# Hybridisation between Oxlip *Primula elatior* (L.) Hill and Primrose *P. vulgaris* Hudson, and the identification of their variable hybrid *P.* ×*digenea* A. Kerner

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ABSTRACT

Hybrids between Oxlip *P. elatior* and Primrose *P. vulgaris* are commonly recorded in mixed populations of the two species, but there has been debate as to whether or not backcrossing and introgression occur. Allozyme electrophoresis has demonstrated that backcrossed or $F_{>1}$ hybrids are frequent in a mixed population of the species in Cambridgeshire (v.c. 29). Molecular analysis reveals that the hybrid or backcrossed plants are very variable in morphology, and some cannot be distinguished from Oxlips in the field. However, whilst some hybrids are intermediate in character and some are identical, or almost identical, to Oxlips, all were easily distinguished from Primrose. Oxlip is easily separated from the widespread hybrid between Cowslip and Primrose, *P. veris* × *vulgaris*.

KEYWORDS: Buff Wood, introgression, *Primula veris*, *Primula* ×*polyantha*, Primulaceae.

## INTRODUCTION

### HYBRIDS BETWEEN YELLOW-FLOWERED PRIMULAS IN BRITAIN

All three of the British yellow-flowered primulas (Oxlip *Primula elatior*, Primrose *P. vulgaris*, and Cowslip *P. veris*) interbreed to produce hybrids (Valentine 1975). Of the three hybrids, the most widespread is that between *P. vulgaris* and *P. veris*, known as False Oxlip *Primula* ×*polyantha*. This plant caused considerable consternation among the botanists of the 19th Century as they debated whether or not the Oxlip was a British plant (Brown 1842; Doubleday 1842; Hill 1842; Leefe 1842; Moxon 1842; Watson 1842; Gibson 1844). The False Oxlip has been recorded as a native from 87 of the 112 Watsonian vice-counties in Britain (Stace *et al.* 1993), and its distribution matches the range of the less widespread parent, *P. veris*, fairly closely (Preston *et al.* 2002). However, the hybrid is rarely present in large numbers (Clifford 1958). The cross between *P. veris* and *P. vulgaris* is more fertile when *P. veris* is the female parent (Darwin 1869), but even so the seeds are less viable than those produced by intraspecific crosses (Valentine 1955). Despite the high viability of seeds from backcrosses to either parent (Valentine 1955), apparent backcross plants or $F_2$s (crosses between hybrids) are rarely reported in the wild (Clifford 1958; Woodell 1965).

As one would expect from the limited range of *P. elatior*, the hybrids that involve this species have a much more restricted distribution than *P.* ×*polyantha*. The hybrid between *P. elatior* and *P. veris*, *P.* ×*media*, is rare. It has been recorded only sporadically from North Essex (Jermyn 1974), Cambridgeshire (Preston 1993), East and West Suffolk (Simpson 1982), East Norfolk (Miller Christy 1922), and Huntingdonshire (Wells 2003). The *P. elatior* × *P. veris* cross very rarely produces viable seed, but when *P. veris*

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is the female parent, a tiny fraction of seeds produced may germinate. Valentine (1952) obtained germination rates of 14/4000 for female *P. veris* × male *P. elatior*, and 0/2000 for the reciprocal cross with *P. elatior* as the female. Offspring have been produced by backcrossing *P. media* to either parent (Valentine 1952), but the only case of backcrossing in the wild that we are aware of is a rather curious-sounding record by Jermyn (1974) of a "hybrid swarm with no *P. veris* present and only a few roots of *P. elatior* near a railway with scattered hybrids and abundant *P. veris*, and a wood with plentiful *P. elatior*". A triple hybrid between all three species, *Primula ×murbeckii*, has been reported from Suffolk where it seems to have been most often found in colonies of *P. elatior* × *P. vulgaris*, but it is extremely rare (Simpson 1982). There is one record from Cambridgeshire, where an apparent cross between native *P. elatior* and cultivated *P. ×polyantha* has been reported (Preston 1993).

