbers forming a short diploid, triploid and tetraploid series. Only these polyploids, along with pentaploid and hexaploid additions to this series, are considered in detail in this paper.

TAXONOMY OF THE GENUS *MECONOPSIS*

David Prain and George Taylor, both once directors of the Royal Botanic Gardens, Kew (RBG, Kew), were primarily taxonomists, and each attempted a formal classification of *Meconopsis*, a complex genus. Later, Taylor published the first detailed taxonomic

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account of the genus (Taylor, 1934). This was based almost entirely on herbarium specimens lent to him from botanic gardens throughout Europe and Asia; he seldom referred to living specimens. This scholarly classification became widely accepted. At that time neither Taylor nor Prain could have had any knowledge of chromosome numbers let alone polyploids. Prain was adventurous and travelled into the Himalayan region, especially Tibet (Xizang), and with regard to the 'Big Perennial Blue Poppies' he classified them under the section Grandes which then comprised four species, *Meconopsis baileyi*, *M. grandis* and the monocarpic *M. simplicifolia* and *M. integrifolia*, which is yellow-flowered. Some alterations to Taylor's classification were made by James Cobb in his book *Meconopsis* (Cobb, 1989). More recently, in 2007, Christopher Grey-Wilson wrote his monograph *Poppies* which included *Meconopsis* (Grey-Wilson, 2000). Today the section Grandes, originally conceived by Taylor, consists of just two species, *M. baileyi*, with two subspecies, and *M. grandis*, with three subspecies as shown in Table 1. Grey-Wilson has now written an updated account of the genus. This detailed treatise is being published by RBG, Kew and will be available in 2014; the author has not seen this article for information or comment.

EXPLORERS AND COLLECTORS OF *MECONOPSIS*

Explorers visited China in the late 1880s and early 1900s, drawn by its huge and varied flora. Rhododendrons were avidly collected and introduced by sponsored expeditions. The two major botanic gardens, Royal Botanic Garden Edinburgh (RBGE) and RBG, Kew, were active in such ventures, as they are today. Some plant hunters had a special interest in collecting the spectacularly beautiful *Meconopsis* that occurred commonly throughout the Sino-Himalayan region. Collectors with a particular interest in *Meconopsis* were Frank Ludlow, George Sherriff, Frank Kingdon-Ward, George Forrest and Ernest Wilson. The French monk Père Delavay discovered *M. grandis*; the type specimen is therefore kept in Paris. It was Prain, however, who first introduced *M. grandis* into Britain. It first flowered at RBGE in 1895 (Grey-Wilson, 2010). *M. grandis* was also brought back to Britain by Frank Kingdon-Ward on several occasions and by Frank Ludlow and George Sherriff in 1934.

George Sherriff introduced many plants and is noted for his introduction of forms of *M. grandis* from eastern Bhutan. The original collector code for this introduction was L&S600, for Ludlow and Sherriff. This became misconstrued as GS600 and a few plants and a large quantity of seeds, thought to be collected from a particular population of *M. grandis*, were distributed far and wide under this erroneous code. It was common in gardens, causing much confusion amongst both amateur growers and professional nurserymen. The *Meconopsis* Group, a study group founded in 1998, took on as its main remit the task of resolving this problem. A well-illustrated account of these studies, up to 2006, has been published (Stevens, 2006) and annual updates are provided on the *Meconopsis* Group website (*Meconopsis* Group, 2012–2013). The main outcome of these studies was the delimitation and naming of a number of new cultivars, which included several good hybrids that have been selected and have received Merit Awards from the RHS (Stevens and Brickell, 2002). Several plants remain to be assigned.

In more recent times several expeditions have visited China and brought back living plants and seed of what are considered to be new forms of *M. grandis*. These are currently being assessed; some plants have shown a lack of fertility, which is a feature of *M. grandis* noted by Taylor (1934) and others. The cause of the sterility encountered in *M. grandis* is not known.

