On the Origins of Observations of Heterostyly in *Primula*

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Summary

In 1862, Charles Darwin published his landmark study on the different forms of flower in *Primula*; he coined the term distyly and subsequently expanded his studies to other species including those with tristyly. Darwin is widely recognised as the first to study pin and thrum flowers in *Primula*, and to provide an explanation for the functional significance of the two floral morphs. Our laboratory is pursuing the genes that underpin floral heteromorphy in *Primula*, a study influenced Darwin's observations. One day, while appreciating a print of *Primula vulgaris* from William Curtis' *Flora Londinensis*, I was struck by the fact that I was looking at images of dimorphic *Primula* flowers captured in a late-1700's copper-plate engraving that predated Darwin's observations by over 70 years. This realisation triggered a journey into archives of botanical texts, herbals and florilegea from the 16th to 19th Centuries, and correspondence archives, in search of earlier documents that could have influenced Darwin and the origins of an idea. Darwin was not the first to observe floral heteromorphy in *Primula*, but he was the first to realise the significance of the two floral morphs. Darwin's insight and exposition of purpose has underpinned all consequent work on the subject.

I) Introduction – the germination of an idea

On Monday 7th May 1860, Darwin wrote to his friend and intellectual confidant J.D. Hooker with some thoughts on pollination, and a description of observations he had made that morning on two forms of flower in Cowslips and Primroses which showed '*balancement of long and short pistils and stamens*' (Darwin, 1860a). This is perhaps the first written reference to Darwin's work on heterostyly in *Primula*. In this letter, Darwin describes both forms of flower and says '*this I have somewhere seen noticed, I think by Henslow*'' (Darwin, 1860a), referring to John Stevens Henslow, his former Cambridge tutor and mentor. Later that week, on Friday 11th May, Darwin wrote to Hooker again on a different matter with a footnote stating that he had examined more Cowslips and Primroses and that these consistently produced two forms of flower (Darwin, 1860b). The following Monday, 14th May, Darwin wrote to Henslow (Darwin, 1860d) to thank him for his support against attacks and criticisms elicited by publication of *On the Origin of Species* (Darwin, 1859) the previous year. As a post script he recalls Henslow's observations on the different pistil lengths in cowslips and primroses and speculates from his own observations that they, and Auriculas, are perhaps dioecious; there is no documented reply. That same day he wrote again to Hooker stating that the evidence on cowslips was becoming '*clearer and clearer*' (Darwin, 1860c). The following Wednesday, 17th May, he wrote again to Henslow (Darwin, 1860e) recounting various detailed points made in his earlier letter to Hooker and asserted that *all* Primroses and Cowslips '*exist in two forms of about equal numbers*', which appeared to be male or female. For one form, the presumed female, he describes low stamens, small oblong pollen, and a long style with rough stigmatic surface above the anthers. In the second form, the presumed male, he describes high anthers, large rounded pollen, a short style and a smoother stigma beneath the anthers.

These five letters, spanning ten days in May 1860, reveal Darwin's key observations, and the germination of an idea that underpins his subsequent realisation of the significance of the two forms of flower. On 21st November 1861 Darwin read his paper '*On the Two Forms, or Dimorphic Condition, in Species of* Primula*, and on their remarkable Sexual Relations*' at the Linnaean Society; the article was published in March the following year (Darwin, 1862). Despite his fascination with primroses, Darwin did not restrict his studies to this species and subsequently

published further works on heterostylous *Linum* (Darwin, 1863b) and *Lythrum* (Darwin, 1864) as well as his Different Forms of Flowers book (Darwin, 1877).

II) Developments since Darwin

In the 153 years since Darwin's original paper (Darwin, 1862), there has been important progress towards understanding heterostyly in *Primula* and other species. We know from genetic analysis that heterostyly in *Primula* is controlled by a di-allelic *S* locus (Bateson & Gregory, 1905); plants producing flowers with a long style, low anthers and small pollen are recessive; those with a short style, high anthers and large pollen carry a dominant *S* allele (Bateson & Gregory, 1905; Ernst, 1928; Dowrick, 1956; Lewis & Jones, 1992). We also know from studies of homostyle plants that the *S* locus comprises a co-adapted linkage group of genes (Ernst, 1928; Pellow, 1928; Haldane, 1933; Ernst, 1936c; Dowrick, 1956; Lewis & Jones, 1992; Richards, 1997) and is has been proposed that recombination within the locus results in long or short homostyle flowers (Dowrick, 1956; Lewis & Jones, 1992), although Ernst originally suggested that these forms arise by mutation (Ernst, 1936b). Darwin showed that reciprocal crosses between the two forms were required for abundant seed set and that within-morph, or illegitimate crosses, were not as productive as crosses between morphs (Darwin, 1862). Darwin's observation that pin and thrum plants are found in equal numbers in the progeny of legitimate crosses (Darwin, 1862), and his observations on the numbers of progeny types arising from illegitimate crosses (Darwin, 1877), prior to recognition of the significance of Mendel's work (Mendel, 1866; Bateson, 1902; Moore, 2001), are consistent with the subsequent demonstration that thrums are heterozygous for a dominant *S* allele and pins are homozygous recessive (Bateson & Gregory, 1905).

Darwin, not surprisingly, speculated on the evolutionary origins of heterostyly (Darwin, 1877), and proposed that the selection and establishment of reciprocal herkogamy preceded the evolution of the self-incompatibility system. He regarded floral heteromorphy as a mechanism to enhance the amount and accuracy of pollen transfer from anther to stigma between the two forms of flower. However, he saw no advantage to a system that rendered a plant unreceptive to pollination by half the population, and considered the self-incompatibility (SI) of within-morph crosses as an incidental

consequence of the adaptation of male and female organs for reciprocal interaction. Subsequent studies have further explored the di-allelic sporophytic SI system (Golynskaya *et al.*, 1976; Heslop-Harrison *et al.*, 1981; Shivanna *et al.*, 1981; Shivanna *et al.*, 1983; Wedderburn & Richards, 1990) which functions to minimise the negative effects of self-pollination, but also acts as a barrier to within-morph crosses.

Darwin considered the initial and primary function of heterostyly as an adaptation to promote the insect-mediated reciprocal transfer of pollen between floral morphs, with SI as a secondary adaptation (Darwin, 1877). Subsequent studies have proposed alternatives scenarios for the evolution of the morphological and physiological aspects of heterostyly, either suggesting that SI and heterostyly evolved together (Mather & De Winton, 1941), or that SI preceded the establishment of di-morphic flowers (Charlesworth & Charlesworth, 1979b; Piper & Charlesworth, 1986; Charlesworth, 2006). Others have concurred with aspects of Darwin's interpretation that reciprocal herkogamy was the key initial step and that cross-pollination was the selective force for the evolution of heterostyly (Lloyd & Webb, 1992a; Lloyd & Webb, 1992b). Ornduff directly measured pollen flow by measuring pollen load on stigmas in a population of *P. vulgaris* but found only limited support for Darwin's hypothesis of reciprocal pollen transfer due to high levels of self pollen on pin and thrum stigmas (Ornduff, 1979). A subsequent study using emasculated flowers which removed the opportunity for contamination by self pollen (Piper & Charlesworth, 1986) enabled the demonstration of significantly greater inter-morph than intra-morph pollen transfer to the stigma surface. Such studies, and more recent consideration of them, has been interpreted as providing strong support for Darwin's proposal that the evolution of heterostyly has been driven by the promotion of out-crossing rather than avoidance of selfing (Lloyd & Webb, 1992b). Further insight into earlier and contemporary thinking on the evolution and function of heterostyly can be found in a number of reviews (Charlesworth & Charlesworth, 1979b; Charlesworth & Charlesworth, 1979a; Ganders, 1979; Barrett, S. C. H., 1992; Lloyd & Webb, 1992a; Lloyd & Webb, 1992b; Barrett & Shore, 2008).