*P. ×digenea*, the hybrid between *P. elatior* and *P. vulgaris*, has a limited distribution, but it seems to be present at all British sites where both parents occur together. It is certainly in all the woods west of Cambridge that contain both *P. elatior* and *P. vulgaris* (Meyer & Meyer 1951), and in all those known to us east of that city (which divides the British range of *P. elatior* into two separate parts). In contrast to the more widespread *P. ×polyantha*, *P. ×digenea* can be present in large quantities where the parent species meet: in Gamlingay Wood (v.c. 29), Peter Walker (unpublished data) counted 3675 Oxlips, 404 Primroses, and 2131 hybrids in 1992. Populations in woods where hybrids are present have been described as hybrid swarms.

The character of the *P. elatior* × *P. vulgaris* hybrid is very variable. Simpson (1982) noted that "almost every conceivable form can be found between the species. There are some that might be mistaken for Primroses, or even pure Oxlips". The large numbers of hybrids, and the presence of plants that are almost, but not quite, identical to either parent, suggested that introgression and backcrossing may be frequent. This was disputed by Miller Christy (1922), who was "not conscious of ever having seen a plant which appeared to be a second-cross hybrid", and by morphological investigations by Valentine (1948) and Woodell (1969). However, Valentine (1961) revised this view after a later study, concluding that "At any rate, at present, introgression is certainly occurring."

The variability of the hybrids, and of *P. elatior* itself, means that it is difficult to use morphological characters to distinguish between first ($F_1$) and later ($F_{>1}$) generation hybrids and backcrosses, and this probably explains the difference in opinion as to whether populations are introgressed.

Using molecular species-specific markers, we have proved that in the well-studied Oxlip population at Buff Wood, Cambridgeshire (v.c. 29), some plants are indeed introgressed or backcrossed (Gurney 2000). Molecular markers also revealed that some plants that were identified as Oxlips using morphological characters were in fact hybrids.

With the interest in hybrids from the new hybridisation and the British flora project (Pearman & Preston 2005), we feel it is timely to review the characters used to identify Oxlips and their hybrids, and to demonstrate the variation that can be found in hybrid swarms. Mixed populations of parent species and putative hybrids are not uncommon in the British flora and have traditionally been investigated by morphological or morphometric studies. Examples include species of *Betula* (Brown *et al.* 1982), *Calamagrostis* (Crackles 1995), *Dactylorhiza* (Heslop Harrison 1949), *Gentianella* (Rich *et al.* 1997), and *Quercus* (Kelleher *et al.* 2003). In some cases cytological evidence has been used to confirm the identity of hybrids in populations where the putative parents differ in chromosome number, such as in the studies of *Eleocharis* by Lewis & John (1961). Only in recent years has it been possible to combine morphological and molecular studies to investigate the identify of putative hybrids, for example in *Potamogeton* (Fant *et al.* 2003), *Trichophorum* (Hollingsworth & Swan 1999), *Salix* (Scottish Montane Willow Research Group 2005), and *Schoenoplectus* (Fay *et al.* 2003). In this study the identity of putative hybrids has been confirmed by allozyme electrophoresis and these plants have been used in assessing the morphological differences between the taxa.

## METHODS

### MORPHOLOGY

The populations of *P. elatior*, *P. vulgaris*, and *P. ×digenea* at Buff Wood, Cambridgeshire (v.c. 29), National Grid Reference TL2850, have been the subject of previous studies of hybridisation (Valentine 1947, 1948, 1961; Walters & Ockenden 1968). Plants in this

population were compared with those from single-species populations of *P. elatior*, *P. vulgaris*, and *P. veris* ("pure populations"). They were examined and photographed, and characters useful for distinguishing them were noted. From these, drawings were made to show the main characters of each species. Plants of known genotypes at Buff Wood were also drawn and photographed to record the variation in hybrids and backcrossed plants. Specimens of these were deposited in the herbarium of the Department of Plant Sciences, University of Cambridge (**CGE**). The Buff Wood plants included 26 hybrids of which 11 were non-$F_1$ hybrids. (Backcrosses are produced by hybrids crossing with one of the parent species, and later generation ($F_{>1}$) hybrids are formed by crosses between hybrids. Both of these could show exactly the same pattern when examined using allozyme electrophoresis, so we could not distinguish between them. We therefore use the term "non-$F_1$ hybrid" to describe backcrosses and later generation hybrids (as distinct from first generation $F_1$ hybrids).)

