



## ***Meconopsis autumnalis* and *M. manasluensis* (Papaveraceae), two new species of Himalayan poppy endemic to central Nepal with sympatric congeners**

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### **Abstract**

Two new species from Nepal, *Meconopsis autumnalis* and *M. manasluensis*, are described and illustrated with notes on diagnostic characters used to distinguish them from allied species. Sympatric speciation and the mechanisms to reproductively isolate the new species are discussed. In *M. autumnalis*, reproductive isolation from the widespread *M. paniculata* is the result of a shift in flowering phenology, whereas possible mechanisms preventing cross-fertilisation between *M. manasluensis* and the sympatric species *M. pinatifolia* remain unclear.

**Key words:** allochronic speciation, assortative mating, Himalaya, Flora of Nepal

### **Introduction**

*Meconopsis* Vig. is the second largest genus of the Papaveraceae and contains about 50 monocarpic or polycarpic species (Mabberley 2008), though with new discoveries and reassessments of species concepts having led to the description of additional novel taxa in recent years (An *et al.* 2009, Cui & Lian 2005, Grey Wilson 2006a, 2006b, Lu & Lian 2006, Ohba *et al.* 2009, Toshio *et al.* 2010). The genus as traditionally defined has a disjunct distribution, with all species found in the Sino-Himalayan region apart from *Meconopsis cambrica* (L.) Viguier (1814: 48), which is confined to Ireland, Britain and the Atlantic fringes of continental western Europe (Webb 1983). However, it is now widely accepted that *M. cambrica* is not congeneric and may thus be reclassified under *Papaver* L. or as a unique genus in its own right (Carolan *et al.* 2006, Jork & Kadereit 1995).

In the Sino-Himalayas *Meconopsis* is found in a variety of habitats ranging from temperate forests and pastures below the tree line at around 2500 m, to alpine meadows, screes and nival zones up to 5500 m. The highest records are of dwarf forms of *M. horridula* Hooker f. & Thomson (1855: 252) *s.s.*, which occur from central Nepal eastwards to Bhutan. Within Central Asia as a whole, the genus has a more or less continuous distribution in a narrow band from the northwestern Himalaya of Pakistan, along the Himalayan range and Tibetan plateau to western China. Twenty two species have been reported from Nepal and eleven of these are endemic and mostly local in distribution (Egan & Shrestha in press). Although several species of *Meconopsis* are currently considered threatened (Sulaiman & Hasnain 1996), the conservation status of the majority remains unknown, with a lack of accurate distribution records and baseline ecological data (population dynamics, demography etc.) hampering formal conservation assessment.

Two new species of *Meconopsis* are here described: *M. autumnalis* P.Egan in the series *Robustae* Prain of subgenus *Eumeconopsis* (Prain) Fedde, and *M. manasluensis* P.Egan belonging to subgenus *Discogyne* G.Taylor. The *Robustae* and *Discogyne* were revised by Grey-Wilson (2006a, 2006b), and an updated key to the Nepalese species of *Meconopsis* will be presented in Volume 3 of the Flora of Nepal (Egan & Shrestha in press). The description of these species follows discoveries made during two expeditions to central Nepal in

2008, in the Manaslu Eco-Tourism Area (Ikeda & Watson 2010) and Langtang National Park and Ganesh Himal (Egan *et al.* 2009, Egan 2010). Like other areas in the region, the Ganesh and Manaslu Himal have rugged topography over a wide elevational range and support a diverse biota. Botanical exploration in these areas has been relatively limited compared with other areas of central Nepal because of the remoteness of the ranges (Baker 1994, Pendry *et al.* 2009, Stainton 1964, Stearn 1993), and rather little information is available even for a conspicuous genus like *Meconopsis*. The first floristic inventory of the Ganesh Himal was carried out relatively recently (Ohba & Ikeda 1999). The species list for the Manaslu Conservation Area has 587 vascular plants, but it is estimated that there may be up to 2500 species present (Bhujju *et al.* 2007).

## Species Descriptions

***Meconopsis autumnalis* P.Egan, sp. nov.** (series *Robustae* Prain) (Fig. 1. & Fig. 3a.)

*Meconopsis autumnalis* a speciebus floribus flavis seriei *Robustae* florescentia multo postea differt.

**Type:**—NEPAL. Central Nepal, Ganesh Himal (Rasuwa District), Tulo Bhera Kharka – Jaisuli Kund, 28°12'N, 85°13'E, 4160 m, Miyamoto *et al.* 9440053 (holotype E!, 2 sheets [E00107717, E00107665], isotypes KATH!, TI).