In 1989, the Kew-Edinburgh Kachenjunga Expedition (collector code KEKE) collected good new forms. A fine, deep-blue flowered plant of *M. grandis* was also collected on the 2004 expedition to Nagaland and Arunachal Pradesh, India (collector code NAPE). This clone is available commercially and is valued by growers. The numerous expeditions to these regions have been described by Christopher Grey-Wilson (Grey-Wilson, 2010). Herbarium specimens of collected variants of *M. grandis*, along with other *Meconopsis* species, are conserved at the British Museum of Natural History (BM) and at RBGE.

EVOLUTION THROUGH NATURAL SELECTION

Charles Darwin published his book *The Origin of Species by Natural Selection* in 1859, and his concept of evolution through natural selection is universally recognised today. This process takes many millennia – tens or even hundreds of millions of years – to complete, a situation impossible to describe or encapsulate. However, studies of *Meconopsis* give some indication of how natural selection operates in the wild. Such inordinately slow evolution is exemplified by two studies of *Meconopsis*.

In 2012, the Chinese botanist F.S. Yang organised an expedition to south-eastern Tibet to collect the yellow-flowered *M. integrifolia* (Yang *et al.*, 2012). The objectives were not only to study evolution but also to determine forms of the greatest medicinal value. *Meconopsis* have been used for this purpose in Tibet and other provinces of the People's Republic of China for centuries. On this expedition the Chinese team collected more than 30 samples of *M. integrifolia*. Plants growing in various habitats were taken back to the laboratory for molecular analysis. The results proved to be interesting; some samples showed distinct molecular differences which are not only of interest medicinally but indicate that the populations are in the process of natural selection. Yang described these mountainous areas of the Qinghai Tibetan Plateau (QTP) as 'a complex of tectonic events and climatic oscillations' with thin soils, very cold temperatures and high winds (Yang *et al.*, 2012). These extreme conditions are demonstrative of the struggle for existence amongst both plant and animal inhabitants and ultimately the survival of the fittest by natural selection as described by Charles Darwin. Although it was once contentious, most people now believe Darwin's theory.

John Mitchell, Alpine Department Supervisor at RBGE, visited the mountain and valley terrain of Tibet and encountered the damp mistiness within these valleys which provides favourable conditions for *Meconopsis* to grow, in particular *M. baileyi*. Different phenotypes could be distinguished, each confined to a different valley or even to opposite sides of the same valley (Mitchell, pers. comm. 2012). These varied forms appear to be the product of incipient geographical isolation, examples of speciation through natural selection observed at a very early stage. The geographical separation of plants by mountain ranges acts as an effective barrier to inter-crossing and gene flow between populations or species and results in genotypes which are reproductively isolated from their progenitors. Natural selection is an extremely slow process, taking many millennia to reach its conclusion, which is ultimately a new species, but it is not the only means of plant speciation.

EVOLUTION OF SPECIES THROUGH POLYPLOIDY

In stark contrast to the inordinately long timescale of natural selection, the evolution of new species through polyploidy can be virtually instant, or take a very short time, although in some instances it may take some years, an example being the evolution of the hexaploid *Meconopsis* 'Lingholm' due to a time gap (see Figs 1, 2 & 3). Polyploids are also subjected to natural selection, like any other organism, so the two evolutionary processes can act together.

Fig. 2 *Meconopsis* 'Lingholm'. Photo: Evelyn Stevens.

Fig. 3 *Meconopsis* 'Lingholm' flower. Photo: Evelyn Stevens.

Stage 1 Hand crossing

M. grandis **tetraploid** **(2n=4x=146)**	×	***M. baileyi*** **diploid** **(2n=2x=82)**	***M. × sheldonii*** **triploid** **(2n=3x=123)**

Time gap of 38 years

Stage 2 Somatic chromosome doubling

M. × sheldonii **triploid** **(2n=3x=123)**	⟶	***M.* 'Lingholm'** **hexaploid** **(2n=6x=246)**

Fig. 1 Mechanisms and pathway leading to the evolution of *Meconopsis* 'Lingholm'.

