

Primula ×*murbeckii* originates from spontaneous hybridisation of wild *P. elatior* with cultivated *P. ‘Colossea’* hybrids in Meise Botanic Garden (Belgium)

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Abstract. – During the study of the subspontaneous flora of Meise Botanic Garden (MBG), several odd *Primula* plants were encountered outside the collections in 2021, within a wild population of *P. elatior*. Due to their similarity to *P. vulgaris*, they were initially regarded as *P. ×digenea*, the hybrid resulting from a cross between these two species. However, further observations in subsequent years displayed traits of *P. veris* as well, proving them to be the triple hybrid *Primula* ×*murbeckii*, which is backcrossing with *P. elatior*. Based on the records of cultivated and wild plants in MBG, they must have arisen as a result of hybridisation of cultivated ‘*Colossea*’ hybrids with wild *P. elatior*.

Résumé. – *Primula* ×*murbeckii* apparu par hybridation spontanée de *P. elatior* avec des hybrides cultivés de *P. ‘Colossea’* au Jardin Botanique de Meise (Belgique). Lors d’inventaires des plantes vasculaires dans le domaine du Jardin Botanique de Meise, des primevères singulières ont été observées en 2021 en dehors des collections, au sein d’une population spontanée de *P. elatior*. En raison de leur ressemblance avec *P. vulgaris*, ils ont d’abord été considérés comme *P. ×digenea*, l’hybride issu du croisement entre ces deux espèces. Néanmoins, des observations faites dans les années suivantes ont fait apparaître des caractéristiques de *P. veris*, ce qui a démontré qu’il s’agit du triple hybride *Primula* ×*murbeckii*, et de rétrocroisements avec *P. elatior*. D’après l’inventaire des plantes cultivées et sauvages du Jardin Botanique, ces plantes sont probablement apparues par croisement entre des hybrides du type *P. ‘Colossea’* et des plantes spontanées de *P. elatior*.

Samenvatting. – *Primula* ×*murbeckii* ontstaat door spontane hybridisatie van wilde *P. elatior* met gekweekte *P. ‘Colossea’*-kruisingen in het domein van Plantentuin Meise (België). Tijdens de studie van de spontane en verwilderde flora van Plantentuin Meise werden in 2021 meerdere buitengewone *Primula* planten aangetroffen buiten de collecties, temidden van een wilde populatie van *P. elatior*. Omwille van hun gelijkenis met *P. vulgaris* werden ze eerst als *P. ×digenea* aanzien, de kruising van deze twee soorten. Verdere waarnemingen in de volgende jaren hebben evenwel ook gelijkenissen met *P. veris* aangegeven, wat aantoont dat het gaat om de drievoudige hybride *Primula* ×*murbeckii*, die aan het terugkruisen is met *P. elatior*. Op basis van de inventaris van gekweekte en wilde planten in Plantentuin Meise, werd er afgeleid dat deze planten ontstaan zijn door spontane kruising van gekweekte ‘*Colossea*’-hybriden met wilde *P. elatior*.

Illustrations:

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Introduction

Meise Botanic Garden (MBG, formerly the National Botanic Garden of Belgium), is located approximately 15 km north of Brussels and occupies a 92-hectare estate with several buildings, large botanical collections and lawns and (semi-) natural grasslands as well as woodlands. Since 2002, regular surveys of the spontaneous and alien flora have been conducted by the author, including the documentation of numerous garden escapes presumed to originate from cultivated material within the domain (Ronse 2011; Ronse & Verloove 2021; Ronse & Verloove 2025).

During these surveys, several unusual *Primula* plants were encountered in 2021 within a spontaneous population of *P. elatior* (L.) Hill. Their large, pale yellow flowers resembled those of *P. vulgaris* Huds., a species not occurring naturally in the Meise area

(Van Rompaey & Delvosalle 1979; Brys in Van Landuyt *et al.* 2006), and their early flowering time further distinguished them from the surrounding *P. elatior* plants. These observations raised the hypothesis that the plants might represent hybrids rather than escapes from cultivation.