### POLLEN STAINABILITY

One flower was collected from plants selected at Foxley Wood, East Norfolk, v.c. 27, and Wayland Wood, West Norfolk, v.c. 28 (*P. vulgaris* only), and Hayley Wood (*P. elatior* only), Cambridgeshire, v.c. 29, and Buff Wood (both species), also v.c. 29, and stored in 70% ethanol. The number of plants used varied between sites (Table 2) because we wanted to use the same individuals sampled for allozyme electrophoresis so that we could be certain of the genetic identity of the plants. Unfortunately, some of these plants had all their flowers removed by herbivores before they dehisced, so not all could be sampled for pollen stainability. Eight months after collection, the fertility of each flower was estimated by counting the number of round, stainable pollen grains in acetocarmine. This method was used by Woodell (1969) and Valentine (1948), but neither gave details of the protocol used. We followed the method in Gurr (1953), using a solution of 0·4 g carmine in 55 ml water and 45 ml glacial acetic acid. An anther was removed from the flower and placed on a microscope slide and a drop of acetocarmine was added. A coverslip was then placed on top and tapped to disperse the pollen grains. A sample of 200 grains was counted and the number of unstained, unswollen grains was recorded. Although staining is not necessarily an accurate measure of fertility, this method has been used to distinguish backcrossed plants in previous studies of introgression in *Primula* (Woodell 1965), and combining the staining results with the electrophoresis should allow an assessment of its effectiveness.

## RESULTS

### MORPHOLOGICAL CHARACTERS OF *P. ELATIOR*, *P. VULGARIS*, *P. VERIS*, AND THEIR HYBRIDS

The most useful characters for distinguishing between *P. elatior* and *P. vulgaris*, based on plants from pure populations, are shown in Figs 1–2 and Table 1. *P. elatior* has smaller flowers than *P. vulgaris*, but there is some overlap. More important are the colour of the flowers and the shape of the markings at their centre, scent, and the hairiness of the pedicels and scape. In the mixed population at Buff Wood, some plants combine characters from both species, and molecular analysis shows that these are a mixture of $F_1$ and non-$F_1$ hybrids. Three examples of these are shown: an "intermediate" hybrid (Fig. 3); an "Oxlip-like hybrid" (Fig. 4); and a "Primrose-like hybrid" (Fig. 5). Drawings of *P. veris* and *P. ×polyantha* are shown for comparison in Figs 6–7. The variation in hybrids confirmed by electrophoresis is illustrated in Plates 1–6, and photographs of the parents from pure populations are shown in Plates 7–8.

There is no difficulty in distinguishing between the species, between *P. ×polyantha* and *P. elatior*, and between *P. ×polyantha* and *P. ×digenea*. Hybrids involving *P. veris* reveal their parentage by a dark orange streak at the base of the petal, by an inflated, more bluntly-toothed calyx, and by shorter hairs. *P. vulgaris* appears much more distinct than does *P. elatior*. Many plants at Buff Wood closely resembled *P. elatior* from pure populations but they showed one or more features suggestive of *P. vulgaris*, such as slightly longer hairs than in the pure populations, or larger flowers. If they had been found in pure populations, these would probably have been considered to be just outside the extremes of variation within *P. elatior* and they more or less grade into it. In contrast, all the plants with *P. vulgaris* characters, such as large, pale flowers, or shaggy hairs, were either obviously