ISOLATING MECHANISMS

Once a new species has evolved it is necessary for its identity or genetic integrity to be retained. This applies to normal diploid plants, the result of long-term natural selection, or short-term rapid evolution through polyploidy. These paramount processes are effected through what has become known as isolating mechanisms. These are many and varied in flowering plants, for example selection by insect pollinators, perhaps aided by modified floral structures. Such a mechanism may not be sufficiently effective on its own in preventing gene flow between a new diploid species and its closest relative. It is more usual for several mechanisms to act together in ensuring more complete reproductive isolation.

The situation in polyploids is simpler and is immediately effective. A neopolyploid is isolated from its immediate progenitor because it is at a different ploidy level. A good example is provided by the *Meconopsis* species and hybrids forming a chromosome series, as shown in Table 3. Each component is effectively isolated by reproductive barriers from its immediate progenitor or any other component of the closely related series.

SPECIAL FEATURES OF POLYPLOIDS

Polyploids in flowering plants have important morphological and physiological differences, which makes them distinct from diploids. Often these are visual enhancements, referred to as 'gigas factors', and are manifest in a more robust growth habit. The mature plants can be taller, with thicker stems and broader, thicker leaves. They generally have larger flowers with petals of good substance. All parts, especially pollen grains and seeds, are bigger. *M. grandis* seeds are about twice the size of those of *M. baileyi*, and the seeds of *Meconopsis* 'Lingholm' are much larger than those of *M. grandis*; an ascending series of seed size can be seen with ascending polyploidy numbers. The fact that these morphological features are often measurably and even statistically different means that

Species	Chromosome no.	Remarks
M. cambrica	2n=2x=28	deleted from genus
M. napaulensis	2n=2x=56	plus other species
M. horridula	2n=2x=56	plus other species
M. integrifolia	2n=2x=76	a unique chromosome number
M. baileyi	2n=2x=82	Now considered to include *M. betonicifolia*
M. grandis	2n=4x=164	1. subsp. *grandis** 2. subsp. *orientalis* 3. subsp. *jumlaensis**

Table 1 Chromosome numbers of *Meconopsis* species.

the likelihood of a plant being a polyploid can be narrowed down without resorting to cytological or molecular investigation techniques, which can be carried out at a later date. Allopolyploids derived as inter-species hybrids have exhibited heterosis or hybrid vigour. Both autopolyploids and allopolyploids are known to show gene dosage effects, with the extra genes emphasising certain traits.

M. integrifolia stands alone with an unusual chromosome number of 2n=76 and is clearly distinct from other species (Ying *et al.*, 2006). A contentious group of hybrids involving *M. integrifolia* have puzzled taxonomists for over a century. They also pose cytogenetic questions because of their improbable combinations of chromosomes, each of which is likely to produce cytological imbalance in the hybrid, and therefore a high degree of sterility is to be expected. None of these hybrids have been cytologically examined and so, at present, must remain putative. Their respective chromosome numbers have been predicted on the basis of the verified numbers of their respective parents, as shown in Table 2.

The two groups with 56 chromosomes (see Table 1) are now recognised as distinct and separate subgenera of *Meconopsis*, They are considered beyond the remit of this article. Having the same chromosome number does not mean that the two are inter-crossable. The many genetic and chromosome differences separating these subgenera would most likely result in sterile hybrids. The *M. baileyi* and *M. grandis* group, the ‘Big Blue Poppies’, form a third subgenus.

Female	Chromosome no.	Male	Chromosome. no.	Hybrid	Chromosome no.
M. baileyi	2n=82	*M. integrifolia*	2n=76	*M. sarsonsii*	2n=79*
M. grandis	2n=164	*M. integrifolia*	2n=76	*M.* × *beamishii*	2n=120*
M. integrifolia	2n=76	*M. simplicifolia*	2n=82	*M.* × *harleyana*	2n=79*
M. ‘Lingholm’	2n=246	*M. integrifolia*	2n=76	*M.* ‘Marit’	2n=161*

Table 2 *Meconopsis integrifolia* hybrids with the Big Blue Poppies.
* indicates the predicted chromosome number.