Others have considered the evolutionary relationships of members of the *Primulaceae* (Conti *et al.*, 2000; Mast *et al.*, 2001; Mast & Conti, 2006; Schmidt-Lebuhn *et al.*, 2012) and recent advances

using classical and molecular genetics approaches in *Primula* (Manfield *et al.*, 2005; McCubbin *et al.*, 2006; Li *et al.*, 2007; Li *et al.*, 2008; Li *et al.*, 2010; Cocker *et al.*, In press; Li *et al.*, In press), and other heterostylous species (Matsui *et al.*, 2004; Yasui *et al.*, 2004; Labonne *et al.*, 2008; Labonne *et al.*, 2009; Labonne *et al.*, 2010; Labonne & Shore, 2011; Ushijima *et al.*, 2012), have made progress towards identifying genes involved in floral heteromorphy. The recent publication of a partial assembly covering 63% of the *P. veris* genome (Nowak *et al.*, 2015) has confirmed the linkage of previously characterised *S*-linked genes (Li *et al.*, 2007; Li *et al.*, 2008; Li *et al.*, 2010) and identified other *S*-linked contigs. This information, together with an integrated genetic and physical map of the *P. vulgaris S* locus (Li *et al.*, In press) and the completion of a genome sequence for *P. vulgaris* (P.M. Gilmartin and co-workers, unpublished) should facilitate identification of the key genes underpinning floral heteromorphy in *Primula*.

The various studies on floral heteromorphy in *Primula* spanning a century and a half have been summarised in numerous papers and reviews on heterostyly (Charlesworth & Charlesworth, 1979a; Ganders, 1979; Barrett, S.C.H., 1992; Lewis & Jones, 1992; Richards & Barrett, 1992; Charlesworth, 2006; Barrett & Shore, 2008; McCubbin, 2008; Owens & Miller, 2009; Weller, 2009; Barrett, 2010), including the Evolution and Function of Heterostyly (Barrett, S. C. H., 1992), the only monograph published since Darwin on heterostyly. Some publications have recognised the historical context of Darwin's findings and one study revealed the significance of Henslow's influence on Darwin's thinking (Kohn *et al.*, 2005), but the majority have focused on work that has been published by and after Darwin although some reference van Dijk's scholarly contribution (van Dijk, 1943). In his *Historical Perspective on Heterostyly* Ornduff (Ornduff, 1992), focused on Darwin' contributions and the influence of his contemporaries, he highlights van Dijk's reference to observations by Clusius in the 16th Century, but does not directly explore published accounts of heterostyly in the intervening 280 years prior to Darwin's 1862 publication (Darwin, 1862).

In this review I explore the origins of observations of floral heteromorphy by reviewing work cited by Darwin (Darwin, 1877), the original texts discovered by van Dijk (van Dijk, 1943), and various early herbals and florilegea dating back to the 16th century in an attempt to document the transition from botanical observation of flower form, to Darwin's insight into the significance of heterostyly in

158 *Primula* (Darwin, 1862). This review is not intended to address the evolution or functional
159 significance of heterostyly, which have been extensively reviews by others to provide
160 contemporary updates on Darwin's observations and interpretations. Table 1 presents a
161 comparison of species names and relevant authorities used in this review, in some cases these
162 predate the Linnaean binomial system (Linneaus, 1735; Linnaeus, 1753), and in other cases reflect
163 name changes as the Linnaean system became adopted; a definitive resolution to this historical
164 complexity was been provided (Brummitt & Meikle, 1993).

165 **The Evolution of Darwin's thinking on heterostyly**

166 Although Darwin observed that the two forms of *Primula* flower contained both pistils and stamens,
167 he initially interpreted the differences as transitions towards dioecy through reduction in size and
168 significance of the male structures in one form, and female structures in the other. In his
169 correspondence with Henslow (Darwin, 1860e) he made the comparison to dioecious Holly, in
170 which '*the Male plant has anthers but no pollen*', in an attempt to explain the differences between
171 the two forms of *Primula* flower. By the following year Darwin had resolved the conundrum and
172 recognised that these forms were not transitions to dioecism, but represented a different breeding
173 system which he called distyly. In a letter to Asa Gray at Harvard in 1861 (Darwin, 1861), Darwin
174 states that both forms of flower are hermaphrodite, and that '*The pollen of A* i*s fitted for stigma of B*
175 *& conversely*'. His letter includes a diagram of (A) pin and (B) thrum flowers (Fig. 1a). Darwin's
176 subsequent paper at the Linnaean Society (Darwin, 1862), and his landmark book, *The Different*
177 *Forms of Flowers on Plants of the Same Species* (Darwin, 1877), both include a now-familiar
178 image (Fig. 1b) produced by the illustrator W.H Fitch of long- and short-styled flowers. This image
179 was prepared from Darwin's hand-drawn sketch (Fig. 1c). The original sketch was sold at auction
180 by Christies in London on 11th November 1998 (Christies, 1998) for £8625, and again on 15th July
181 2004 at Bonhams, London, this time fetching £7,170 (Bonhams, 2004). Like the sketch he sent to
182 Gray, Darwin's image shows long stamen filaments rather than differentiating between the two
183 forms based on the point of anther attachment (Fig. 1c). Fitch's image in the published work (Fig
184 1b) however depicts the two forms of flower with astounding accuracy.

Following publication of his *Primula* paper (Darwin, 1862), Darwin exchanged notes on heterostyly in *Primula* and *Linum* with Freidrich Hildebrand in Bonn. In a letter dated 10th November 1863 (Hildebrand, 1863a), Hildebrand summarises his observations on *P. sinensis*, but is unable to comment on experiments on *P. officianalis* (*elatior*) and *P. veris* as these were '*destroyed by children in the botanical gardens*' (Hildebrand, 1863a). This event may explain the focus of Hildebrand's subsequent publications on heterostyly in *P. sinensis* (Hildebrand, 1863b; Hildebrand, 1864), and contrasts with Darwin's experience described in a letter to Hooker, that his children had helped gather 522 flower stalks for his studies (Darwin, 1860c). Darwin also corresponded extensively with John Scott, Head Gardener at the Royal Botanic Gardens, Edinburgh and communicated Scott's comprehensive manuscript describing heterostyly in several *Primula* and other species to the Linnaean Society (Scott, 1864). These various correspondences helped Darwin further develop his thoughts on heterostyly which were included, with numerous other studies on floral dimorphism, in his treatise *Different forms of Flowers* (Darwin, 1877). Additional insight into the interactions between Darwin and his contemporaries on heterostyly can be found in Ornduff's earlier review (Ornduff, 1992)

In both his original publication (Darwin, 1862) and subsequent book (Darwin, 1877), Darwin used the terms pin-headed and thrum-eyed to distinguish the floral morphs, although in the original paper (Darwin, 1862) thrum is misspelt as thumb. Pin-headed flowers are so called after the appearance of the long style and globular stigma which resembles the head of a pin inserted into the flower. In his *Different Forms of Flowers* book Darwin defines thrum, according to Johnson's dictionary, as the ends of weaver's threads (Darwin, 1877). The fact that these terms were in use in 1861 when Darwin read his paper at the Linnaean Society (Darwin, 1862) suggests that the two forms of flower were already familiar before Darwin described them.

A potential insight into earlier observations on heteromorphy appears on page 43 of *Different Forms of Flowers* (Darwin, 1877), where Darwin cites observations by Kerner on heteromorphy in *P. auricular* in 1835; 27 years before Darwin's original publication. A search for these references revealed referencing errors; the articles actually appeared in 1875 (Kesner, 1875d; Kesner, 1875a; Kesner, 1875b; Kesner, 1875c) and do not therefore reveal precedence on Darwin's observations.