Hybridisation in the type section of *Primula* is well documented but restricted to a small group of closely related species. *Primula elatior* can hybridise with *P. vulgaris* and *P. veris* L., as well as with four geographically more restricted taxa: *P. grandis* Trautv., *P. juliae* Kusn., *P. megaseifolia* Boiss. & Balansa and *P. renifolia* Volgunov (Schmidt-Lebuhn *et al.* 2012). In Western Europe, the first two species are the most relevant. All three common yellow-flowered species – *P. elatior*, *P. vulgaris* and *P. veris* – are strongly self-incompatible due to floral dimorphism, yet they hybridise readily

when growing in close proximity (Stace *et al.* 2015). Their known hybrids include *P. ×digenea* (*P. elatior* × *P. vulgaris*), *P. ×polyantha* (*P. veris* × *P. vulgaris*), and *P. ×media* (*P. elatior* × *P. veris*), all of which have been reported from several European countries according to Plants of the World Online (POWO; Royal Botanic Gardens, Kew), including Belgium (Verloove & Van Rossum 2023). A triple hybrid, *P. ×murbeckii* Lindq. (*P. elatior* × *P. veris* × *P. vulgaris*), is known only from Great Britain and Denmark. Many cultivated ‘Polyanthus’ plants also derive from hybrid combinations involving *P. veris* and *P. vulgaris*, although their exact parentage is often complex and not fully documented (Köhlein 1984; [Missouri Botanical Garden 2025](#)).

Distinguishing the three species and their hybrids requires attention to a suite of morphological characters. Relevant traits include the presence and length of the scape, the number of flowers per inflorescence, corolla colour and diameter, petal shape, the form and colour of the central floral mark, pedicel length, the presence of dark green stripes on the calyx, the degree of calyx inflation, the type and length of hairs on scape and pedicels, the pilosity of the adaxial leaf surface, and the colour and shape of the leaf base. These diagnostic traits, synthesised from Anchisi *et al.* (1987), Gurney *et al.* (2007), Stace *et al.* (2015), Tendal *et al.* (2018), and Verloove & Van Rossum (2023), are summarised in Table 1.

	<i>P. vulgaris</i>	<i>P. elatior</i>	<i>P. veris</i>
Scape length	0 (rarely max. 100)	100-250	100-250
Flowers/inflorescence	1	3-12	5-30
Corolla colour	very pale yellow	yellow	dark yellow
Corolla diameter	20-30	10-18	6-12(-15)
Petal shape	rounded; notched on top	rather narrow	rounded; not notched
Flower mark shape	star (pentagon)	ring	streaks
Flower mark colour	orange	dark yellow /orange	dark orange
Pedicel length	50-100	5-20(-25) *	5-20(-25)
Calyx: green stripes	present	present (dark green)	absent
Calyx inflated	no	no	yes
Hair type of scape/pedicel	shaggy	straight	straight
Hair length/type of scape/pedicel	≥ 2 / long, shaggy	< 1 / short	short
Adaxial leaf surface	glabrous	hairy	hairy
Leaf base colour	often reddish	usually not reddish	not reddish
Leaf base shape	cuneate	gradually narrowing	suddenly narrowing
Petiole	no	winged	winged in upper part

* mostly shorter than the calyx length

Table 1: Distinctive morphological characters of *Primula elatior*, *P. vulgaris* and *P. veris*. (all measurements in mm).