Species or hybrid	**Chromosome no.**	**Ploidy level**	**Authority for chromosome nos**
Single genome or chromosome set	n=x=41	haploid	Not applicable
M. baileyi	2n=2x=82	diploid	Ratter (1968)
M. × *sheldonii* *M.* × 'Slieve Donard' *M.* × 'Crewdson Hybrid'	2n=3x=123	triploid	McAllister (1998)
M. grandis Many cultivars. Some new introductions	2n=4x=164	tetraploid	McAllister (1999)
Not yet ascertained	2n=5x=205*	pentaploid	Not yet determined
Species name not yet accorded	2n=6x=246	hexaploid	McAllister(1999)

Table 3 Chromosome numbers of the Big Blue Poppies – a polyploid series.
* chromosome numbers not yet determined; the predicted number is shown.

The chromosome number of *M. grandis* is precisely double the number of *M. baileyi*. This suggests that *M. grandis* has probably been formed from *M. baileyi*, or its close allies, by chromosome doubling. *M. grandis*, as a polyploid, is likely to have arisen spontaneously and at random. This could occur in the wild or in cultivation.

The genomic or haploid chromosome number for this subgenus, better known as the 'Big Blue Poppies', is (n=x=41). Each component of the possible extended chromosome series, including hybrids, is separated by one complete genome containing 41 chromosomes, as shown in Table 3. The two new additions suggested to complete the series are a hybrid pentaploid and a hexaploid species. Relatively short chromosome series, diploid (2n=2x) to hexaploid (2n=6x) are fairly common in flowering plants. I have experience of three such polyploid series: in *Papaver*, the wild field poppies; in *Brassica*, the synthesis of a complete series using colchicine; and an essay on the value of triploid forms of *Galanthus* (snowdrops) as garden plants.

Diploid details

There is only one species of concern in this rather simplified classification and that is *M. baileyi*. It is widespread throughout the Himalayas and beyond and was discovered by Colonel F.M. Bailey during an expedition to the Tsangpo region of Tibet. *M. baileyi* has become common in cultivation where it is normally reproduced from seed. Seed-grown plants are, not surprisingly, very variable. Two distinct forms have been selected, *M. baileyi* 'Alba' and the attractively coloured *M.* 'Hensol Violet'. *M. betonicifolia* was formerly considered to be a subspecies of *M. baileyi* but it is now considered to be a separate species (Grey-Wilson, 2009).

Triploid details

Triploids are important components of the polyploid series in this subgenus of *Meconopsis*. They are formed by hybridisation between the tetraploid species *M. grandis* and the diploid species *M. baileyi*, and are therefore technically allotriploids. Since triploids are highly sterile they cannot be species, which by definition should be fully fertile. Triploids have their own genetic identity and this is reflected in their characteristic traits. They have proved to be long-lived hardy perennials which flower over a long period.

In theory allotriploids could occur in the wild provided that the parental species are closely sympatric to allow cross-pollination. Triploid *Meconopsis*, involving *M. baileyi* and *M. grandis*, have never been located in the wild and are unlikely to be found because of geographical separation between these two species. All triploids, whether verified or putative, have been formed in cultivation, either arising naturally and spontaneously

Fig. 4 *Meconopsis* ‘Slieve Donard’ flower. Photo: Evelyn Stevens.

in gardens or produced artificially by controlled hand-pollination, as in the cases of *M.* × *sheldonii* and *M.* 'Slieve Donard' (Fig. 4). Several presumed triploids have been regarded as distinct; they have been given cultivar names and have proved to be good, reliable garden plants. The integrity of each cultivar has been maintained by simple division. These include *M.* × *sheldonii*, *M.* 'Slieve Donard' and *M.* 'Crewdson Hybrid'. Only the triploid cultivars listed in Table 3 have been verified cytologically as triploid; others remain putative (*Meconopsis* Group, 2012–2013).