213 Darwin was also aware of homostyle variants of cultivated *Auricula* (Darwin, 1862) and had
214 observed homostyles in *P. veris* x *P. vulgaris* hybrids, but was surprised to hear (Darwin, 1863a) of
215 a long homostyle native Cowslip described in a letter from John Scott on 21st May 1863 (Scott,
216 1863). It seems Darwin regarded homostyly as a consequence of hybridisation and cultivation; we
217 now recognise that homostyles can occur by mutation or recombination within the *S* locus.
218 *Different Forms of Flowers* (Darwin, 1877) contained detailed observation on various homostyled
219 plants. Perhaps one of the earliest illustrations of a long homostyle, which predates Darwin's and
220 Scott's correspondence, comes from Alcide D'Orbingy's *Dictionnaire Universel d'Histoire Naturelle*
221 (D'Orbingy, 1849) (Fig. 2). Another image published forty eight years later in Edward Step's
222 *Favourite Flowers of Garden and Greenhouse* (Step, 1897) depicts a short homostyle (Fig. 3).

223 In Darwin's paper (Darwin, 1862) he did not refer to earlier studies on distyly in *Primula*, although
224 he did cite Asa Gray's work on different floral morphs in the *Rubiaceae* (Gray, 1856). However, in
225 *Different Forms of Flowers*, Darwin not only credits the contributions of Gray, Hildebrand and Scott,
226 but dedicates the volume to Gray (Darwin, 1877). In this book he also recognises the contributions
227 of John Scott, by referring to his *Primula* observations on several occasions, and acknowledges
228 Hildebrand's use of the term heterostyly as superior to his own term, distyly (Darwin, 1877). At the
229 same time he rejects Gray's proposal for the term heterogonous (Gray, 1877; Ornduff, 1992), as
230 the term heterostyled had '*by this time become accepted in various countries'* (Darwin, 1877). In
231 *Different Forms of Flowers*, Darwin clearly recognises the intellectual contributions of others and
232 also cites earlier observations on heterostyly in *Primula* species, and the water violet *Hottonia*
233 *palustis*, through reference to Sprengel's 1793 description of heterostyly in *Hottonia* (Sprengel,
234 1793), and to Persoon as having first observed heterostyly in *Primula* in 1794, as cited by von Mohl
235 (von Mohl, 1863). As these cases were not cited in the original *Primula* paper (Darwin, 1862), it
236 can be assumed that he only became aware of them in the years between the two publications;
237 these earlier observations cannot therefore have influenced his original thinking.

238 **Influences on Darwin's thinking**

What did perhaps influence Darwin's thinking on *Primula* was the unpublished work of Henslow (Kohn *et al.*, 2005) who had drawn both forms of flowers in 1826 (Fig. 4), 34 years before Darwin's letters of discovery. As revealed by his 1860 correspondence with Henslow (Darwin, 1860c) and Hooker (Darwin, 1860a), Darwin did recall the earlier description, possibly from his Botany studies with Henslow as a student at Cambridge between 1829 and 1831 (Kohn *et al.*, 2005). Henslow was however not the first to document the two forms of flower, three earlier representations exist. The first in Francoise-Pierre Chaumeton's *Flore Medicale,* illustrated by Pierre Jean Francoise Turpin, and published in 8 volumes between 1814 and 1820. In volume 5, published in 1818 (Chaumeton & Turpin, 1818), Turpin presents images of pin and thrum flowers of *P. veris*. However, the text only describes the pin form and the figure legend refers only to the thrum as '*provenant d'un autre individu'* (from another individual). The different forms of flower were clearly recognised and documented (Chaumeton & Turpin, 1818) but the significance and relevance were not. Henslow's 1826 drawings are therefore predated by Turpin's in 1818. A second example appears in Wilibald Artus' *Hand-Atlas sammtlicher medicinisch-pharmaceutischer Gewachse* illustrated by Kirchner (Artus & Kircher, 1848) which shows a dissected *P. veris* pin flower and a second corolla without style but anthers in the thrum position (Fig. 6). The text refers to flowers having either high or low anthers, but only refers to the long style. An even earlier representation of pin and thrum flowers can be found in William Curtis' *Flora Londinensis* (Curtis, 1777-1798a); it is this image that triggered this review. It is perhaps surprising that Darwin was not familiar with Curtis' publication.

Curtis uses the Linnaean binomial system and follows his *Systema Sexuale* classification system (Linneaus, 1735) based on reproductive organ number; this focus on reproductive structures perhaps explains the depiction of dissected flowers alongside the whole plants in *Flora Londinensis*. Curtis' copper-plate image of *P. vulgaris* (Fig. 7) shows the whole plant and dissected flowers that show both forms of flower. The accompanying text describes the two forms and names them as pin-eyed and thrum-eyed. This is perhaps the earliest record of these terms, nearly 100 years before Darwin used them.

Flora Londinensis is considered one of the foremost 18th century illustrated Floras (Walpole, 1976) and was published in 72 parts each comprising 6 plates, and is typically dated between 1777-1798 (Walpole, 1976), although the first parts were released in 1775 (Stevenson *et al.*, 1961; Nelson, 1980). The complete work comprises 432 plates depicting 435 species in six *fasciculi* grouped into two volumes; each *fasciculus* contains 12 parts with 72 plates, each volume comprises 3 *fasciculi*. The serial publication over 23 years, the limited number of intact copies, and the order of plates in the different bound copies, obscures dates for individual plates. However, an 18th Century review (Schrank, 1793) published contemporaneously with Curtis' work, includes an ordered list of plates for *Flora Londinensis*. Without Schrank's list it would not be possible to date individual plates.

In Flora Londinensis, *P. farinosa*, *P. officianalis* (*veris*) and *P. acaulis* (*vulgaris*) are included in volume 2 of the 1st edition and indexed and bound as Plates 14, 15 and 16 respectively in the final 6th *fasciculus* (Curtis, 1777-1798c; Stevenson *et al.*, 1961). Plate 16, *P. acaulis* (*vulgaris*) was published 1st March 1791; Plate 15, *P. officianalis* (*P. veris*) was published by 10th April 1793, and *P. farinosa* was published sometime during 1795. Plates depicting *P. elatior* and *P. scotica* were not included in the 1st edition (Stevenson *et al.*, 1961) but were included in the later Hooker edition (Curtis *et al.*, 1815-1828). Despite clear descriptions and images of pin and thrum flowers of the primrose (Curtis, 1777-1798a), other *Primula* species are not depicted with both forms of flower and the text does not refer to them. Images show *P. veris* and *P. farinosa* as thrums (Curtis, 1777-1798a), the second edition shows *P. elatior* as a pin and *P. scotica* as a homostyle with dissected flowers showing high anthers and a long style (Curtis *et al.*, 1815-1828).

Flora Londinensis was edited and republished as an expanded 'Hooker Edition' in 1815 by George Graves and William J. Hooker (Curtis *et al.*, 1815-1828; Walpole, 1976); W.J. Hooker was J.D. Hooker's father; at the time of his correspondence with Darwin, J.D. Hooker was Assistant Director at Kew (Desmond, 2007). The lack of reference to *Flora Londinensis* in their correspondence suggests neither Hooker (J.D.) nor Darwin were aware of Curtis' description and images of pin and thrum *Primula* flowers. Although J.D. Hooker may not have been aware, his father certainly was; in the later edition, Hooker edited Curtis' original *P. acaulis* (*vulgaris*) text with a footnote discussing flower stalk length in comparisons to *P. elatior* (Curtis *et al.*, 1815-1828).