Primula vulgaris has by far the largest flowers, that are very pale yellow to almost greenish, with rather roundish petals with usually sharper notches, with a distinctive orange star shaped mark at the centre, formed by a diamond-shaped mark at the base of each petal. Each flower sits on a long pedicel but very rarely flowers are inserted on a scape. The pedicels/scape as well as the calyx are covered in (≥ 2 mm) long shaggy hairs. The leaves are cuneate, without distinct petiole, and often reddish at the base. *P. elatior* has smaller flowers, inserted on short pedicels above a scape with short (< 1 mm) hairs, and usually nodding and facing to one side. They have clear yellow, often rather narrow petals, and the flowers display a dark yellow to orange ring shaped mark centrally at their base; the calyx displays distinctive dark green stripes. The

usually rather broad leaves often have a distinct petiole, and are mostly not reddish at the base. *P. veris* has the smallest flowers, and mostly not all facing the same way. They are deep yellow and with short roundish petals that display a sharp dark orange streak at their base inside; the calyx is broad and inflated, without green stripes, with very short crisped hairs and broader teeth (see Fig. 1, right). The flowers are inserted on short pedicels above a long scape that is also covered with very short crisped hairs. The leaves are sharply truncate, glabrous above, and very shortly hairy beneath.

Not surprisingly, the morphology of the hybrids is more variable than that of the species, as many combinations of traits of the parent species can occur. *P. ×digenea* (*P. elatior* × *P. vulgaris*) often

shows intermediate corolla size and colour, relatively short scapes and conspicuously long white hairs on the calyx (Fig. 1, left), though some backcrossed individuals resemble *P. elatior* closely and flower earlier than the surrounding *P. elatior* population (Gurney *et al.* 2007). The identity of these later generation hybrids can only be confirmed by molecular-genetic analyses. *P. ×media* (*P. elatior* × *P. veris*) typically exhibits *veris*-like calyx inflation combined with *elatior*-like flower shape or orientation, as illustrated by spontaneous hybrids photographed in Belgium (Fig. 1, right). *P. veris* differs by its smaller flowers, with a more bluntly toothed and inflated calyx. *P. ×polyantha* (*P. veris* × *P. vulgaris*) is highly variable and may show umbellate inflorescences with a dark orange streak at the petal base, while cultivated forms display a broad range of colours and morphologies (Gurney *et al.* 2007; Tendal *et al.* 2018). ‘Polyanthus’ plants often have dark green and deeply textured leaves, and umbellate inflorescences with 4–12 flowers on stout stalks above the foliage (Missouri Botanical Garden, accessed on 12.09.2025). The triple hybrid *P. ×murbeckii* (*P. elatior* × *P. veris* × *P. vulgaris*) is characterised by an umbellate inflorescence reminiscent of *P. ×polyantha* but with clear *P. elatior* influence, such as a bicoloured green calyx (Stace *et al.* 2015). This hybrid occurs mainly when the fertile *P. ×digenea* wild hybrid crosses with *P. veris* (wild, or sometimes coloured garden strains), and less often when fertile garden ‘Polyanthus’ plants hybridise with wild *P. elatior*. Later-generation hybrids and backcrosses may resemble one parent more strongly, making detailed morphological assessment essential (Tendal *et al.* 2018).



Figure 1: *Primula* flowers: Left: *P. ×digenea* with long white hairs on the calyx. Right: *P. veris*, *P. ×media* and *P. elatior* (from left to right).

The unusual *Primula* plants observed in MBG displayed combinations of characters not fully consistent with any of the three species, suggesting hybrid origin. To clarify their identity and provenance, multi-year field observations were combined with herbarium sampling and morphometric analysis. The aim of this study is to determine whether these plants correspond to known hybrid taxa, including the rare triple hybrid *P. ×murbeckii*, and to assess how their occurrence can be explained in relation to the wild and cultivated *Primula* taxa historically and currently present in Meise Botanic Garden.

Material and methods

A targeted literature survey was conducted to identify morphological characters that reliably distinguish *Primula elatior*, *P. vulgaris*, *P. veris* and their known hybrids. Based on this synthesis, a set of diagnostic traits was selected for use in the morphological assessment of the plants encountered in Meise Botanic Garden (MBG). These traits were subsequently measured on herbarium

material collected over several years at the site.