Erect monocarpic herbs, 110–160 cm. Stem 2.2–3.1 cm in diameter at base; taproot elongated, to 3 cm wide, yellow-orange lactiferous. Indumentum densely puberulent with scattered 5–9 mm pale fawn to orange barbellate bristles. Basal leaves in large rosettes, pubescent throughout, though glabrous at maturity, leaving only slender capillary bristles (to 10 mm) on the margins; petioles 11–25(–31) cm; lamina distinctly pinnatisect at base, pinnatifid only shortly from leaf apex, broadly oblong, 33–55 × 8–16 cm; segments noticeably parted in 3–5 opposite to sub-opposite pairs, oblong or ovate, to 4.0 × 2.2 cm, pinnatilobate at the margin, the lobes acute to obtuse. Cauline leaves with indumentum similar to basal leaves; petioles present in lower cauline leaves, sessile in upper; lamina progressively smaller upwards, deflexed on stem and semi-amplexicaul attached, with large auricles prominent at the base, narrow-oblong, pinnatilobate to pinnatifid, the lobes entire and broadly rounded or subacute. Inflorescence densely paniculate and markedly columnar in outline, 50–250 flowered; cymules laterally branched, 3–8(–12)-flowered, the uppermost flowers solitary. Flowers bowl to saucer-shaped, semi-nutant to lateral-facing. Bracts leaf-like, at base of peduncles and pedicels. Peduncles 11–21 cm, widely spreading during anthesis, elongating to 15–29 cm and ascending in fruit. Pedicels 6–17 cm. Buds broadly ellipsoidal to ovoid, sparsely covered with ascending, barbellate bristles. Petals 4(–6), pale yellow, obovate to suborbicular, 4.3–5.6 × 4.1–5.5 cm, occasionally widely spaced, only overlapping a short distance from the base. Filaments pale yellow, anthers yellow-orange. Ovary obviously stipitate and with large receptacle, densely covered with orange ascending bristles. Style 8–25 mm, stout. Stigma yellow, capitate, (3–)5–8 mm, 6–8-lobed. Capsule ovoid to ellipsoidal, 1.5–2.7 × 0.9–1.4 cm, dehiscent by 6–8 valves; indumentum moderately dense, spreading to ascending.

**Flowering:**—Late July–September.

**Ecology:**—Sub-alpine pastures, stream margins and grassy alpine slopes on edges and in openings of *Abies* forest, in association with *Rumex*, *Arisaema*, *Stellaria*, *Nepeta*, *Persicaria*, *Aster*, *Swertia*, and dwarf shrubs such as *Berberis*, *Rhododendron* and *Juniperus*, in stony, humus-rich soils. Locally abundant.

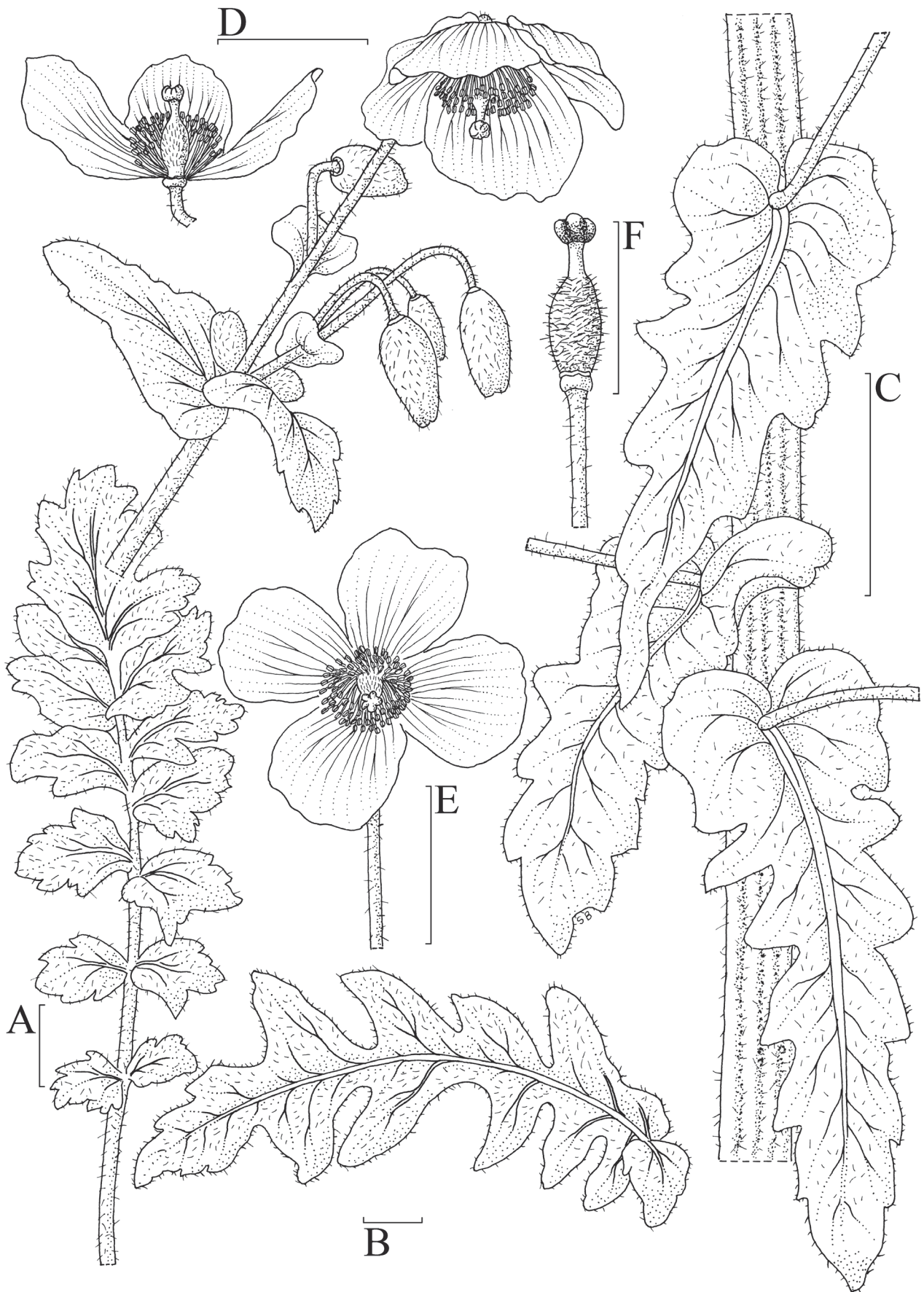
**Elevational range:**—3300–4200 m.