There is a similar familial record of Curtis' *Flora Londinensis* in Darwin's family. His Grandfather, Erasmus Darwin corresponded directly with William Curtis in November 1781 expressing his delight with the *Flora Londinensis* '*which he had taken ever since it was published*'(Darwin, 1781); although Erasmus is curiously not listed as one of the founding subscribers (Curtis, 1777-1798b). Although Erasmus would no doubt have seen Curtis' depiction of the two forms of *Primula* flower, these did not influence his various writings. Primroses and cowslips are poetically introduced without description in his *Botanic Garden* (Darwin, 1791a; Darwin, 1791b), although he does describe the adhesions of stamen filaments to the inner corolla in what was most likely a pin flower in his *Phytologia* (Darwin, 1800), On page 106 of his 1787 translation of Linneaus' *Families of Plants*, the *Primula* entry describes a pin flower (Linneaus, 1787). Erasmus' failure to highlight the two forms of flower is perhaps surprising given his interest in '*the loves of the plants*' (Darwin, 1791b). Erasmus died seven years before his grandson Charles was born so perhaps Darwin was unaware of his Grandfathers enthusiasm for Curtis' Floral Londinensis. In those elements of Darwin's library donated to the Botany Department in Cambridge by his son Francis, there is no record for *Flora Londinensis,* there is however a record of Volumes 1 and 2 of another of William Curtis' publications, the Botanical Magazine (Rutherford, 1908). In these two volumes, the only *Primula* species illustrated is *P. villosa* (Vol. 1, Plate14) (Curtis, 1790) but the image does not show any flower detail that could have influenced Darwin.

III) Darwin and the historical landscape of botanical illustration

It is surprising that neither Darwin nor Hooker were aware of *Flora Londinensis* and the engravings and descriptions of pin and thrum flowers that it contains. Henslow was however aware of the images therein, as revealed in his article '*On the Specific Identity of the Primrose, Oxlip and Cowslip and Polyanthus*' (Henslow, 1830). In this article he concludes, based on his own observations, and those of Reverend William Herbert, of the mixture of Primrose, Cowslip and Oxlip progeny obtained from a single flowering umbel of ''*an highly manured Red Cowslip*' (Herbert, 1822) that the plants are merely varieties of the same, rather than distinct species (Henslow, 1830). It is perhaps surprising, given his experimental approach to hybrid crosses, that Herbert did not recognise the two forms of flower. Henslow cites Hooker's edition of Curtis' *Flora*

Londinensis as providing an example of *Primula* plants with single and compound scapes, possibly influenced by Hooker's footnote, but he does not refer to the pin and thrum flowers illustrated there. The clear intellectual focus at the time on whether primroses, cowslips and oxlips represented a single, or multiple species, may perhaps explain why the details of heterostyly were overlooked. Henslow had however by this date illustrated the two forms of flower, but had not published them (Kohn *et al.*, 2005); had he done so he may well have cited Curtis' prior observations of pin and thrum *P. vulgaris* flowers in *Floral Londinensis*.

The contemporaneous *English Botany* with copper plate engravings by James Sowerby and text by James Edward Smith was published between 1790 and 1813 (Sowerby & Smith, 1790-1813). It is curious that *Primula* species illustrated in *English Botany* are not shown with both forms of flower; perhaps more surprising given the fact that Sowerby contributed engravings to both publications (Stevenson *et al.*, 1961), although the *Primula* engravings in the *Flora Londinensis* are attributed to Sydenham Edwards not James Sowerby (Curtis, 1777-1798a; Stevenson *et al.*, 1961). Of the five species described in *English Botany*, *P. vulgaris* and *P. veris* show only whole flowers illustrated as thrums. The dissected flower images for *P. elatior* and *P. farinosa* show pin and thrum flowers respectively. For *P. scotica*, the intact flower shows both anthers and sigma, suggesting a long homostyle (Sowerby & Smith, 1790-1813).

The majority of 18th and 19th century botanical illustrations depict intact, not dissected, flowers. Such images do not typically permit distinction between pin and thrum flowers, unless the mouth of the flower is clearly visible. In pre-Darwinian texts this may reveal a lack of appreciation of the two floral forms, but in some later Victorian flower books it may reflect a more aesthetic, artistic or poetic view of the importance of flowers (Seaton, 1985), as opposed to seeing them as botanical specimens of reproductive importance. An example is John Ruskin's *Proserpina* (Ruskin, 1888) in which he illustrates the '*Four stages in the Young Life or a Primrose*' showing four stages of flower bud development (Fig. 8). Ruskin uses intact flowers which obscure any reproductive detail, perhaps reflecting attitudes of the era or, as proposed by Smith (Smith, 2006), as a statement of rejection to Darwin's view on the significance and importance of reproductive structures. The

primrose images in Ruskin's *Proserpina* (Ruskin, 1888) probably provide the earliest representation of *Primula* flower bud development.

In Frederick Edward Hulme's *Familiar Wild Flowers* (Hulme, 1878), *Primula* images show only pin *P. vulgaris*, *P. veris* and *P. elatior*. Similarly Anne Pratt's earlier books '*Wild Flowers*' (Pratt, 1852) and '*The Flowering Plants of Britain*' (Pratt, 1855-1866) do not distinguish between the two forms, although the former does include a detailed description of stamen and pistil position, with an illustration of a dissected pin Primrose flower; text in the latter book describes the location of stamens in *Primula* as within the tube of the corolla. The illustration from '*The Flowering Plants of Britain*', Fig. S1 shows flowers of the five British *Primula* species, depicting Cowslip as thrum, Oxlip as pin, *P. farinosa* and *P. scotica* with high anthers, and curiously, primrose as a long homostyle; a thrum *H. palustris* is also included (Pratt, 1905).

Notable exceptions to the depiction of intact flowers in 18th Century texts comes from three works with high quality images of dissected *Primula* flowers which clearly display pin or thrum forms without reference to their significance. These are Elizabeth Blackwell's *Curious Herbal* (Blackwell, 1737-1739), The *Flora Danica* (Oeder, 1761-1883) and Johannes Zorn's *Icones Plantarum Medicinalium* (Zorn, 1780). The *Curious Herbal* was originally published weekly as four images and a text page, and subsequently republished in 1750 and 1757 (Blackwell, 1757). The first edition shows intact *P. vulgaris* and *P. veris* flowers (Blackwell, 1737-1739); the 1757 edition however provides much greater anatomical detail for *P. veris* (Fig. S2) with dissected thrum flowers (Blackwell, 1757). Zorn's 1780 image of a dissected *P. veris* flower reveals details of a pin flower (Fig. S3). In the *Flora Danica*, *P. vulgaris* and *P. elatior* are depicted as pins, and *P. veris* as a thrum (Oeder, 1761-1883). The *P. vulgaris* image (Fig. S4) was published around 1765, the *P. veris* and *P. elatior* images date from around 1767 (Oeder, 1761-1883). The lack of consistency between illustrators in presenting images of whole flowers or dissected flowers in 18th and 19th Century herbals and florilegia suggests that the differences in floral organ arrangements were not recognised as important, although the botanical accuracy captured by Blackwell (Blackwell, 1737-1739), Zorn (Zorn, 1780) and in *Floral Danica* (Oeder, 1761-1883) show significant attention to this detail.