Any triploid has the potential to produce a small number of fertile hexaploid seed. All triploids are open to spontaneous mutation which could occur at any time and at any location. The mutation rate in general is estimated to be one in a million and so it is an extremely rare occurrence. This explains why the evolution of the hexaploid *Meconopsis* 'Lingholm' is a very rare event and seems so far to be unique.

Tetraploid details

Meconopsis grandis (2n=4x=164) has a chromosome number which is precisely twice that of the diploid species *M. baileyi* (2n=2x=82). An early chromosome count of 2n=118–120 by Ratter (Ratter, 1968) was found to be erroneous. It is most likely that McAllister's counts for *M. grandis* are the first for this species (*Meconopsis* Group, 2012–2013). *M. grandis* is the only tetraploid species in the series, just as *M. baileyi* is the only diploid. Both species have been closely related phylogenetically, being paired together in a tree ascertained by Elliott & Kenicer (2009). They are also paired together in several botanical keys such as the one shown in the *Flora of China* (Zhang Mingli & Grey-Wilson, 2008).

Both *M. grandis* and *M. baileyi* are polymorphic, each showing considerable variation. Some forms of these two species are very similar and they can be confused, but flower and leaf size are distinctive, as illustrated by Grey-Wilson (2012). They can also be identified by seed size as depicted by Cobb (1989). All this verified information leads to the logical deduction that *M. grandis* forms have been derived by spontaneous chromosome doubling, which could occur in the wild or in cultivation. In order to substantiate this theory, *M. grandis* and *M. baileyi* should be found sympatric in the wild or planted together in gardens. Neopolyploids of *M. grandis* should remain within reasonably close range of their diploid progenitors. Such a deduction of the evolution of *M. grandis* may be incorrect, as *M. grandis* and *M. baileyi* have not so far been found together in the wild (Grey-Wilson, pers. comm. 2012).

It is important that the existing chromosome counts for *M. grandis* are cemented by others, on a wider range of genotypes, ideally including all three new subspecies, as determined by Grey-Wilson (Grey-Wilson, 2012). They may or may not be different cytotypes or even species. The only feasible strategy is DNA analysis. The phytogenetic relationship between *M. grandis* and *M. baileyi* needs to be determined in a detailed study, perhaps confirming or denying the theory that *M. grandis* has evolved directly from *M. baileyi sensu lato*, by chromosome doubling.

HEXAPLOID DETAILS AS EXEMPLIFIED BY *MECONOPSIS* 'LINGHOLM'

The story of *Meconopsis* 'Lingholm' began in 1934 when W.G. Sheldon of Oxted in Surrey hand-pollinated a Sikkim form of *M. grandis* with *M. baileyi*, introduced from Tibet. Plants raised from the seed produced turned out to be entirely sterile and have remained so ever since. It was officially named *M.* × *sheldonii* after its raiser. It was described and illustrated by George Taylor and officially recognised by the Royal Horticultural Society (Taylor, 1936). *M.* × *sheldonii* had to be propagated clonally because of its sterility and this was mainly done by simple division. This clone may not exist today.

A chromosome count was obtained by McAllister in 1998 for *M.* × *sheldonii* showing it to be a triploid (2n=3x=123) (*Meconopsis* Group, 2012–2013). Plants were circulated far and wide by various nurseries. Some found their way to Cumbria and were grown by Dr L. Nelson in his garden in Brampton in Cumbria. This garden may be the site of the evolution of *Meconopsis* 'Lingholm' as it was here that fertile plants were first found. Seed was distributed and the plants found their way to Lingholm Garden near Keswick, which was owned by the Nelson family. Many years later, this resulted in the plants being given the cultivar name *Meconopsis* 'Lingholm' (*Meconopsis* Group, 2012–2013). In the author's opinion, this is a misnomer as this was not the site of its origin, an irritating and confusing deviation from traditional naming.