**Distribution:**—Restricted to southeast Ganesh Himal, central Nepal.

**Etymology:**—Named for its autumn flowering.

**Additional specimen seen (paratype):**—NEPAL. Central Nepal, Ganesh Himal (Rasuwa District), Jaisuli Kund (Jagesor Kund), 28°14'N, 85°11'E, 3965 m (13,000 ft), *Stainton 4028* (BM!, 4 sheets).

*Meconopsis autumnalis* is a member of the series *Robustae* Prain, which is characterised by long, branched inflorescences, large overwintering rosettes, and a monocarpic-perennial habit in which flowering usually only occurs after 3–5 years. Unlike most other series of *Meconopsis* that have centres of distribution in south-



**FIGURE 1.** *Meconopsis autumnalis* P.Egan **A.** Basal (rosette) leaf. **B.** Lower cauline leaf. **C.** Deflexed upper cauline leaves. **D.** Peduncle and flower section. **E.** Flower showing widely spaced petals. **F.** Gynoecium, with large receptacle. Scale: 4 cm. Illustration credit: S. Bradley.

western China (Chuang 1981), series *Robustae* is almost exclusively Indo-Himalayan (Table 1.) and seems to represent a monophyletic lineage (Yuan *et al.* 2002) of 12 species, seven of which are endemic to Nepal. In the aggregate of yellow-flowered species of the series, *M. autumnalis* is morphologically intermediate between *M. napaulensis* De Candolle (1824: 121) (*sensu* Grey-Wilson 2006b) and *M. paniculata* (D. Don) Prain (1896: 316), but clearly differs from the former by its significantly taller stature, larger flowers, both wider and longer leaves, larger capsules and orange pubescence (fawn in *M. napaulensis*), and from the latter in its smaller size (and subsequent greater density of the inflorescence), yellow-green stigmas, narrower capsules with spreading as opposed to densely appressed pubescence, and in its largely auriculate, deflexed cauline leaves (usually lateral-facing in *M. paniculata*). *Meconopsis autumnalis* differs from both *M. napaulensis* and *M. paniculata* in its distinctly larger stigmas and longer pedicels (a mean of 10 cm in *M. autumnalis* during anthesis, and 7 cm and 6 cm in *M. napaulensis* and *M. paniculata* respectively).

Delimitation of *M. autumnalis* has required particularly careful examination of the morphological relationship with the closely related *M. paniculata*; a partially sympatric and highly variable species widely distributed over a large geographic area (Giri & Lal 1989, Kingdon-Ward 1930), as listed in Table 1. However, despite the reputation of *M. paniculata* as one of the most polymorphic species of *Meconopsis*, surprisingly few infraspecific taxa have been delimited. Only *M. paniculata* var. *elata* Prain (1896: 316) has been described, although this was not maintained in a subsequent monograph (Taylor 1934). Leaves vary considerably in *M. paniculata*, while pubescence and stigma characters are much less variable and are diagnostic of the species (Cobb 1989, Grey Wilson 2006b). In the field it was observed that these characters were sufficiently distinct even in sympatric populations to consistently separate the two species. Furthermore, the upper inflorescence of *M. autumnalis* retains wide laterally-branched peduncles with long pedicels, which render a distinctly columnar outline (Fig. 3a.), whereas that of *M. paniculata* is much less branched and shortly pedicellate. *Meconopsis autumnalis* and *M. paniculata* scarcely overlap in their respective flowering times, allowing an ecological differentiation to be made between the two species (as further discussed below).