Looking back to even earlier representations of *Primula* flowers, 17th Century herbals and florilegia typically used wood block prints which lacked the quality of resolution required to capture detail of floral architecture (Gerard, 1597; Besler, 1613; Parkinson, 1629). However, at the end of the 17th Century, copper plate printing was replacing wood block printing (Arber, 1912) and this new technology enabled fine details of floral form to be captured. One such example is *Hortus Floridus* by Crispin van de Pass the Younger, which contains copper-plate images of plants drawn '*true to life*' (van de Passe, 1614) and arranged by the four seasons. Plate 7 of the 'Spring' section of *Hortus Floridus* depicts two mutant forms of *P. veris*, one showing double flowers, the other *Hose in Hose* flowers (van de Passe, 1614). We now know that *Hose in Hose* is linked to the *S* locus (Ernst, 1936a; Webster & Grant, 1990; Li *et al.*, 2010), however there is insufficient detail in the image to determine whether the *Hose in Hose* plant depicted is a pin or a thrum.

In Plate 8 of *Hortus Floridus* van de Pass presents two forms of *Auricula Ursi*; both images show anthers in the mouth of the flower (Fig. S5), these are possibly the earliest illustration of a *Primula* thrum flower (van de Passe, 1614). *Hortus Floridus* was published in two parts, the *Altera Pars* (the other part) (van de Passe, 1603) is arranged not by season as in *Hortus Floridus*, but presents plants in different arrangements as food or medicinal plants. Although *Altera Pars* is sometimes regarded as an appendix to *Hortus Floridus*, it likely predates it; although the exact publication date, around 1605, is not clear (Savage, 1923; Gerard, 1996). Plate 27 of *Altera Pars* depicts a *P. vulgaris* plant with the stigma in the mouth of the flower; this image (Fig. S6), along with the copper-plate images of pin flowers in de Reneaulme's *Historiae Plantarum Plantae* (Fig. S7) (de Reneaulme, 1611), may be the earliest images of *Primula* pin flowers.

IV) The historical work cited in Darwin's 'The Different Forms of Flowers' book.

By 1877, when the *Different Forms of Flowers* was published, Darwin had discovered that heterostyly had been observed and documented previously, both in *Primula* (Persoon, 1794) and *Hottonia* (Sprengel, 1793). Darwin had clearly read Sprengel's work on *Hottonia* which precisely describes some flowers as having '*anthers located within the corolla tube, and the style extended above, and others with stamens longer than the corolla tube and shorter styles'* (Sprengel, 1793).

He even notes Sprengel's sagacity (his term) (Darwin, 1877) in suggesting that this is not just fortuitous but a device of Nature, although unlike Darwin, Sprengel does not speculate on the reason for the differences (Sprengel, 1793). For *Primula*, Darwin cites Persoon's work as '*according to Von Mohl'* in the Botanical Zeitung in 1863 (von Mohl, 1863), the year after his *Primula* paper (Darwin, 1862). Von Mohl is aware of Darwin's preceding paper and cites Darwin's work, he also provides an important link to the earlier work of Persoon (von Mohl, 1863).

Review and translation of Persoon's original description of *Primula* flowers, which appeared in Latin in Pauli Usteri's *Annalen der Botanick* in 1794 (Persoon, 1794) is interesting for two reasons. Firstly, it describes the different forms of flower in three species of Primula. *P. inodora* (*elatior*), *P. odorata* (*veris*) and *P. acaulis* (*vulgaris*). In his description of *P. inodora* Persoon defines two forms of flower: *prominula* (prominent), with an exerted pistil and anthers inserted into the tube, and *latitans* (hiding) with anthers in the throat of the flower and a shorter pistil. His description of the two forms of *P. odorata*, as *exserta* (protruding) and *abscondita* (hidden) also refer to the style length and he describes the '*situs staminium & pistilli diversa longitudo'* – 'different positions of the stamens and pistil lengths'. For the descriptions of *P. acaulis* (*vulgaris*), which he discusses alongside *P. odorata* (*veris*), he uses the anther height rather than the style length to distinguish the two forms, or varieties (Var.) of flower: Var. α *Antheris prominulis* (anthers prominent) and Var. β *Antheris latitantibus* (anthers hiding). The second and most striking element of Persoon's descriptions comes from his reference to Curtis' *Floral Londinensis* in relation to *P. odorata* (*veris*), and after his own full description of the two forms of flower – '*Ex observatione Curtisii'* – 'from the observations of Curtis' (Persoon, 1794).

Given the date of Persoon's article he must have been referring to the 1st edition of *Floral Londinensis* (Curtis, 1777-1798a) in which pin and thrum flowers of *P. acaulis* (*vulgaris*) were described and illustrated. Persoon published his observations in *Annalen der Botanick* in 1794 (Persoon, 1794), three years after the primrose was illustrated by Curtis'; Schrank's review of *Floral Londinensis* also appeared in *Annalen der Botanick* a year before Persoon's (Schrank, 1793). It is therefore likely that Persoon had seen Schrank's earlier article and that this may have

prompted him to explore *Floral Londinensis*, if he was not already aware of it, where he discovered Curtis' precedence for the description of pin and thrum flowers.

The text from Flora Londinensis reads: '*While we are thus describing the varieties to which this plant is subject, it may not be amiss to observe that the stamina also vary greatly in their situation, being sometimes found low down in the tube of the blossom, sometimes at its mouth, in the former instance the pistil which varies also in length shows its round stigma, and with its attendant style looks like a pin stuck in the centre of the flower; such flowers in the Polyanthus are termed pin-eyed, while those in which the anthers close the mouth of the tube, are called thrum-eyed, and this latter appearance in the opinion of the florist is an essential requisite in a good flower'*.

Curtis' point on the '*requisite of a good flower*' is further borne out by an article in the 1st edition of Gardener and Practical Florist (unknown, 1843) on the properties of the Polyanthus, which states: '*The tube should be nearly filled up with the six anthers, which are technically called the thrum, and the flowers should not exhibit the pistil*. A footnote reveals: *Some Polyanthus show the pistil, and are called pin-eyed; these are considered worthless* (unknown, 1843). Clearly early gardeners did not recognise the mutual dependence of both forms and the importance of pins for reproductive success. It is interesting that Darwin uses the exact same terms as Curtis, pin-eyed and thrum-eyed, in his first *Primula* paper (Darwin, 1862). Although Persoon recognised and cited observations by Curtis as his primary source of the descriptions of two forms of flower (Persoon, 1794), he did not use the terms pin and thrum even though these were already in use by 1791 (Curtis, 1777-1798a). Had Darwin pursued von Mohl's reference (von Mohl, 1863) back to Persoon's original article (Persoon, 1794), he would have made the link to Curtis' earlier observations, and been able to provide the reference that is conspicuously absent in *Different Forms of Flowers* (Darwin, 1877). With the discovery of Curtis's *Flora Londinensis* as the source of Persoon's descriptions, and Schrank's review which may have alerted Persoon to *Flora Londinensis*, it might seem that this closes the chapter on the origins of the earliest descriptions of two forms of flower in *Primula*, but this is not the case; the history of floral heteromorphy goes back even further.

V) The insights of Clusius and de Reneaulme and the influence of Linnaean thinking

In 1943, van Dijk (van Dijk, 1943) published a remarkable analysis of the Latin texts of Carolus Clusius (Clusius, 1583; Clusius, 1601) and Latin and Greek descriptions by Pauli de Reneaulme (de Reneaulme, 1611) to provide a historical perspective on the origins of observations on floral heteromorphy, details of which have been overlooked by citation of van Dijk without retrospective analysis or interpretation of the original texts that he uncovered. Perhaps this lack of analysis is due to publication of van Dijk's monumental analysis in French, with no subsequent English version of this or the 16th Century texts that he cites. However, translation of van Dijk's original work (van Dijk, 1943) reveals his outstanding depth of perception into the 16th Century botanical world.