The main concentration of putative hybrid plants in MBG is located in sector 54 (conifer collection), within the boundaries of a spontaneous *P. elatior* population. This area was visited repeatedly during the flowering period (March–April) between 2021 and 2026, specifically on 18 March 2021, 24 March 2023, 5 April 2023, 17 April 2024, 25 April 2025 and 3 April 2026. During each visit, detailed field observations were made, photographs were taken, and herbarium vouchers were collected. All specimens are deposited in BR, the herbarium of Meise Botanic Garden. Additional hybrid individuals were also collected in adjacent sectors, including sector 51 (Cronquist Garden) and sector 53. Morphological measurements were carried out on a selection of these specimens, using the diagnostic characters identified in the literature as distinctive for the three species and their hybrids.

Results

1. Field observations of putative *Primula* hybrids

During the first observation in March 2021, several plants with large, pale yellow flowers borne on a short scape were recorded in sector 54. Their morphology, combined with their markedly early flowering compared to the surrounding *Primula elatior* population, suggested that they represented *P. ×digenea*, likely F₁ or early-generation hybrids (Fig. 2).



Figure 2: Putative F₁ *Primula ×digenea* (left: n° 1*), 8 March 2021. *: plant numbers refer to the numbers in table 2.

Other individuals displayed slightly smaller and darker yellow flowers, mostly arranged on a relatively short scape, although some plants also produced one or more flowers on conspicuously long pedicels (Fig. 3). These plants likewise appeared to represent early-generation hybrids, but with a different combination of parental traits than n° 1: two flowers each on a separate pedicel with smaller corollas with a dark yellow pentagon-shaped mark, and a calyx with green stripes but clearly inflated—an attribute otherwise restricted to *P. veris*.

Plant n°	1	2**	3	4	5	6	7	8	9	10	11	12	13	14	15
Herbarium n°	AR4931	AR4932	AR5753	AR5754	AR6264	AR6279	AR6278	AR6715	AR6717	AR6716	AR6719	AR6638	AR6639	AR6640	AR6722
Date	17.03.21	17.03.21	16.04.24	16.04.24	25.03.25	16.04.25	16.04.25	06.03.26	06.03.26	06.03.26	17.03.26	03.04.26	03.04.26	03.04.26	20.04.26
Scape length	65	110	157	303	120	115	38	123	156	109	238	149	180	245	244
N° of flowers	10	14 (+2)	11	12	7	12	13	7	6	2	17	4	11	15	8
Corolla colour	pale yellow	yellow	red	(pale) yellow	(bright) yellow	yellow	(/)	yellow	dark yellow	± dark yellow	yellow	yellow	pure yellow	± dark yellow	yellow
Corolla diameter*	23.5 19-28	13.7 11.5-15	21.3 21-22	19.3* 18-21	16.7* 16-17	24 24	//	21.6 20-24	10.0 6-12	10.5 10-11	12.4 10-15	21.6 21-22	23.5 16-26	20.4 20-21	12.0 10-14
Flower mark shape	PENT	(PENT)	RING	(PENT)	RING	RING	/	RING	RING	RING	RING	± (PENT)	(PENT)	RING	RING
Flower mark colour	dark yellow	yellow	dark yellow	dark yellow	yellow	yellow	/	orange	dark yellow	dark yellow	dark yellow	light orange	light orange	light orange	dark yellow
Petal shape	broad, notched	± narrow, notched	± narrow, notched	± narrow, notched	± narrow, notched	broad, notched,	/	± broad notched	narrow, notched	broad, notched	± narrow, notched	broad ± notched	broad notched	± broad notched	± broad, notched
Pedicel length	15.8 7-22.5	6.2 2-11	10.4 9-11	4.3* 2-12	8.6* 3-15	28.9 26-33	14.1 8-22	26.6 16-33	7.0 5-13	5.5 5-6	6.8 3-14	6.7 5-10	13.4 7-23	10.7 2-22	11.6 2-22
Calyx stripes	No	(Yes)	Yes	Yes: broad	Yes	Yes: broad	Yes: broad	Yes	Yes	Yes	Yes: broad	Yes	Yes	Yes	(Yes)
Calyx inflated	1	1	2	1	2	2	2	1.5	0	1	1	2	1	2	2
Hair type	shaggy	straight	shaggy	(shaggy)	(shaggy)	shaggy	straight	shaggy	straight	shaggy	(shaggy)	straight	(shaggy)	shaggy	shaggy
Hair length (max.)	1.0	0.2 (0.3)	0.5 (-0.7)	0.2 (0.3)	0.4	1.2	0.3	1.3	0.5	0.5	0.6	0.3	0.9	1.0	1.0
Adaxial leaf pilosity	--	---	/	--	-	/	/	++	--	++	+	--	+	+	++
Leaf base colour	green	green	/	(reddish)	(reddish)	/	/	green	green	green	green	green	red-purple	reddish	green
Petiole winged	no	no	/	narrowly	Upper only	/	/	no	yes	no	no	yes	yes	/	no