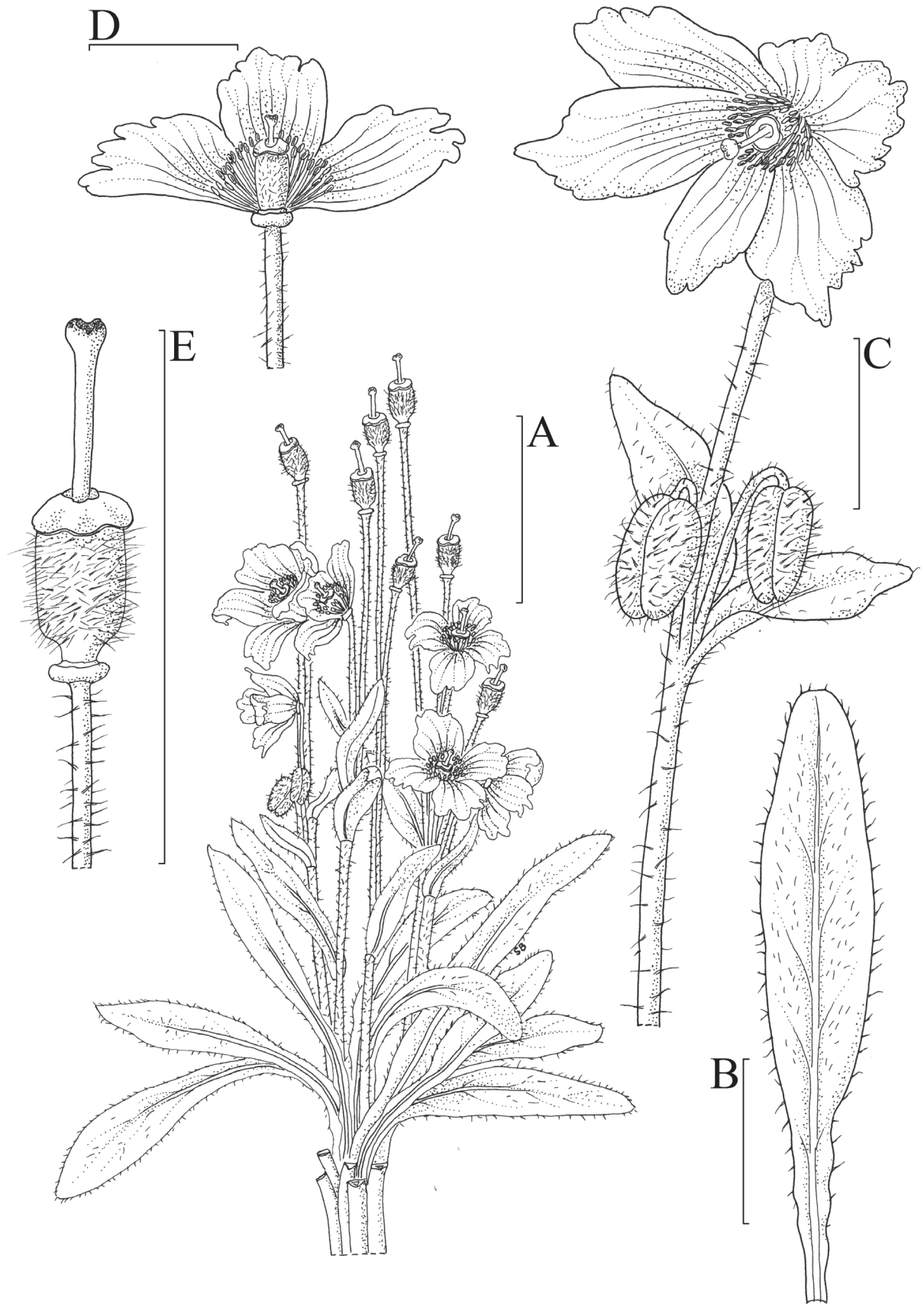
The field notes for *Stainton 4028* (reproduced in part in Grey-Wilson 2006b) separate *M. paniculata* from what was noted as a second ‘easily distinguishable’ species of *Meconopsis* subsequently collected in the Ganesh Himal, and, when growing together, ‘no intermediate forms were seen’. Despite suggestion as to its novelty, the specimen (which now refers to *M. autumnalis*) remained as ‘*Meconopsis* sp.’ without formal status afforded, though two later determinations included *M. longipetiolata* G. Taylor (1932: 41). However, neotypification of *M. longipetiolata* by Debnath & Nayar (1987) placed this species type locality as Langtang valley, Rasuwa district; thereby justifying synonymy under *M. napaulensis* (*sensu* Grey-Wilson 2006b) after the complex surrounding the latter was clarified (see Table 1.).

***Meconopsis manasluensis* P. Egan, sp. nov.** (subgenus *Discogyne* G. Taylor) (Fig. 2. & Fig. 3b.)

*Meconopsis manasluensis* a *M. tibetica pedicellis longioribus, gemmis et capsulis anguste ovoideis vel cylindricis et disco styli majore differt.*

**Type:**—NEPAL. Central Nepal, Manaslu Himal (Gorkha district), east of Samdo on south side of Sanam Khola river valley, 28°38'N, 84°38'E, 4000 m, Ikeda *et al.* 20815156 (holotype E! [E00360728], isotype E! [E00360729]).