Van Dijk's narrative states says that he was '*by chance'* reading *Rariorum Plantarum Historia* (Clusius, 1601) when the descriptions of differences between long and short style forms of *Primula* caught his attention (van Dijk, 1943). He pursued his research back to 1583 and an earlier publication, *Rariorum Aliquot Stripum, per Pannoniam, Austriam, & vicinas quasdam provincias observatarum Historia* (Clusius, 1583). Within these two volumes, similar Latin text describes the different forms of *Primula* flower (Clusius, 1583; Clusius, 1601). Although Clusius divides his descriptions into *Primula* and *Auricula*, he recognised their relatedness. Linnaeus would similarly classify these plants 170 years later, and link them with *Hottonia palustris* in his *Systema Naturae* (Linneaus, 1735). Molecular studies have since confirmed and advanced the validity of this classification and evolutionary relationships between species (Conti *et al.*, 2000; Mast *et al.*, 2001).

Clusius grouped *P. veris* with *P. farinosa* but differentiated these from *Auricula Ursi* (Bears Ears) which were popular with horticulturalists, then as now. In describing *Auricula Ursi*, he describes one variety as '*stilo inter stamina nonnumquam prominente, interdum autem nullo*' – sometimes a prominent style between the stamens, sometimes not – and refers to a prominent style in another recognised variety, *Auricula Ursi IIII carnie colors flora* (Clusius, 1583). Clusius also recognised another variety, *Auricula Ursi minima V,* with '*nullo prominente stilo*' – without a prominent style (Clusius, 1583). What Clusius was describing in 1583 were different floral morphs, not distinct

485 varieties. It would therefore seem that he noted the different forms of flower in different varieties
486 and species, but did not make the connection between the two forms within one variety or species
487 (van Dijk, 1943). Van Dijk takes this interpretation a stage further and expresses his surprise that
488 Clusius, who was clearly focussed on detailed observation, did not describe the short style within
489 the corolla tube of thrum flowers and concludes that Clusius did not dissect the flowers (van Dijk,
490 1943). Had he done so, he could have provided us with the earliest description of the two forms of
491 flower 279 years before Darwin's paper (Darwin, 1862).

492 In *Historia Plantarum Rariorum* Clusius also noted an association between flower colour and floral
493 morph. *'Illud autem hoc flora in obervavi, ut intensius rubeat, pistillum sive Stilum prominentem*
494 *Habeat, qumedmodum nonnullarum Primularum flores: at dilutior minimal' (Clusius, 1601)*. Which
495 translated from van Dijk's French (van Dijk, 1943), reads '*The darker red flowers possess a*
496 *prominent pistil, as found in flowers of different Primulas, but the paler flowers do not*'. Van Dijk
497 was not aware of colour associated with floral form in contemporary literature (van Dijk, 1943).
498 However, genetic studies in the early 1900's on *P. sinensis* had provided one of the first examples
499 of linkage in plants, namely, linkage between the *S* locus and the *B* locus which controls flower
500 colour (Gregory, 1911; Bridges, 1914; Altenburg, 1916; Gregory *et al.*, 1923; De Winton &
501 Haldane, 1933; De Winton & Haldane, 1935). Kurian and Richards subsequently identified two
502 flower pigment loci in *P. vulgaris* that co-segregate with the *S* locus (Richards, 1997). Although
503 Clusius did not recognise the significance of the two forms of flowers, he did recognise them in
504 different species, and observed linkage of flower colour to floral morph (Clusius, 1601).

505 Perhaps the first recognition of the relevance of different flower forms comes from Pauli de
506 Reneaulme's *Specimen Historiae Plantarum* (de Reneaulme, 1611). Like Clusius (Clusius, 1583),
507 de Reneaulme attempted to classify plants by morphology, in contrast to Besler (Besler, 1613) and
508 van de Passe (van de Passe, 1614) who focused their groupings on seasons and flowering time;
509 prior to Linnaeus (Linneaus, 1735), classification was complex. As noted by van Dijk (van Dijk,
510 1943), de Reneaulme focused on single Greek or Latin words to describe plants, rather than long
511 descriptive names favoured by Besler (Besler, 1613), Clusius (Clusius, 1601) and van de Passe
512 (van de Passe, 1614). De Reneaulme defined *Primula* as Phlosmikos (ΦΛΟΜΙΣΚΟΣ) and

described two forms: a, Makrostylos (ΜΑΚΡΟΣΤΨΛΟΣ) (long style) and b, Anostemon (ΑΝΩΣΤΗΜΩΝ) (short style). He described the short stamens and long style in the Makrostylos form **a**, and the long style and lower stamens of the Anostemon form b (de Reneaulme, 1611), Persoon subsequently used similar terms, variety α and variety β, to distinguish the two forms (Persoon, 1794). Perhaps Persoon was not only familiar with Curtis' work but also recognised de Reneaulme's classification system. Another revelation comes from de Reneaulme's description of the two forms of *Primula*, he states *'Minutas istas persequi differentias non est vanum. Deus siquidem & natura non frustra distinxere'* – 'These minute details are not in vain for God and Nature distinguish these for a reason'. Sprengel voiced a similar view in relation to *Hottonia* (Sprengel, 1793), as did Darwin when he provided an explanation and rationale for the two forms of flower (Darwin, 1877), but in Darwin's case with a focus on the role played by Nature rather than God.

Van Dijk takes his analysis further and contrasts de Reneaulme's conviction that these differences are not without reason, with Linnaeus' view that *'Varietates levissimas non curat botanicus'* – the botanist is not concerned with slight variations (Linneaus, 1792). Intriguingly, Linnaeus uses *Primula* as an example where '*flower enthusiasts focus on small floral details that no sane Botanist would consider important'* (Linneaus, 1792). Van Dijk speculates that it is this difference in attention to detail and the dominance of Linnaean thinking during the 18th and 19th centuries that led to the failure to recognise the significance of such important floral morphologies. It seems remarkable, that a classification system based on the *Systema Sexualis* (Linneaus, 1735) could obscure the relevance of floral heteromorphy by using the number, rather than the defining differences between reproductive structures, as the basis for classification. The recognition of two forms of flower by Clusius, de Reneaulme, Persoon, Sprengel, Curtis, Henslow and then Darwin, demonstrate not only that careful observation can reveal the importance of the *varietates levissimas* or small differences, that Linnaeus rejected, but the need to understand the reason for the difference that is important. This is what Charles Darwin did where other had only observed and not sought to explain. In his autobiography Darwin wrote: *'no little discovery of mine ever gave me so much pleasure as making out the meaning of heterostyled flowers' (Darwin, 1887).* Although Darwin was not able to test his hypothesis on the meaning of heterostyly, subsequent

541 ecological studies have, and the current availability of molecular genetic tools and resources now
542 provide the opportunity to identify the genes underpinning the '*balancement of long and short*
543 *pistils and stamens*' that Darwin first noted in *Primula* in the spring of 1860.

544

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559

Figure Legends

Figure 1 Darwin's *Primula* images (1861)

Figure 8 Darwin's hand drawn sketch of pin (A) and thrum (B) Primula flowers from his letter to Asa Gray on 16th September 1861, anther and stigma are labelled (Darwin, 1861). **B)** Wood block print engraved by W.H. Fitch showing long styled form (pin) and short styled form (thrum) of *Primula veris* flowers that was used to illustrated Darwin's publications (Darwin, 1862; Darwin, 1877). **C)** Darwin's hand drawn sketch of the two forms of *Primula* flower, short stamens or pin-headed (left) and long stamens (right), pistil, calyx stamens and corolla are labelled (Christies, 1998). A) with permission, The Asa Grey Library, Harvard University, b) photograph from the original by the author, c) with permission, Sotheby's London and Bridgman Art Library.