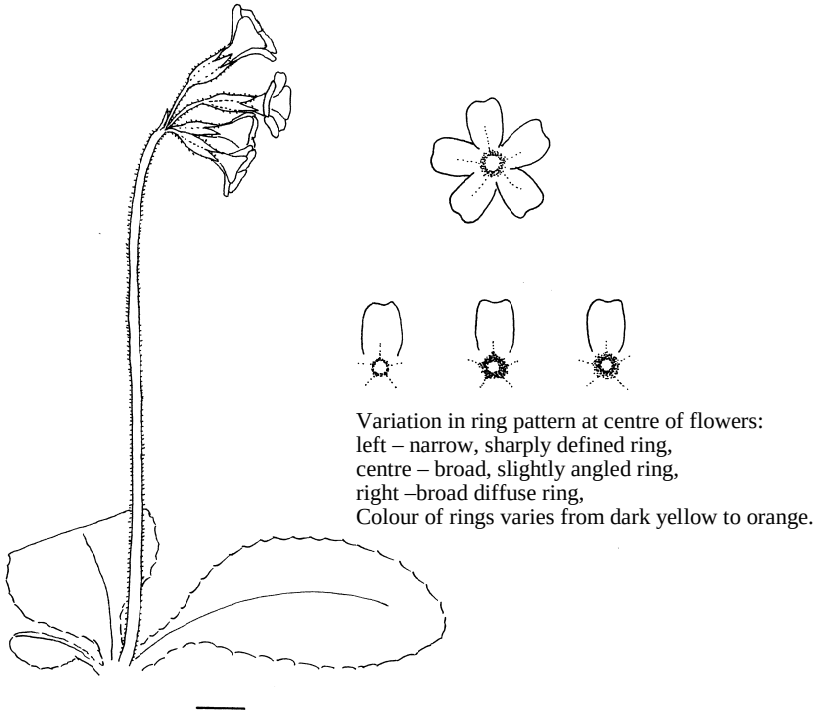


FIGURE 1. *Primula elatior*. Calyx rather narrow. Flowers usually facing to one side. Flowers clear yellow, petals often rather narrow. Leaves hairy, often with distinct petiole, usually rather broad and not reddish at base. Scape shortly hairy. Short pedicels. Scale bar = 1 cm.

FIGURE 2. *Primula vulgaris*. Flowers larger than those of *P. elatior*, with more rounded petals and usually sharper notches. Very pale, almost greenish, yellow flowers with distinct orange star shape at centre, formed by diamond-shaped mark on each petal. Leaves cuneate, with no distinct petiole, often reddish at base. Flowers in a stalk-less umbel. Very rarely on a scape, which is covered in shaggy hairs. Flowers on long pedicels. Pedicel and calyx covered in long shaggy hairs. Scale bar = 1 cm.

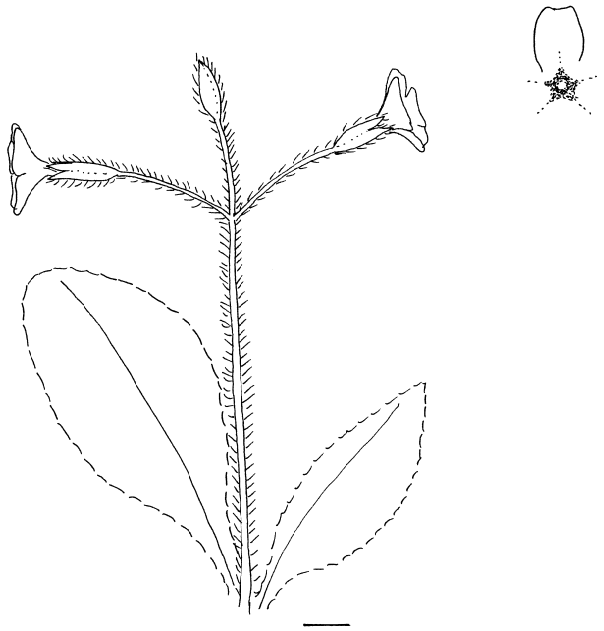

FIGURE 3. *Primula* ×*digenea* (intermediate). Flowers on longer pedicels than in *P. elatior*, creating more open inflorescence, and not all facing same way. Flowers variable, but usually paler than in *P. elatior*, and with pentagon or weakly-formed star at centre. Scape, pedicels, and calyx with long shaggy hairs. Leaves broader than in *P. vulgaris*, but with less distinct petiole than in *P. elatior*. Scale bar = 1 cm.