Erect monocarpic herbs, 30–60 cm. Stems multiple, partially fusing above the rootstock crown, to 1.5 cm in diameter at base; taproot twisted, fleshy, 2.5–3.0 cm wide. Indumentum a sparse to moderately dense cover of 3–6 mm fawn or orange barbellate bristles. Basal leaves in rosettes, pubescent on both surfaces and petioles; petioles 3–5 cm, winged; lamina tapered at the leaf base, sub-acute or rounded at the apex, obelliptic to narrow oblanceolate, 6.5–15.5 × 1.5–3.0 cm; margins entire. Cauline leaves gradually decreasing in size upwards, otherwise resembling basal leaves; lower leaves shortly petiolate, uppermost leaves and bracts sessile. Inflorescence racemose, 30-flowered, the flowers borne singly on the central axis and multiple, leafy lateral stems. Flowers saucer-shaped, lateral-facing to subsasendant. Pedicels conspicuously elongate, 1.5–7.5 cm, decurrent on stem, curved throughout anthesis, though erect at fruiting. Buds ellipsoidal, with sparse



**FIGURE 2.** *Meconopsis manasluensis* P.Egan **A.** Stems (scale: 10 cm). **B.** Basal leaf. **C.** Upper stem and pedicels. **D.** Flower section. **E.** Gynoecium, showing stigmatic disc. Scale: 3 cm, except where otherwise stated. Illustration credit: S. Bradley.

cover of long ascending, flexuose bristles. Petals 4 or 5(–8), scarlet with darker, purple patches towards the base, broadly ellipsoidal to obovate, 2.0–3.0 × 1.0–2.0 cm. Filaments red-purple, anthers yellow-orange. Ovary densely covered with fawn to orange ascending bristles. Style 7–12 mm, slender, with stylar-disk to 8 mm in diameter projecting beyond edge of ovary. Stigma yellow, capitate, 3–4 mm, generally 6-lobed. Capsule narrowly ovoid to cylindric, 0.8–1.6 × 0.4–0.7 cm, dehiscent by 8-valves; indumentum of sparsely spreading bristles.

**Flowering:**—July–August.

**Ecology:**—Herb-rich alpine grasslands with scattered shrubs (*Berberis*, *Lonicera*, *Salix*, etc.) and dwarf trees of *Betula utilis*. Found amongst boulders in moist, humus-rich soils. Locally common.

**Elevational range:**—ca. 4000 m.

**Distribution:**—Currently only known from locality of type collection, Manaslu Himal, central Nepal.

**Etymology:**—The species is named after the mountain range to which it is endemic; the Manaslu Himal, and in honour of the Flora of Nepal Manaslu 2008 Expedition, during which it was discovered.

Subgenus *Discogyne* G.Taylor is defined by the possession of a substylar disc surmounting the ovary, a feature clearly distinguishing it from the rest of the genus. *Meconopsis manasluensis* is easily distinguished from all other species of this subgenus because it is the only one with multiple flowering stems, unlike the single prominent fleshy stem in the other five species. Although the subgenus was first proposed by Taylor (1934) based only on *M. discigera* Prain (1906: 356) and *M. torquata* Prain (1906: 355), known from the Indo-Himalaya and south-central Tibet respectively, this number has grown in the intervening decades with discoveries of species centred upon the central Himalaya (Grey-Wilson 2006a, Zhou 1979).

**TABLE 1.** Political & floristic distribution of species of the series *Robustae*.

Species	Bhutan	India	Myanmar (Burma)	Nepal	Tibet (Xizang)	Western China	Floristic province <sup>†</sup>
<i>M. autumnalis</i>				•			EH
<i>M. chankeliensis</i> *				•			WH
<i>M. dhwojii</i>				•			EH
<i>M. ganeshensis</i> *				•			EH
<i>M. gracilipes</i>				•			EH
<i>M. napaulensis</i> *				•	○		EH
<i>M. paniculata</i> ~	•	•	○	•	○		WH, EH, NB
<i>M. robusta</i>		•		•			WH
<i>M. staintonii</i> *				•			WH, EH
<i>M. violacea</i>			•		○		NB
<i>M. wallichii</i> *	•	•		•	○		EH
<i>M. wilsonii</i>			○		○	•	NB, SY
Total no. spp.	2 (17%)	3 (25%)	3 (25%)	10(83%)	5 (42%)	1 (8%)	
Total no. endemic spp.	0	0	1	7	0	0	