Figure 2 Long homostyle (1849)

Hand coloured copper plate print of polyanthus *Primula*, engraved by Vc. Fournier, from Charles D'Orbigny's *Dictionnaire Universel d'Histoire Naturelle* published in 1849, showing dissected long homostyle flower at left as well as seed capsules and seed. Stigma and anthers are visible in the corolla mouth of the intact flowers (D'Orbingy, 1849).

Figure 3 Short homostyle (1897)

Polyanthus *Primula variabilis* from Edward Step's *Favourite Flowers of Garden and Greenhouse* published in 1897 showing whole plant with thrum flowers and dissected thrum flower at lower left, and dissected short homostyle at lower right (Step, 1897).

Figure 4 Henslow's *Primula* images (1826)

Hand drawn sketch by John Stevens Henslow of var. (varieties) in Cowslip *Prim. Off.* (*P. veris*, formerly (*P. officianalis*) showing dissected and intact flowers of pin (above) and thrum (below). Dated 18th April 1826 and signed J.S.H. (Kohn *et al.*, 2005). With permission, Cambridge University Botanic Gardens.

Figure 5 Turpin's Cowslip (*P. veris*) (1818)

Hand coloured copper plate print, engraved by Pierre Turpin, from volume 5 of Françoise-Pierre Chaumeton's *Flore médicale* published in 1818 of a Cowslip (*P. veris*) plant. Dissected pin (1) and thrum (2) flowers are illustrated. Seed capsules (3, 4, 5) and seed (7) are also shown (Chaumeton & Turpin, 1818).

Figure 6 Kirchner's Cowslip (*P. veris*) (1848)

Hand coloured copper plate print, engraved by F. Kirchner for Wilibald Artus' *Hand-Atlas sammtlicher medicinisch-pharmaceutischer Gewachse* published in 1848 of a Cowslip (*P. veris*) plant (A). A dissected pin flower (B) is illustrated with ovary (a) and anthers (b) labelled. A dissected anther (1) and cross section of the stigma (2) and various stages of seed capsule (3, 4, 5, 6) are shown. The dissected corolla and anthers (C) represent a thrum flower. Intact and dissected seed (7, 8, 9, 10) are also shown (Artus & Kircher, 1848).

Figure 7 *P. vulgaris* from Curtis' *Floral Londinensis* (1777-1798)

Hand coloured copper plate print, engraved by Sydenham Edwards for William Curtis' Flora Londinensis published between 1777 and 1798. This image of *P. acaulis* (*P. vulgaris*) published on 1st March 1791 shows pin stigmas in the mouths of the intact flowers. The images at bottom left show a calyx (1) and a dissected thrum flower showing corolla (2) and high anthers (3). The images at bottom left show a dissected pin flower with corolla (2) and low anthers (4) with enlarged anther (5) and carpel with ovary (6),style (7) and stigma (8) identified (Curtis, 1777-1798a).

Figure 8 Ruskin's developing Primrose (*P. vulgaris*) flowers (1888)

Print from wood engraving by Arthur Burgess of four stages of Primrose flower development drawn by John Ruskin for his *Proserpina* published in 1888 (Ruskin, 1888). With permission from Cambridge University Library.

Figure S1 Anne Pratt's posy of *Primula* species (1855-1856)

Engraving of the five native *Primula* species as labelled and *Hottonia paustris* from Anne Pratts originally published by Anne Pratt's *The Flowering Plants of Great Britain* published in five volumes

between 1855 and 1866. This image, originally in Volume 3 of the first edition, is from a 1905 reprint of the original. The image shows a *P. veris* thrum, *P. elatior* pin, and a *P. vulgaris* long homostyle. Anthers are visible in the mouth of *P. 24arinose* and *P. scotica* flowers. The *H. palustris* flowers thrum (Pratt, 1905).

Figure S2 Elizabeth Blackwell's Cowslip (*P. veris*) (1757)

Cowslip (*P. veris*) engraving from reissued edition of *Elizabeth* Blackwell's *Curious Herbal, Herbarium Selectum Emendatum et Auctum* published in 1757. Two umbels are show but neither reveals the form of flower. A dissected corolla with anthers at top right are from a thrum flower. Various insets depict calyx, carpels, capsule and seed (Blackwell, 1757).

Figure S3 Zorn's Cowslip (*P. veris*) (1780)

Hand coloured copper plate engraving of Cowslip *(P. veris,* formerly *P. officianalis*) (a) from an original by B. Thanner, engraved by Johann Sebastian Leitner (J.S.L.), for Johannes Zorn's *Icones Plantarum Medicinalum.* The intact flowers do not distinguish the plant as pin or thrum. Insets show calyx (b), whole flower (c) anther (c), dissected pin flower (d) and pistil (f); there is no (e).

Figure S4 *Primula vulgaris* from *Flora Danica* (1761-1883)

Hand coloured copper plate engraving of Primrose (*P. vulgaris*) from Georg Christian Oeder's *Floral Danica* published in parts between 1761 and 1863. This image is dated was published around 1765. The pin style is visible in some of the flowers on the plant, and the inset at top left shows a dissected corolla with low anthers (Oeder, 1761-1883).

Figure S5 Crispin van de Passe's Auricula (1615)

Extract of a wood block print of Auricula Ursi (Bears Ears) from Crispin van de Passe's *Hortus Floridus* (1615). Anthers are clearly visible in the mouth of the flowers defining the plant as a thrum (van de Passe, 1614). With permission, The John Innes Centre.

Figure S6 Crispin van de Passe's Primrose (~1605)

Extract of a wood block print from *Hortus Floridus Altera Pars*, attributed to Crispin van de Passe and published around 1605. No anthers are visible at the mouth of the flowers which present what appears to be a round pin stigma (van de Passe, 1603).

Figure S7 Pauli de Reneaulme's Cowslip (1611)

Extract of a wood block print from Pauli de Reneaulme's *Specimen Historiae Plantarum* showing an umbel of Cowslip flowers. No anthers are visible at the mouth of the flowers and the round stigma visible in the flowers at the top of the image identifies this as a pin. With permission, Cambridge University Library.

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Current binomial	***P. vulgaris* Huds.**[1]	***P. veris* (L.) Hill**[2]	***P. elatior* (L.) Hill**[2]	***P. farinosa* L.**[3]	***P. scotica* Hook**[4]	***P. auricula* L.**[3]
Common name	Primrose	Cowslip	Oxlip	Birdseye Primula	Scottish Primula	Auricula
Nomenclature used by Linnaeus[3]	*P. veris* var. *acaulis*	*P. veris* var. *officinalis*	*P. veris* var. *elatior*	*P. farinosa*		*P. auricula*
Names used by Curtis [7]	*P. acaulis*	*P. officinalis*	*P. elatior*	*P. farinosa* L.	*P. scotica*	
Names used by Persoon [8]	*P. acaulis* (L.) Hill[2]	*P. odorata* Gilib.[5]	*P. inodora* Hill[2]			
pre-Linnaean descriptive names	Descriptive names include Primula veris sylvestris flora pallido[9] (primrose) and Primula veris pallido flore elatior[9] (cowslip), others which cannot be aligned to current species include Auricula Ursi III [10], Auricula Ursi minima V [10], and Bear's Ears[11]					
Horticultural varieties	*P. acaulis* is sometimes used for commercial Primrose varieties; and *P. x polyantha* Mill.[6] for Polyanthus.					Auricula

Notes: References to authorities for species names: [1] (Hudson, 1762), [2] (Hill, 1759-1775), [3] (Linnaeus, 1753), [4] (Curtis *et al.*, 1815-1828), [5] (Gilibert, 1782), [6] (Miller, 1768), and publications using these names: [7] (Curtis, 1777-1798a), [8] (Persoon, 1794), [9] (Besler, 1613), [10] (van de Passe, 1614), [11] (Weinmann, 1737).