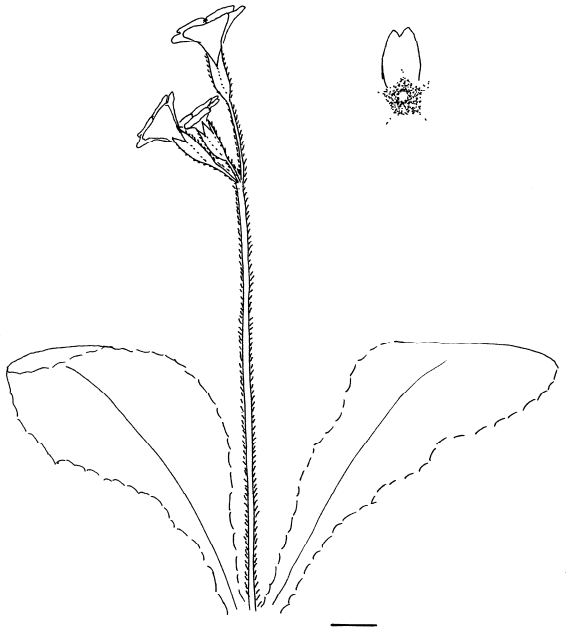

FIGURE 4. *Primula* ×*digenea* (Oxlip-like). Flowers on short pedicels, all facing same way. Flowers pale yellow with clear pentagon mark at centre. Leaves not truncate and not with obvious petiole, but still within range of variation found in *P. elatior*. Shortly hairy scape. Scale bar = 1 cm.

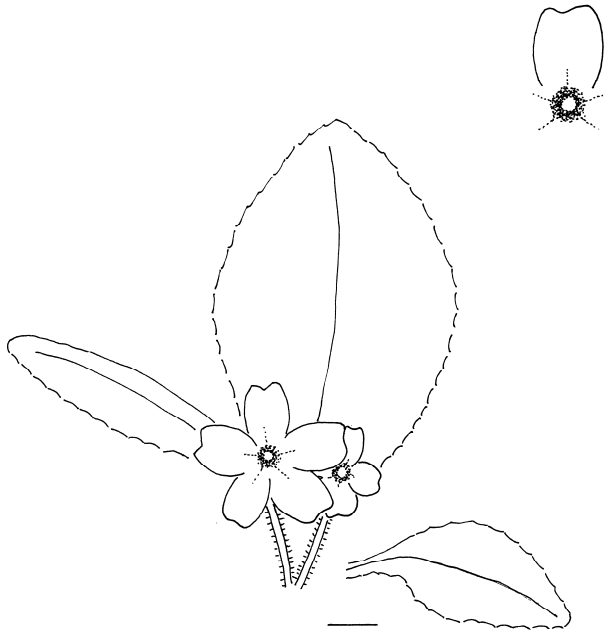

FIGURE 5. *Primula* ×*digenea* (Primrose-like). Flowers close to *P. vulgaris* in colour, in stalkess umbel, but with broad diffuse ring at centre. Flowers like *P. vulgaris* in size and shape. Pedicels with short hairs. Leaves broader than in *P. vulgaris.* Scale bar = 1 cm

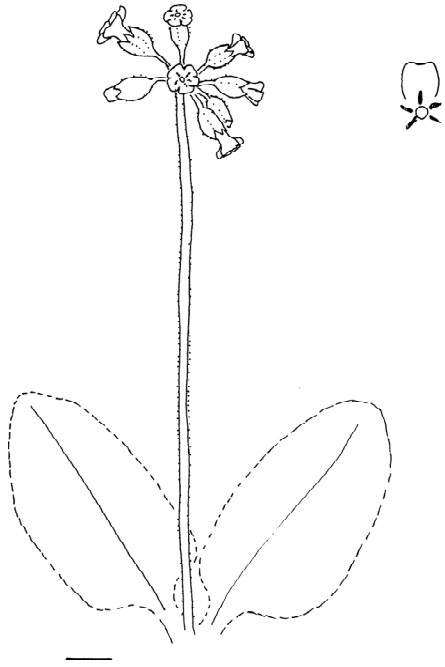

FIGURE 6. *Primula veris*. Broad, inflated calyx with blunt teeth. Flowers with short, round petals. Deep yellow, with sharp dark orange streak at the base of petals. Short pedicels. Leaves glabrous above, very shortly hairy beneath. Leaves sharply truncate. Scape, pedicels, and calyx with very short crisped hairs. Flowers not often facing all same way. Scale bar = 1 cm.