Dr Roger Nelson, present owner of Brampton House, informed me that as a birthday present for his father, he bought three plants from his local garden centre, then Hayes of Ambleside, purchased with the label *M.* × *sheldonii*. They were planted together in the garden at Brampton isolated from other *Meconopsis* plants (Dr R. Nelson, pers. comm. 2012). Dr Nelson was unable to recall any relevant dates or further details as he had made the purchase around 50 years previously. He enthusiastically explained the upkeep and refurbishment of the large border of *M.* 'Lingholm' plants which flourishes at Brampton House today. It provides abundant seed which he packages and sends out worldwide since 'Lingholm' is now propagated mainly from seed. The Brampton seed will produce plants most closely resembling the original clone.

Earlier publications state that *M.* × *sheldonii* is the progenitor of *M.* 'Lingholm'. Others including Stevens (Stevens, pers. comm. 2012) believe that it was actually *M.* 'Slieve Donard', which is of different genetic origin. This information is now published on the *Meconopsis* Group's website (*Meconopsis* Group, 2012–2013). This supposition is based on the close morphological resemblance between *M.* 'Slieve Donard' and *M.* 'Lingholm'. The two plants would then probably be isogenic. This is feasible if somatic chromosome doubling was the mechanism involved. This could be confirmed or denied by a suitable molecular technique.

MECHANISMS AND PATHWAYS

Mechanisms and pathways are words commonly used in modern genetics to describe evolutionary processes. A mechanism can be defined as a process that enables something to happen; chromosome doubling is an excellent example. A pathway is defined as leading to the emanation of a new form or even a new species; a good example of these processes is the occurrence of a new hexaploid species, exemplified in *Meconopsis* 'Lingholm'.

There are two ways in which a polyploid can be formed: the first is due to a failure of meiosis leading to the formation of unreduced gametes which pair to give a zygote with double the chromosome number. The second is an asexual vegetative process in which mitosis is inhibited, leading to the formation of a plant with double the chromosome number, a process known as somatic chromosome doubling.

Meconopsis 'Lingholm' cannot have evolved by sexual or reproductive chromosome duplication since its known progenitor is a sterile triploid and does not produce viable gametes. Under these circumstances the only feasible mechanism through which it could have occurred is an asexual one, the vegetative process of somatic chromosome doubling.

Production of a hexaploid through somatic doubling involves two stages: the first stage, chromosome doubling, takes place within the apical meristem of the sterile triploid plant (Fig. 5). In the case of *Meconopsis* 'Lingholm' this is thought to have occurred in the shoot meristem but such mutations are also known to occur in roots and root nodules. A random mutation occurs which interferes with the process of normal mitotic cell division, resulting in a single polyploid cell. This cell multiplies to form a group of hexaploid cells. Later, the doubled cells proliferate and then differentiate to form floral organs which eventually produce pollen and egg cells.

The second stage is reproductive. At anthesis diploid pollen is released, very probably resulting in self-pollination. Male and female balanced euploid gametes with

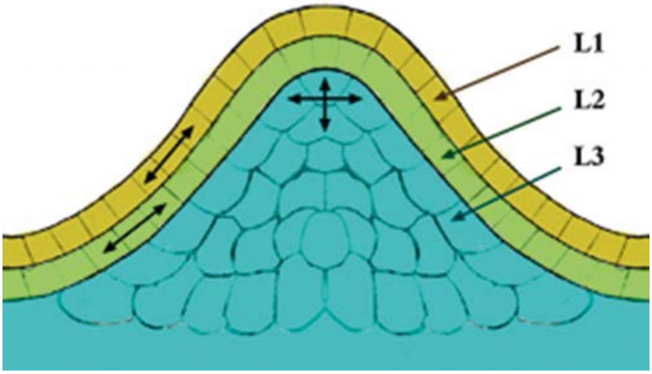

Fig. 5 Longitudinal section of a typical apical meristem. The epidermal (L1) and subepidermal (L2) layers form the outer layers which divide sideways, keeping these layers distinct. The inner (L3) layer divides in all three planes. This is where a single polyploid cell developed in *Meconopsis* 'Lingholm', leading to the formation of a group of hexaploid cells.