/ only overblown flowers

* without measures of not fully developed/ overblown flowers

** n° 2 displayed three basal flowers on a separate pedicel of resp. 5 and 5.6 cm long, the third one on a not fully grown pedicel

PENT: pentagon-shaped; (PENT): pentagon-like; ± (PENT): more or less pentagon-like

Table 2: Morphology of hybrid *Primula* in BGM. **Bold**: average value (All measures in mm).



Figure 3: Hybrid with rather small flowers and inflated calyx; three flowers on a separate pedicel (n° 2), 8 March 2021.

In March 2023, four additional putative F₁ *P. ×digenea* individuals were observed (Fig. 4), together with a larger number of plants resembling *P. elatior* but with slightly larger and paler flowers and a more inflated calyx (Fig. 4, bottom, in background). At that time of year, most *P. elatior* plants in the population were not fully flowering.

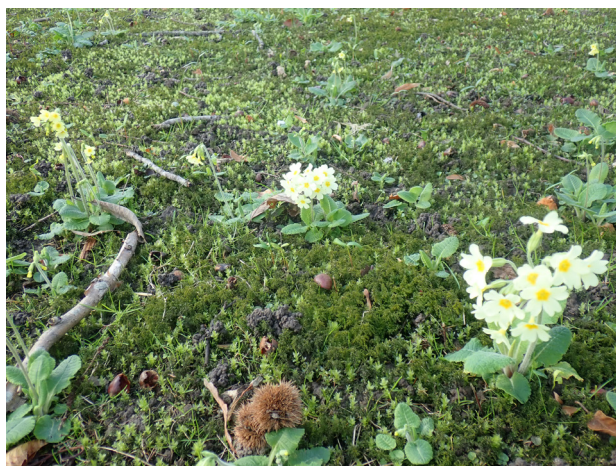


Figure 4: (↑↑) Putative F₁ *Primula ×digenea* in sector 54, 24 March 2023. (↑) With *P. elatior*-like plants in background.

On 16 April 2024, when the majority of *P. elatior* individuals were still non-flowering, one hybrid plant with double flowers was recorded (Fig. 5, top). Other flowering individuals displayed various intermediate combinations of parental characters. Many resembled *P. elatior* but flowered slightly earlier and showed a distinctly inflated calyx, particularly plant n° 6, which also had unusually long pedicels. One plant (n° 3) bore purplish-red flowers – not present in any wild *Primula* in Belgium – on a scape of average length (Fig. 5, bottom).



Figure 5: (↑↑) Double flower of hybrid plant. (↑) *P. elatior*-like inflorescences of n° 4, n° 3, and n° 6 (from left to right), April 2024. Note the variable pedicel lengths.

In 2025, one hybrid with clear *P. vulgaris* influence was still present, characterised by large pale flowers on a short scape. Several plants with more intermediate combinations of traits (n° 5–7) were also recorded, while rather many *P. elatior*-like individuals flowered slightly earlier than the bulk of the species. On 6 March 2026, a few plants with *P. vulgaris*-like traits were again observed, including individuals with relatively large flowers on a short scape and long pedicels (e.g. n° 8). One month later, numerous intermediate plants (n° 12–15) were present. Additional putative hybrids were also found in sectors 51 (Cronquist Garden) and 53.