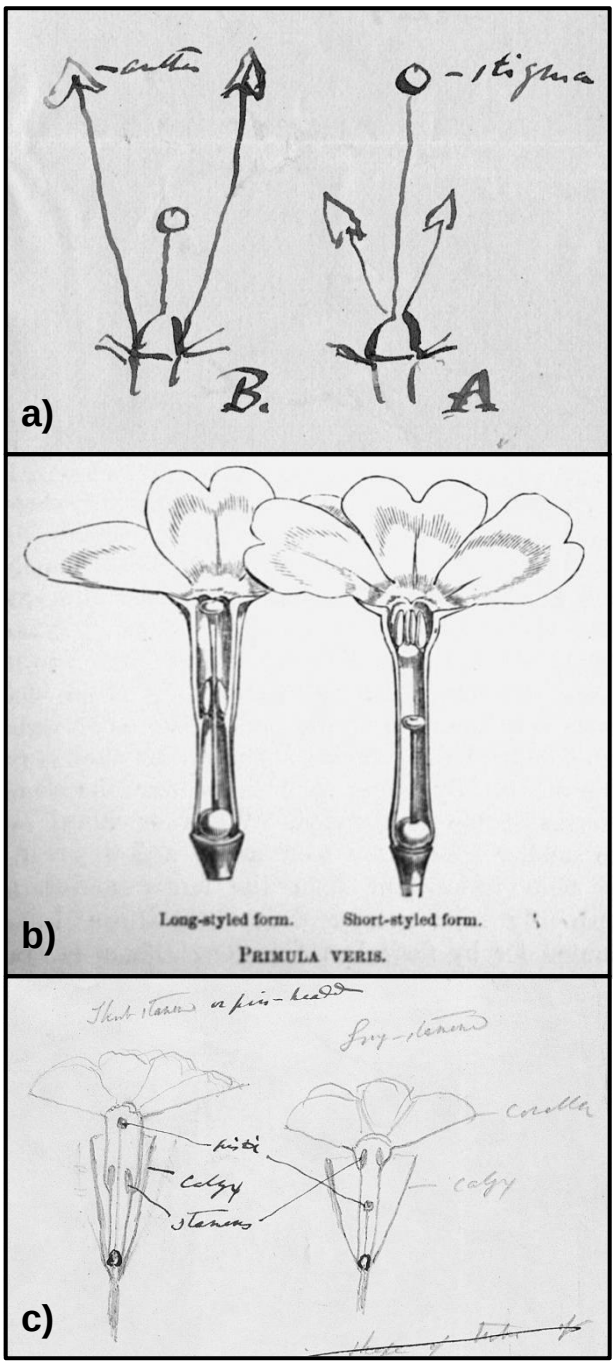
a)
B.
A
b)
Long-styled form.
Short-styled form.
PRIMULA VERIS.
c)
corolla
calyx
calyx

Figure 1

Figure 2

Figure 3

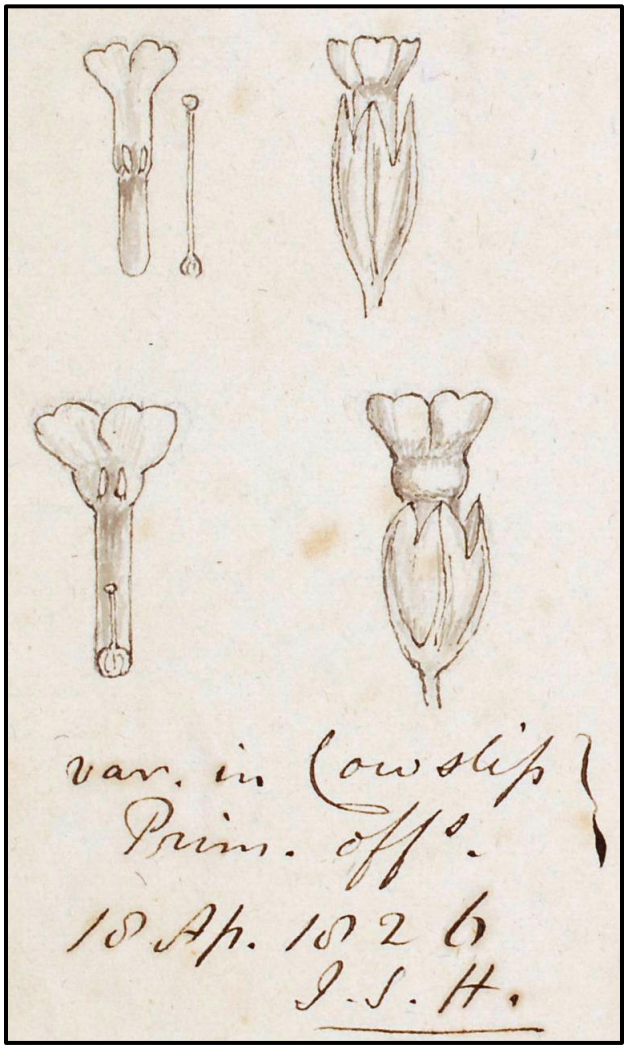

Figure 4

Figure 5

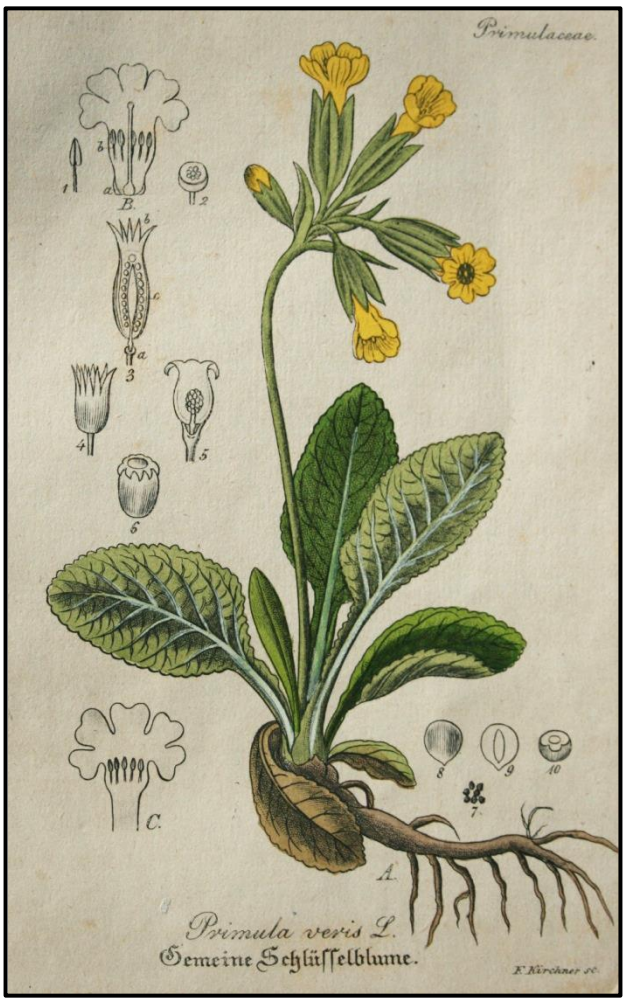

Figure 6

Figure 7

Figure 8


1 . WATER VIOLET
Hottonia palustris
2 . COMMON PRIMROSE
Primula vulgaris
3 . JACQUINS OXLIP
P. elatior
4 . COWSLIP

Figure S1


II
I
Paralyſis
1–9. Blüthe
10–16. Frucht
17–19. Saame
Schlüſſel Blume.

Figure S2

Figure S3

Figure S4

Figure S5


27
L. Primula veris
G. Pfinz vere, ou Blaies de Coeu
A. Primrose
Ge. Schlusselblumen.

Figure S6

Figure S7