n=x=123 chromosomes unite to form a zygote with exactly double the number of chromosomes 2n=6x=246. Such cells then proliferate mitotically to form an embryo, seed, seedling and eventually a mature flowering plant, a hexaploid in the case of *M.* 'Lingholm'. Because somatic chromosome doubling results in euploid gametes with the precise triploid chromosome number the product of their fusion must also be chromosomally balanced with the precise (2n=6x=246) number irrespective of chromosome loss, technically known as shedding, which may occur in later generations. This is a common phenomenon in later generations of neopolyploids with high chromosome numbers. Shedding results in aneuploidy and chromosome imbalance which may or may not affect seed fertility or morphology. Plants with high chromosome numbers can tolerate loss of several chromosomes better than those with few, where the loss of only one or two could prove drastic or even lethal. The 2n=6x=240 count obtained by McAllister in 1999, from plants grown at Ness Botanic Garden, is lower than the euploid number predicted by somatic chromasome doubling. Chromasome shedding may have occurred during the 30-year period which had elapsed.

In the case of *M.* 'Lingholm' this probably happened once only as it was just a single capsule on the sterile triploid plant that produced seed. It seems therefore that *M.* 'Lingholm' is self-compatible. This is confirmed by the copious seed obtained from the original clone of the plant when it was growing in isolation.

It seems that today *Meconopsis* 'Lingholm' stands alone as an example of a hexaploid species. An application should be made for a new hexaploid species and not for *M.* 'Lingholm' *per se*. It should consist of a clear, concise and correct genetical account of the origin and status of *M.* 'Lingholm' together with historical, morphological and cultural details which have already been written on the *Meconopsis* Group website and could remain largely unaltered.

POSSIBILITY OF PENTAPLOIDS

Other cultivars previously grouped along with *Meconopsis* 'Lingholm' as part of the Fertile Blue Group (Stevens, 2006) seem not to be hexaploid but to belong to some other group yet to be defined. Two of these, *Meconopsis* 'Mop-head' and *M.* 'Louise', are in fact not fully fertile and there are plans to reclassify them (Stevens, pers. comm. 2013). The author believes that they are higher polyploids but not hexaploids, due to their sterility and general robust appearance with large flowers. It is suggested, by the author, that these plants could be pentaploids, with five sets of chromosomes and a predicted chromosome number of 2n=5x=205. This is a ploidy level not so far encountered in this group of plants. If this were proved to be so it would complete the one remaining gap in the proposed extended polyploid series. Chromosome studies of *M.* 'Mop-head', *M.* 'Louise' and other large flowered, sterile or even partially fertile, plants could prove revealing. Stevens believes that some may be triploid (Stevens, pers. comm. 2013), however all verified triploids are totally sterile, a fact which, along with their relatively small flowers, seems to set them apart.

In order for a pentaploid to be produced, a hexaploid and a tetraploid must inter-cross. In this example, *M.* 'Lingholm' and *M. grandis* could inter-cross but this could only occur in gardens where they are planted together. There is some circumstantial evidence that *M.* 'Lingholm' and *M. grandis* have cohabited in gardens for some time and certainly may do so today. In general, such crosses are more successful when the plant with higher ploidy level is the seed parent, so pentaploid hybrids may be more likely to be found amongst seedlings obtained from *M.* 'Lingholm' than from *M. grandis.*

The sterile *Meconopsis* 'Jimmy Bayne', discovered by the Head Gardener from Kilbryde Castle, may be a pentaploid. The strikingly tall, elegant *M.* 'Dalemain' which got its name from the garden in Cumbria where it forms a large floriferous colony may be another. Others such as *M.* 'Susan's Reward' and *M.* 'Barney's Blue' may also be pentaploids.