2. Morphometric analysis

Between 2021 and 2026, sixteen herbarium specimens representing the observed morphological variation were selected for detailed measurement using the diagnostic traits summarised in Table 1. The results are presented in Table 2.

The earliest specimen (n° 1, 2021) exhibited nearly all diagnostic characters of *P. vulgaris*: large pale yellow flowers with a pentagon-shaped mark, absence of green stripes on the calyx, long

shaggy hairs on pedicels and scape, a green leaf base, and an almost entirely glabrous adaxial leaf surface. In subsequent years, plants with large flowers continued to occur, but increasingly in combination with traits of the other species.

From 2024 onwards, plants with intermediate morphologies became more frequent. Two individuals collected that year (n° 3 and 4) both had relatively large corollas, but differed markedly: n° 4 bore pale yellow flowers with a pentagon-shaped mark on a long scape, whereas n° 3 had purplish-red flowers with a ring-shaped mark on a scape of average length.

In 2025 and 2026, repeated visits allowed the detection of a broader range of trait combinations, including individuals with high flower numbers (e.g. n° 2, 7 and 10). Overall, traits attributable to *P. elatior* became increasingly common, which is expected given the location of the hybrids within a large spontaneous population of this species. This trend is reflected most clearly in the frequent presence of green stripes on the calyx, absent only in specimen n° 1. The influence of *P. veris* is most evident from the widespread occurrence of an inflated calyx, present in all but one plant (n° 9), though to varying degrees. Small corolla size and late-season flowering also suggest *P. veris* influence, as seen in specimen n° 15 (late April 2026). Several plants collected earlier in 2026 (n° 9, 10 and 12) likewise had small corollas (10–12.5 mm) and an inflated calyx, except for n° 9.

Because the earliest surveys focused on early-flowering individuals under the assumption that the plants represented *P. ×digenea*, sampling effort differed between years. Consequently, direct year-to-year comparisons are not possible. Nevertheless, the population as a whole displays traits of all three parental species. Over time, characters attributable to *P. vulgaris* appear to decline most strongly, although these are also the most conspicuous traits and may therefore have been overrepresented in early field observations.

A complete list of examined herbarium specimens (BR) is provided below. All specimens correspond to *Primula ×murbeckii*, including individuals showing varying degrees of backcrossing with *P. elatior*:

A. Ronse 4931, Meise Botanic Garden, coniferetum s 53, forest understory, among *P. elatior*, flowers paler yellow and much larger, on ± short scape, 17.03.2021 (n° 1); A. Ronse 4932, Meise Botanic Garden, coniferetum s 53, forest understory, some flowers on a long pedicel, 17.03.2021 (n° 2); A. Ronse 5753, Plantentuin Meise, sector 54, spontaneous, purple flowers, only 1 plant (?), 16.04.2024 (n° 3); A. Ronse 5754, Plantentuin Meise, sector 54, coniferetum, with distinct petiole but slightly reddish at base, 16.04.2024 (n° 4); A. Ronse 6264, Meise, Botanic Garden, sector 54, close to hybrid *P. ×digenea*, 25.03.2025 (n° 5); A. Ronse 6279, Meise Botanic Garden, sector 54, n° 3, with seeds, 16.04.2025 (n° 6); A. Ronse 6278, Meise Botanic Garden, sector 54, 16.04.2025 (n° 7); A. Ronse 6715, Meise, Botanic Garden, sector 54, 03.04.2026 (n° 8); A. Ronse 6717, Meise, Botanic Garden, sector 54, 03.04.2026 (n° 9); A. Ronse 6716, Meise, Botanic Garden, sector 54, n° 2, 06.03.2026 (n° 10); A. Ronse 6719, Meise, Botanic Garden, sector 54, 17.03.2026 (n° 11); A. Ronse 6638, Meise, Botanic Garden, sector 54 Coniferetum, hybrid n° 1, 4 flowers, 03.04.2026 (n° 12); A. Ronse 6639, Meise, Botanic Garden, sector 54 Coniferetum, hybrid n° 2, 03.04.2026 (n° 13); A. Ronse 6640, Meise, Botanic Garden, sector 54 Coniferetum, hybrid n° 3, 06.03.2026 (n° 14); A. Ronse 6722, Meise, Botanic Garden, Herbetum, spontaneous in collections, 20.04.2026 (n° 15).