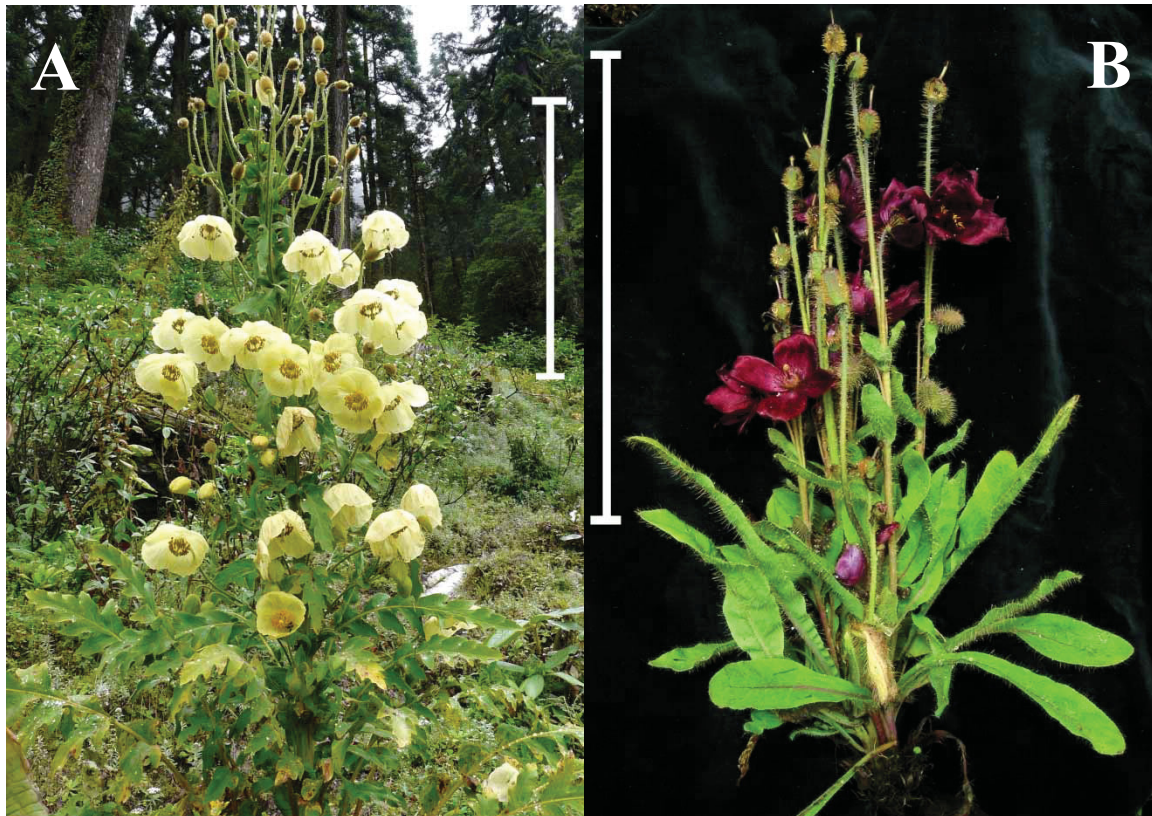
○ Minor occurrence • Major occurrence • Strict or near endemic

† EH= Eastern Himalayan, WH= Western Himalayan, NB= Northern Burmese, SY= Sikang-Yunnan

~ Occurrence in Myanmar controversial, see Kress *et al.* (2003)

\* Newly described or reinstated/recircumscribed by Grey-Wilson (2006b)

In Nepal, only a single species, namely *M. simikotensis* Grey-Wilson (2006a: 220) and the yellow form of *M. discigera*, are reported from the west and east of the country respectively, whereas the species *M. pinnatifolia* C.Y.Wu & H.Chuang ex L.H.Zhou (1979: 114) and *M. manasluensis* are known from central Nepal, and occur in partial sympatry in the Manaslu Himal. *Meconopsis manasluensis* is distinguished from *M. pinnatifolia* by its entire versus pinnately cleft leaves, and dark red versus purple flowers. It differs from the closely related *M. tibetica* Grey-Wilson (2006: 222) by its elongated pedicels, narrowly ovoid or cylindric buds and capsules (versus subglobose capsules found in *M. tibetica*), and in the projection of its stylar disc beyond the edge of the ovary. *Meconopsis manasluensis* is also geographically separated by some 260 km of rugged terrain from *M. tibetica*, which thus far is only known from several small populations located north west of Mount Everest in the Xizang Region of China.



**FIGURE 3.** **A.** Habit of *M. autumnalis* (photo taken 17 August 2008, credit: P. Egan). **B.** Habit of *M. manasluensis* (photo taken 8 August 2008, credit: M. Watson). Scale: 30 cm.

## Discussion

The Asian species of *Meconopsis* are noted for high rates of polymorphism (Taylor 1934) and consequent controversies over species delimitations and major differences of species concepts between generic revisions (Kingdon-Ward 1926, Prain 1896, 1906, Taylor 1934). Taylor's (1934) subgeneric classification remains the most comprehensive and widely accepted treatment, and was not superseded by Wu & Chuang's (1980) account. In the genus it is evident that geographic isolation (which in mountainous areas may be present even across relatively short distances) has served as an important prelude to speciation events and the formation of infraspecific taxa. However, sympatric speciation has not previously been proposed as a mechanism for the creation of new taxa in *Meconopsis*. Divergence in flowering phenology within and between congeneric species can be critical in the establishment and maintenance of genetic differentiation (Devaux & Lande 2008,

Ollerton 2005), with formation of reproductive isolation and subsequent speciation possible if positive assortative mating is maintained over a sufficient period of time (Widmer *et al.* 2009).

During the expedition to Langtang and Ganesh *M. autumnalis* was found twice in early to mid August growing in the vicinity of *M. paniculata*. It was noted that the upper fruit capsules of all individuals of *M. paniculata* were already fully ripe with seed, whilst *M. autumnalis* had only just begun flowering (this phenology is also seen in the type specimens of *M. autumnalis*, collected July 30<sup>th</sup>, 1994). It is proposed that this difference serves to maintain genetic isolation and morphological integrity even in populations in such close proximity. This is especially interesting considering the propensity of *Meconopsis* to form natural hybrids in the wild (Cobb 1989, Grey-Wilson 2006b). A divergence in flowering period could potentially be favoured by natural selection due to reduction in competitive interaction between the two species, through partition of key resources like pollinators (Hou *et al.* 2008, Lack 1982). Elsewhere in the genus, only *M. wallichii* (1852: 4668), also in *Robustae* and found from east Nepal to Bhutan, flowers as late in the season as *M. autumnalis*. *Meconopsis wallichii* is also known to partially overlap with *M. paniculata* over its entire distributional range.