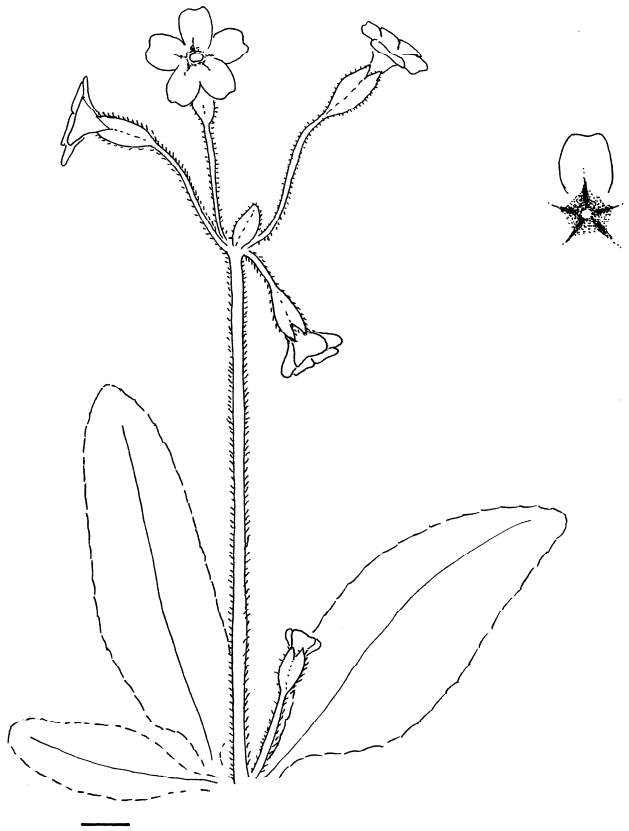

FIGURE 7. *Primula* ×*polyantha*. Long pedicels, flowers not all facing same way. Flowers larger than in *P. veris*, more like *P. vulgaris* in shape. Pale yellow, with orange pentagon at centre, and dark streak on each petal. May rarely have *P. veris*-like flowers at base. Leaves rounded to truncate, shortly hairy. Scale bar = 1 cm.

intermediate between the two species or looked exactly like pure *P. vulgaris*. An example of a plant that looks superficially like *P. vulgaris* is shown in Fig. 5, but even this is easily distinguished from Primrose by its shortly hairy pedicels and very broad leaves. Therefore, the only possible confusion arises with plants that seem to be close to *P. elatior*, but could be first or later generation hybrids or backcrosses.

POLLEN STAINABILITY

The results of the pollen staining are presented in Table 2. The *P. elatior* samples from the mixed population at Buff Wood and the pure population at Hayley Wood both have very high levels of stainability. This seems to be slightly reduced in the hybrids at Buff Wood, but the *P. vulgaris* from Buff Wood and from the two pure populations also have lower levels of stainability. Pollen stainability can therefore not be used to differentiate between hybrids and *P. vulgaris*, but there is rarely any difficulty in distinguishing between them using morphological characters anyway. Pollen stainability may be more useful in distinguishing between *P. elatior* and hybrids and backcrosses, but the sample from the pure population at Hayley Wood includes *P. elatior* plants that have relatively low pollen stainability, so this measure is not conclusive. Unfortunately the leaves sampled from these plants degraded before allozymes could be extracted, so we could not combine pollen staining results with those from allozyme electrophoresis.

Our values for stainability are noticeably lower than those of Woodell (1969), and they have higher standard errors. This seems to be

TABLE 1. MAIN CHARACTERS FOR SEPARATING COWSLIP *PRIMULA VERIS*, PRIMROSE *P. VULGARIS*, OXLIP *P. ELATIOR* AND THEIR HYBRIDS

| | Cowslip<br>*P. veris* | Cowslip × Primrose<br>*P. ×polyantha* | Primrose<br>*P. vulgaris* | Primrose × Oxlip<br>*P. ×digenea* | Oxlip<br>*P. elatior* |
|---|---|---|---|---|---|
| Flower colour | Deep yellow. | Very variable, from deep to pale yellow, but most typically pale pure yellow. | Pale to very pale cold yellow. | Very variable, but usually paler than in Oxlip. Pure to pale yellow. | Pure yellow. |
| Markings on flowers | A narrow dark orange streak at the base of the petals. | Usually with an orange streak at the base of the petals, though this may be much more diffuse than in Cowslip. | An orange star or pentagon in the centre formed by diamonds at the base of the petals. | Often with an orange pentagon or diffuse star at the centre, but may have a broad ring. | A narrow to broad dark yellow to orange ring at centre. Ring may be angled and almost pentagonal. |
| Scent | | | Almost soapy. | Often soapy, but not as strongly as in Primrose. | Rather peachy. |
| Hairs on pedicels, calyx, and scape. | Short and crisp. | Short, but not so crisp as in Cowslip. | Shaggy and long. | Medium to long, may appear shaggy. | Medium to long, but never shaggy as in Primrose. |
| Calyx | Inflated, with blunt teeth. | Usually slightly inflated, and with blunter teeth than in Primrose. | Narrow, with long teeth. | Narrow, with medium to long teeth. | Narrow with medium teeth. |
| Inflorescence | Flowers on short pedicels at top of a scape. Flowers usually, but not always, spreading and facing in different directions. | Flowers at the top of a scape or in an umbel. Pedicels usually longer than in Cowslip. | Very rarely with a scape. Pedicel usually longer than the calyx. | Usually with a scape. Flowers often on long pedicels and not so numerous as in Oxlip. | Flowers on short pedicels at top of a scape. Often, but not always, facing the same direction. |