There are numerous others described by the *Meconopsis* Group under the 'Sterile Blue Group'; this is not a definitive classification but a temporary grouping (Stevens, 2006). It is predictable that the taller hybrids are pentaploids with five sets of chromosomes. These hybrids are sterile or only partially fertile and, like the triploid hybrids, are maintained vegetatively as clones. At present both sets of hybrids are grouped together as the Infertile Blue Group. This is not a botanical classification and is insufficiently diagnostic, and should be changed.

A proper classification of these tall, large-flowered plants cannot be made without some form of chromosome analysis. They may or may not be pentaploids; if not, what are they? Molecular DNA studies of a few carefully selected subjects could resolve contentious problems; the author's highest priority would be to confirm the extent of homology or genetic similarity between the tetrapoid *M. grandis* and its possible diploid progenitor *M. baileyi*. They are the only species at present comprising the 'Big Blue Poppies'. The official recognition of a new hexaploid species is very long overdue; comprehensive supporting evidence is given in this account. Many species have been recognised on far less information.

CONCLUSION

It has become obvious that hybrids have superseded species as garden plants. With regard to evolution there are polyploid species that have been considered. The possibility of the tetraploid species *M. grandis* evolving from the diploid species *M. baileyi* is discussed without reaching any conclusion. The evolution of the so far unrecognised hexaploid has been described in detail, represented by a single cultivar, a rare event. This has been described, demonstrating that a high ploidy level has been attained through somatic chromosome doubling, a vegetative mechanism.

The various ploidy levels form a diploid to hexaploid polyploidy series which could be added to by pentaploids. With so much cytotaxonomy being based on supposition there is a clear need for detailed chromosome analysis. The rapid improvements in the efficiency of molecular techniques and their lower cost of use might enable further studies in the genus *Meconopsis*.

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GENERAL REVIEWS ON POLYPLOIDY AND PLANT SPECIATION WHICH HAVE INFORMED SOME OF THE DISCUSSION IN THIS PAPER

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GLOSSARY

Allopolyploid: A polyploid derived from two distinct species.

Allopatric: Referring to species or populations which are geographically isolated.

Aneuploid: An individual or gamete with a chromosome number that is one or a few chromosomes above or below the normal chromosome number.

Anthesis: The shedding of pollen by dehiscence of the anthers.

Autopolyploid: A polyploid derived from one species only, such as autotriploid (2n=3x) or autotetraploid (2n=4x).

Euploid: Having a chromosome number that is the exact multiple of the haploid number of the species.

Glabrous: Smooth, free from hairs.

Homeologous: Referring to partially homologous chromosomes, usually indicating some ancestral original homology.

Homologous: Chromosomes which have a close relationship and precise chromosome pairing.

Hybrid: The product of a cross between two species.

Meiosis: The process in cell division that reduces the number of chromosomes from diploid to haploid, as in the formation of gametes, gametogenesis.

Mitosis: An asexual process that occurs in the nuclei of vegetative cells leading to their division into daughter nuclei with the same chromosome numbers as the parent.

Monocarpic: Flowering once and then dying.

Neopolyploid: A new polyploid, recently formed.

Polymorphic: Literally ‘having many forms’, phenotypically variable.

Polyploid: An organism with three or more sets of chromosomes.

Progenitor: A parent; a biologically related ancestor.

Species: Definitions are many and varied, some are inadequate and do not include seed fertility as a criterion. The author’s definition would be based on seed fertility together with morphological distinctiveness.

Subspecies: An immediate derivative of a species, inter-fertile with that species and with any other subspecies of the same parentage.

Sympatric: An ecological term referring to plants occupying the same habitat.