Although the level of divergence and extent to which introgression may still occur between *M. autumnalis* and *M. paniculata* is not known, it is postulated that temporal boundaries to fertilization has minimized gene flow between the species, thus maintaining genetic and morphological integrity of sympatric populations. Preliminary results from a forthcoming genus-wide phylogenetic study of *Meconopsis* have verified a close genetic relationship between the two taxa (W. Xiao personal communication). This study has also suggested that due to incongruence between the different genetic markers employed, *M. autumnalis* may be of hybrid origin. This result is consistent with the emergence of *M. autumnalis* under an allochronic model of sympatric speciation, as gene flow between sympatric populations would have been unavoidable at least during initial stages of divergence. It is unclear by what mechanisms sympatric populations of *M. pinnatifolia* and *M. manasluensis* are reproductively isolated and further investigations will be required to clarify this.

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## References

- An, L.Z., Chen, S.Y. & Lian, Y.S. (2009) A new species of *Meconopsis* (Papaveraceae) from Gansu, China. *Novon* 19: 286–288.
- Baker, W.J. (1994) Three men and an orchid. *Bulletin of the Alpine Garden Society of Great Britain* 62: 99–114; 62: 181–199.
- Bhujju, U.R., Shakya, P.R., Basnet, T.B. & Shrestha, S. (2007) *Nepal Biodiversity Resource Book. Protected Areas, Ramsar Sites, and World Heritage Sites*. International Centre for Integrated Mountain Development, Ministry of Environment, Science and Technology, in cooperation with United Nations Environment Programme, Regional Office for Asia and the Pacific, Kathmandu, 128 pp.
- Carolan, J.C., Hook, I.L.I., Chase, M.W., Kadereit, J.W. & Hodkinson, T.R. (2006) Phylogenetics of *Papaver* and related genera based on DNA sequences from ITS nuclear ribosomal DNA and plastid trnL intron and trnL-F intergenic spacers. *Annals of Botany* 98: 141–155.
- Chuang, H. (1981) The systematic evolution and the geographical distribution of *Meconopsis* Viguiet. *Acta Botanica Yunnanica* 3: 139–146.
- Cobb, J. (1989) *Meconopsis*. Timber Press, London, 125 pp.
- Cui, Z. & Lian, Y. (2005) A new variety of *Meconopsis* from Gansu. *Guihaia* 25: 106.