Plate 1. The petals of this individual are rather narrow and the flowers are rather large. Otherwise this plant is very similar to *P. elatior.*

Plate 2. This plant is almost indistinguishable from *P. elatior*. Note, however, the pentagonal ring.

Plate 3. Another plant that is very close to *P. elatior*, but the pedicels are perhaps too shaggily hairy for that species.

Plate 4. An obvious hybrid, with large flowers, long pedicels, a pentagon at the base of the petals, and slightly shaggy hairs on the pedicels. Perhaps superficially similar to *P.* ×*polyantha*, but that hybrid has a distinct streak at the base of each petal and much shorter hairs.

Plates 1–4. *Primula elatior* × *P. vulgaris* at Buff Wood. The allozyme patterns of these plants is incompatible with that of an $F_1$, and they are either backcrosses or later generation hybrids.

Plate 5. Note large flowers with narrow petals and star shape at base of petals, rather shaggy hairs on scape, and red base to leaves.

Plate 6. An obvious hybrid. The flowers are large and pale with a star-pentagon at the base, all facing in different directions, and with narrow petals. The scapes are shaggily hairy and the leaves are narrowed into a petiole.

Plates 5–6. *P.* ×*digenea* from Buff Wood. These plants have allozyme patterns consistent with them being $F_1$ hybrids.

Plate 7. *Primula elatior*. Note the compact flowers and secund inflorescence.

Plate 8. *Primula vulgaris*. Large, cold-toned flowers with a star at the centre.

Plates 7–8. Oxlip *Primula elatior* and Primrose *Primula vulgaris* from pure populations.

TABLE 2. POLLEN STAINABILITY IN OXLIPS *P. ELATIOR* (O), PRIMROSES *P. VULGARIS* (P), AND HYBRIDS (H)

| Site | Pollen stainability (%) | | | | | | n | Mean | S.E.M |
|---|---|---|---|---|---|---|---|---|---|
| | 20–60 | 61–70 | 71–80 | 81–90 | 91–95 | 96–100 | | | |
| Hayley (O) | | | 1 | 1 | 1 | 8 | 11 | 96·1 | 1·89 |
| Buff (O) | | | | 1 | 1 | 8 | 10 | 96·8 | 1·16 |
| Buff (H) | | | 1 | 2 | 2 | 1 | 6 | 88·8 | 3·49 |
| Buff (P) | | | 1 | 4 | 2 | 2 | 9 | 89·7 | 2·36 |
| Foxley (P) | 1 | 1 | 2 | 1 | 1 | 6 | 12 | 86·3 | 4·74 |
| Wayland (P) | 1 | 1 | 2 | 2 | 4 | 2 | 12 | 80·5 | 6·26 |
| Marley (P) | | | | | | 60 | 60 | 99·9 | 0·01 |
| Lawn (O) | | 1 | 1 | | 1 | 57 | 60 | 98·9 | 0·66 |

Hayley Wood, Foxley Wood, and Wayland Wood contain only one of the species, Buff Wood has both. Woodell's (1969) data for 'characteristic' (i.e. single-species) populations at Marley and Lawn Woods are also included for comparison. n = number of plants in sample, S.E.M. = standard error of the mean. The ranges are inclusive (i.e. 20–60 = 20·00…–60·99…).

due to a lower number of plants with very high (96–100%) stainability, especially in *P. vulgaris*.