3. Actual and past presence of cultivated and wild *Primula elatior*

P. vulgaris, *P. veris* and hybrids in MBG

Primula elatior occurs naturally in several areas of MBG, including sector 54 (Coniferetum). Plants from these wild populations were planted in the Cronquist Garden (formerly Herbetum) and the Garden of Medicinal Plants in 1983 and 1996, but have since disappeared.

Primula vulgaris has been cultivated in several locations, including the Cronquist Garden, using both commercial material and plants collected from a Belgian wild population in 2008. Most plantings have disappeared, except for a thriving white-flowered accession ('English Snow') in the Dahlgren Arboretum and a commercial accession planted in 2019 in the new Medieval Garden near the main entrance.

Neither *Primula ×digenea* nor *P. ×murbeckii* is recorded as cultivated in MBG. However, *P. ×polyantha* 'Colossea' was grown in sectors 19 and 24, both near the Meise Village entrance and approximately 1 km from the spontaneous hybrids in sector 54. These red-flowered plants were removed several years ago during redevelopment of the displays.

Primula veris has been cultivated in various locations, including the Cronquist Garden and the Medicinal Garden, using several Belgian wild accessions. All plantings have since disappeared.

Discussion

The first unusual *Primula* plants observed in 2021 within the spontaneous *P. elatior* population in MBG displayed large, pale yellow flowers borne on a short scape and marked by a pentagon-shaped corolla pattern. Their early flowering, combined with several traits reminiscent of *P. vulgaris*, initially suggested that they represented *P. ×digenea* (*P. vulgaris* × *P. elatior*). This interpretation was consistent with the flowering phenology reported by Tendal *et al.* (2018), who noted that *P. vulgaris* typically flowers one to two weeks earlier than *P. elatior*, albeit with substantial overlap. However, continued observations over several years gradually challenged this hypothesis.

A turning point occurred in 2024, when a late-flowering individual with a striking purple-red corolla was discovered. This unexpected colour variant raised questions about the identity and provenance of the hybrids. Further investigation revealed that purple-red flowered forms of *P. vulgaris* do occur, namely in subspecies *rubra* (Sm.) Arcang., but this taxon has never been cultivated at MBG. The observation therefore cast doubt on the interpretation of the hybrids as *P. ×digenea* and prompted a more detailed examination of the entire hybrid population. Additional observations revealed traits not attributable to *P. vulgaris* or *P. elatior* alone, most notably the frequent presence of an inflated calyx, a character diagnostic for *P. veris*. Since *P. veris* can hybridise with both *P. elatior* and *P. vulgaris*, its involvement provided a more coherent explanation for the observed morphological diversity. The combination of characters from all three species strongly indicated that the plants represent the triple hybrid *P. ×murbeckii* (*P. elatior* × *P. veris* × *P. vulgaris*), which is known to exhibit umbellate inflorescences resembling *P. ×polyantha* but with clear *P. elatior* influence, such as a bicoloured green calyx (Stace *et al.* 2015).

Over the course of the study, hybrids with a wide range of floral and vegetative trait combinations were recorded, including individuals with smaller, darker yellow flowers and others with unusually long pedicels or high flower numbers. The population displayed a continuous morphological gradient, with an apparent increase over time in traits attributable to *P. elatior*. This pattern is consistent with ongoing backcrossing, which is expected

given the location of the hybrids within a large, well-established *P. elatior* population. Ecological factors may reinforce this trend: *P. elatior* is better adapted to shaded woodland conditions, whereas *P. veris* tolerates drier, more open habitats (Whale 1983, 1984). The presence of the triple hybrids on the more elevated, better-drained parts of sector 54 aligns with these ecological preferences.