- De Candolle, A.P. (1824) Papaveraceae. In: *Prodromus Systematis Naturalis Regni Vegetabilis*, Volume 1, pp. 117–124.
- Debnath, H. & Nayar, M. (1987) Short communication. Neotype of *Meconopsis longipetiolata* G.Tayl. ex Hay (Papaveraceae) and some additional note. *Bulletin of the Botanical Survey of India* 27: 244–245.
- Devaux, C. & Lande, R. (2008) Incipient allochronic speciation due to non-selective assortative mating by flowering time, mutation and genetic drift. *Proceedings of the Royal Society B-Biological Sciences* 275: 2723–2732.
- Egan, P.A. (2010) Expedition *Meconopsis*. *The Rock Garden* 124: 46–61.
- Egan, P.A. & Shrestha, S. (in press) *Meconopsis*. In: Watson *et al.* (ed.), *Flora of Nepal Volume 3*. Royal Botanic Garden Edinburgh.
- Egan, P.A., Swords, C., Eeftens, M.R. & Ram Poudeyal, M. (2009) *Ethnobotany Nepal Himalaya Project 2008 - Final Report*. University of Aberdeen (privately published), 26 pp.
- Giri, G.S. & Lal, J. (1989) Distributional record of *Meconopsis paniculata* (D.Don) Prain (Papaveraceae) from Arunachal Pradesh. *Journal of Economic & Taxonomic Botany* 12: 365–366.
- Grey-Wilson, C. (2006a) A new *Meconopsis* from Tibet. *Alpine Gardener* 74: 212–225.
- Grey-Wilson, C. (2006b) The true identity of *Meconopsis napaulensis* DC. *Curtis's Botanical Magazine* 23: 176–209.
- Hooker, J.D. & Thomson, T. (1855) Papaveraceae. In: *Flora Indica: Being a Systematic Account of the Plants of British India, Together With Observations on the Structure and Affinities of Their Natural Orders and Genera*. W. Pamplin, London, pp. 248–257.
- Hooker, W.J. (1852) *Meconopsis Wallichii*. Dr. Wallich's *Meconopsis*. *Curtis's Botanical Magazine* 78: 4668.
- Hou, Q.Z., Meng, L.H. & Yang, H.L. (2008) Pollination ecology of *Gentiana siphonantha* (Gentianaceae) and a further comparison with its sympatric congener species. *Journal of Systematics and Evolution* 46: 554–562.
- Ikeda, H. & Watson, M.F. (2010) Plant collecting around Mt. Manaslu in 2008. *Newsletter of Himalayan Botany* 43: 11–13.
- Jork, K. & Kadereit, J. (1995) Molecular phylogeny of the Old World representatives of Papaveraceae subfamily Papaveroideae with special emphasis on the genus *Meconopsis*. In: Jensen U. & Kadereit J.W. (eds.), *Systematics and evolution of the Ranunculiflorae* (Plant Systematics and Evolution, supplement 9). Springer, New York, pp. 171–180.
- Kingdon-Ward, F. (1926) Notes on the genus *Meconopsis*, with some additional species from Tibet. *Annals of Botany* 40: 535–546.
- Kingdon-Ward, F. (1930) The Seinghku and Delei Valleys, North-East frontier of India. *Geographical Journal* 75: 412–432.
- Kress, W. J., DeFilipps, R. A., Farr, E. & Kyi, D.Y.Y. (2003) A checklist of the trees, shrubs, herbs, and climbers of Myanmar. *Contributions from the United States National Herbarium* 45: 1–590.
- Lack, A.J. (1982) Competition for pollinators in the ecology of *Centaurea scabiosa* L. and *Centaurea nigra* L. 1. Variation in flowering time. *New Phytologist* 91: 297–308.
- Lu, M. & Lian, Y. (2006) *Meconopsis punicea* Maxim. var. *glabra* M.Z.Lu et Y.Sh.Lian (Papaveraceae), a new variety from Gansu, China. *Bulletin of Botanic Research* 26: 8–9.
- Mabberley, D. (2008) *Mabberley's plant-book: a portable dictionary of plants, their classification and uses*: Cambridge University Press, 1021 pp.
- Ohba, H. & Ikeda, H. (1999) *A contribution to the flora of Ganesh Himal, Central Nepal* (Nature and Culture, No. 5). University Museum-University of Tokyo, 84 pp.
- Ohba, H., Yoshida, T. & Sun, H. (2009) Two new species of *Meconopsis* (Papaveraceae) from southern Biluo Xueshan, Yunnan, China. *Journal of Japanese Botany* 84: 294–302.
- Ollerton, J. (2005) Speciation - flowering time and the wallace effect. *Heredity* 95: 181–182.
- Pendry, C.A., Watson, M.F., Shrestha, K. & Rajbhandari, K.R. (2009) Building capacity for plant biodiversity, inventory and conservation in Nepal: Activities of the recent Darwin Initiative Project in Nepal. *Newsletter of Himalayan Botany* 42: 16–27.
- Prain, D. (1896) Some additional Papaveraceae. *Journal of the Asiatic Society of Bengal* 64: 303–327.
- Prain, D. (1906) A review of the genera *Meconopsis* and *Cathcartia*. *Annals of Botany* 20: 323–370.
- Stainton, J.D.A. (1964) *Notes on a journey in East and Central Nepal 1964 with brief notes on journeys in East Nepal 1956 and in Central Nepal*. British Museum (privately published), 51 pp.
- Stearn, W.T. (1993) John Williams (1915–1991) and Adam Stainton (1921–1991), botanical explorers of Nepal. *Taxon* 42: 901–905.
- Sulaiman, I.M. & Hasnain, S.E. (1996) Random amplified polymorphic DNA (RAPD) markers reveal genetic homogeneity in the endangered Himalayan species *Meconopsis paniculata* and *M. simplicifolia*. *Theoretical and Applied Genetics* 93: 91–96.
- Taylor, G. (1932) Two new species of *Meconopsis* from Nepal. *The Gardener's Chronicle* 92: 41.
- Taylor, G. (1934) *An account of the genus Meconopsis*. New Flora and Silva, London, 130 pp.
- Toshio, Y., Hang, S.U.N. & Boufford, D.E. (2010) New species of *Meconopsis* (Papaveraceae) from Mianning, southwestern Sichuan. *Acta Botanica Yunnanica* 32: 503–507.

- Viguiér, A.L.G. (1814) *Meconopsis*. In: *Histoire Naturelle, Médicale et Économique des Pavots et des Argemones*. Université Montpellier, pp. 48–49.
- Webb, D. (1983) The flora of Ireland in its European context. *Journal of Life Sciences of the Royal Dublin Society* 4: 143–160.
- Widmer, A., Lexer, C. & Cozzolino, S. (2009) Evolution of reproductive isolation in plants. *Heredity* 102: 31–38.
- Wu, C. & Chuang, H. (1980) A study on the taxonomic system of the genus *Meconopsis*. *Acta Botanica Yunnanica* 2: 371–381.
- Yuan, C., Shi, S. & Boufford, D.E. (2002) Phylogenetic analysis of *Meconopsis* Viguiér (Papaveraceae) based on chloroplast and nuclear ribosomal DNA sequences. In: Yuan, C., *The phylogeny, systematics and biogeography of Meconopsis Viguiér (Papaveraceae) and Craigia W.W.Sm. & W.E. Evans (Tiliaceae)*. PhD thesis.
- Zhou, L. (1979) New taxa of *Meconopsis* from Qinghai - Tibet Plateau. *Acta Phytotaxonomica Sinica* 17: 112–114.