## DISCUSSION

### MORPHOLOGICAL CHARACTERS AND INTROGRESSION

*P. elatior*, *P.* ×*polyantha*, and *P.* ×*digenea* all have constant characters that allow them to be separated with certainty. Confusion between *P. elatior* and *P.* ×*polyantha* probably arose amongst botanists of the 18th and 19th Century because few of them had ever seen *P. elatior* in the field, and they based their opinions upon dried specimens or written descriptions. Many of the useful characters (flower colour and markings, shape of the inflorescence, scent) are not preserved in herbarium specimens, and may not have been emphasised in the written descriptions.

The main identification problem occurs in mixed populations of *P. elatior*, *P.* ×*digenea*, and *P. vulgaris*. Whilst there is no problem in identifying some hybrids (the classic "intermediate" types), or *P. vulgaris*, separating *P. elatior* from other hybrids becomes difficult for two reasons. First, *P. elatior* is rather variable in its hairiness, flower size and markings, and leaf shape and colour, more so it seems than native British *P. vulgaris* and *P. veris*, and some of the characters that are useful in distinguishing backcrossed or later generation hybrids from most Oxlips can be found in pure populations of *P. elatior* (e.g. cuneate leaves). Whether or not this variation, even in "pure" Oxlip populations, reflects historic introgression with *P. vulgaris* must remain an open question. However, it is of note that we did not find any populations where hybrids were detectable only through molecular methods: the hybrids were all in woods with populations of Oxlips, Primroses, and obviously intermediate plants. Second, the amount of backcrossing and introgression means that some hybrids can be very close genetically and morphologically to *P. elatior*, and the boundaries of "Oxlip", and "hybrid" become rather arbitrary and meaningless in hybrid swarms. Pollen fertility cannot be used to clarify the situation as it can in many other hybrid complexes, such as that involving Creeping Cinquefoil *Potentilla reptans*, Trailing Tormentil *Potentilla anglica*, and Tormentil *Potentilla erecta* (Harold 2006).

The other potential pitfall is the rare Cowslip × Oxlip hybrid, *P.* ×*media*. We have not been able to confirm this hybrid using molecular methods, and this would be a useful area of future work if plants could be found for analysis. We have found plants in mixed populations of *P. veris* and *P. vulgaris* that had obvious Cowslip characters, such as dark streaks on the petals, rather short hairs, and slightly inflated calyces, but these were tempered by longer hairs and larger and paler flowers than in *P. veris*. As either Oxlip or Primrose could have provided these features, determining which species is the other parent is more a matter of proximity than of morphology.

The presence of small flowers in a stalkless umbel in *P. elatior* is not associated with any sign of hybridisation (it is found in "pure" populations), and is part of the normal range of variation of the plant. It was noted by Miller Christy (1897), although he does not mention that the flowers were smaller than those on scapes. Miller Christy's flowers were produced only early in the season, and we have seen them on plants before the normal inflorescences are produced. However, they are still in evidence later in the season, although they are much less obvious following the growth of the leaves and other vegetation, and it is possible that Miller Christy overlooked them. Tabor (1998) mentions a second flowering in some plants in June and July, in which the scape is very short. This differs from the sessile umbels that we have described in that the flowers are not carried on long pedicels (see photograph on page 97 of Tabor's article), and we have not seen this ourselves, although similar looking inflorescences can rarely be found on plants during the normal flowering time. Other rare abnormalities we have found in *P. elatior* include the bracts being replaced by small leaves, the development of a second inflorescence lower down the scape, six-petalled flowers, flowers with two ovaries, and flowers with bright red stigmas (the last being a reasonably frequent phenomenon).

### EXTINCTION THROUGH HYBRIDISATION: MILLER CHRISTY'S HYPOTHESIS

The view that in Buff Wood *P. elatior* seems to grade into *P.* ×*digenea*, whilst *P. vulgaris* remains a discreet entity could be seen as supporting Miller Christy's (1897) suggestion that the "modest and retiring Oxlip is, in this country at least, being gradually hybridized out of existence by the more aggressive Primrose". However, this hypothesis has been rejected by Woodell (1969) and Rackham (1999). Our own investigations (Gurney 2000) found no reduction in fertility or seed production in Oxlips in Buff Wood when compared to those in "pure" populations, and we agree with Rackham that climate, woodland management, and herbivory are likely to be much more important in determining the species' fate.

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