To reconstruct the origin of *Primula* $\times$ *murbeckii* in the Coniferetum, the historical and current presence of potential parental taxa in MBG was examined. Hybridisation of *P. elatior* is only possible with other members of the type section (*P. vulgaris*, *P. veris*, *P. grandis*, *P. juliae*, *P. megaseifolia* and *P. renifolia*), but the latter four species have never been cultivated in MBG and can therefore be excluded. Although red or purple *P. juliae* $\times$ *P. vulgaris* hybrids (e.g. *P. $\times$ pruhonicensis* Zemmann ex Bergmans, including the cultivar ‘Wanda’; Stace *et al.* 2015), could theoretically account for the red-flowered individual, these have likewise never been planted in MBG. In contrast, *P. elatior*, *P. vulgaris* and *P. veris* have all been cultivated in the garden at various times, and *P. elatior* is abundant in the wild flora of the domain.

The presence of a red-flowered hybrid suggests the involvement of a cultivated parent with anthocyanic pigmentation. A plausible candidate is the red-flowered *P. $\times$ polyantha* ‘Colossea’, which was historically grown in several locations near the Meise Village entrance, approximately 1 km from the hybrid population. Although these plants were removed around 2020, their earlier presence provides a credible source of *P. vulgaris* $\times$ *P. veris* genetic material capable of hybridising with wild *P. elatior*. The horticultural background of ‘Colossea’ is poorly documented, but its morphology – umbellate inflorescences, numerous flowers, and a wide range of colours – strongly suggests that it belongs to the ‘Polyanthus’ hybrid group.

The formation of *Primula* $\times$ *murbeckii* through spontaneous hybridisation has been documented previously. In the UK, Simpson (1982) and Sanford & Fisk (2010) have reported yellow flowered triple hybrids arising where wild fertile *P. $\times$ digenea* hybridises with wild *P. veris*; Stace *et al.* (2015) also mention one hybrid in his garden, adjacent to a single cultivated plant of *P. elatior* and about 30 m from ‘Polyanthus’ plants. Additional records exist from Denmark (POWO) as well as a probable observation from Switzerland (iNaturalist, 2023). In one case only, red-flowered *P. $\times$ murbeckii* plants were recorded in a woodland fragment in Cambridgeshire (UK), at 100 m distance from the nearest wild *P. elatior* and 500 m from cultivated ‘Polyanthus’ plants in gardens (Preston 1993). The situation in MBG closely parallels these cases, with spontaneous hybridisation occurring in a mixed landscape of wild *P. elatior* and formerly cultivated ‘Polyanthus’-type hybrids.

The increasing prevalence of *Primula elatior* traits in the MBG population suggests that backcrossing with this species is ongoing. This interpretation is consistent with Stace *et al.* (2015), who noted that *P. $\times$ murbeckii* hybrids are capable of producing seed, although detailed fertility data remain scarce.

Conclusion

The unusual *Primula* plants observed within a *P. elatior* population at Meise Botanic Garden represent a spontaneously formed population of *P. $\times$ murbeckii*, the triple hybrid between *P. elatior*, *P. veris* and *P. vulgaris*. The hybrid most likely originated through crosses between wild *P. elatior* and cultivated ‘Polyanthus’-type hybrids formerly grown at MBG, notably the red-flowered ‘Colossea’ accession. Hybridisation probably occurred before 2021, the year in which the unusual *Primulas* were first recorded and also the

year when the cultivated ‘Polyanthus’ hybrids were removed. As the site had not been surveyed during the early flowering season prior to 2021, the original *P. $\times$ murbeckii* individuals may have gone unnoticed. The morphological diversity of the plants in the population and their evolution in time reflect multiple generations of hybridisation and subsequent backcrossing with *P. elatior*, the dominant species at the site. This study provides the first documented occurrence of *P. $\times$ murbeckii* in Belgium and illustrates how cultivated garden hybrids can contribute to complex hybridisation dynamics within semi-natural plant populations.

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