Hybridisation between *Gentianella amarella* (L.) Boerner and *G. anglica* (Pugsley) E. F. Warb. (Gentianaceae)

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ABSTRACT

A morphological investigation of *Gentianella anglica* (Pugsley) E. F. Warb. subsp. *cornubiensis* Pritchard indicates that it is the hybrid between *Gentianella amarella* (L.) Boerner and *G. anglica*. The hybrid is named as **Gentianella** × **davidiana** T. C. G. Rich, **hybr. nov**. It is recorded from the southern English v.cc. 1, 4, 10, 14 and 16, and may also occur elsewhere. A lectotype is selected for *Gentiana amarella* L. var. *praecox* Townsend, the basionym for *G. anglica*. The current evidence indicates hybridisation may be a threat to survival of some but not all populations of *G. anglica*.

KEYWORDS: Early gentian, *Gentiana amarella* var. *praecox*, *Gentianella anglica* subsp. *cornubiensis*, *Gentianella* × *davidiana*.

INTRODUCTION

Gentianella anglica (Pugsley) E. F. Warb. is a rare, English endemic. It is protected under Schedule 8 of the *Wildlife and Countryside Act 1981* (as amended). It is also listed in Appendix 1 of the *Bern Convention* and Annexes II and IV of the European Community *Habitat and Species Directive*.

Plantlife began conservation work on *G. anglica* in Surrey in 1993 at the request of Mrs Joyce Smith, the B.S.B.I. vice-county recorder, and began monitoring populations and carrying out habitat management work (Rich 1993, 1994, 1995a, b). In 1994 and 1995, the work was extended to Gloucestershire (Rich, Kitchen & Kitchen 1995), Kent (Rich & Phillip 1995), Lincolnshire (Rich & Weston 1995) and Sussex (Rich 1995c). After a review of the status of *G. anglica* subsp. *cornubiensis* Pritchard had identified that hybridisation with *G. amarella* (L.) Boerner might be a threat to *G. anglica* (Rich, Murphy & Margetts 1995), the Cornish plants were investigated in 1995. Populations are also being investigated independently in the Isle of Wight by Mrs Susan Telfer (Telfer 1994, 1995). A reasonably up-to-date distribution map of *G. anglica* is given by Chatters (1994).

Our current understanding of the taxonomy of *G. anglica* is based on work by Pritchard (1959), which suggested that there are striking differences between plants from dunes and cliff tops in Cornwall and plants from elsewhere in England. The Cornish plants were described as having a higher average number of internodes, slightly contracted terminal internodes, longer corollas,

axillary flowers and were seldom branched from the base. Pritchard suggested that the position of the Cornish plants was somewhat intermediate between *G. anglica* and *G. amarella*, though closer to the former, and chose to recognise this variation by describing the Cornish plants as a subspecies of *G. anglica* based on the morphological and ecological differences and disjunct distribution on one hand, and the morphological similarities and the similar flowering time on the other.

At the time, an alternative explanation of the intermediate Cornish plants as hybrids seems to have been dismissed due to the apparent differences in flowering time of the two species, with Cornish and other *G. anglica* reported flowering early in the year to 12 July, and *G. amarella* later in the season from 22 July onwards (Pritchard 1959). Pritchard (1972) later stated "A very few specimens have been questioned as possible intermediates, but I have seen no populations which suggest any measure of hybridisation". Hybridisation with *G. amarella* was, however, recognised in closely related taxa such as *G. uliginosa* (Willd.) Boerner and *G. germanica* (Willd.) Boerner (Pritchard 1959, 1961).

The first report of hybridisation between *G. anglica* and *G. amarella* was of a huge hybrid swarm found at Penhale Sands (Gear Sands), Cornwall in 1966 by L. J. Margetts (Margetts & David 1981), and hybrids were later reported from Braunton Burrows, Devon (Margetts 1987). During field work in 1994 and 1995 populations of *G. anglica*, *G. amarella* and morphologically intermediate plants were seen flowering at the same time in Sussex and Kent.

A more detailed analysis of populations with intermediate plants and subsp. *cornubiensis* was therefore carried out in 1995. These morphological comparisons of populations have led the authors to the view that the variation in Cornwall is due to hybridisation, and that subsp. *cornubiensis* cannot be maintained as a separate subspecies.

METHODS

The comparative morphology of *Gentianella* was investigated mainly in the field. The low numbers of plants in most *G. anglica* populations mean it is undesirable to collect plants as voucher specimens or take seed for cultivation experiments (*Gentianella* has also proved difficult to cultivate; Pritchard 1959, Zopfi 1991). There is very little isozyme variation in *Gentianella* (A. Lack & Q. O. N. Kay, pers. comm. 1995), and the chromosome numbers of *G. anglica* and *G. amarella* are both 2n = 36 (J. P. Bailey, pers. comm. 1995).

Population sizes of *G. anglica* are generally very small, and variable from year-to-year partly due to its biennial habit. Wherever possible, a random sample of at least 15 plants in each separate population or sub-population (e.g. separate dune slacks) was measured, though only smaller populations were present at some sites and smaller samples available in some herbarium collections. Damaged plants were not measured. Some populations were visited twice to record early- and late-flowering plants. Pritchard (1959) does not indicate the numbers of plants included in his analysis.

Some historical herbarium specimens in **BM**, **BRISTM**, **E**, **K**, **NMW**, **OXF** and **SLBI** were examined including the type of subsp. *cornubiensis* (Perranporth, heathland by roadside, Cornwall, 20 June 1919, *F. Robinson*, **BM**). These included specimens seen by Pritchard.

After an initial screening of the characters used to separate *G. amarella* from *G. anglica* and its two subspecies, those best suited for measurement and distinguishing the taxa were narrowed down to four (Fig. 1):

1. Corolla size (mm), measured from the base of the calyx to the tip of the lobes on the terminal flower or the next largest if this was unavailable.
2. Number of internodes. It was not always easy to distinguish between the basal rosette and the lowest node; the first obvious gap was taken as the lowest internode. A number of plants had an extra solitary, small leaf above the terminal node; this leaf was ignored.
3. Height of main stem (mm), measured from the basal rosette to the terminal node on the main stem.
4. Length of terminal internode (mm), measured from the terminal node to the node below. In plants with one internode this length was measured to the basal rosette.

For some plants where flowering had finished, no corolla measurements were available. Observations of plants in Cornwall suggest that the stem, terminal internode and especially pedicels

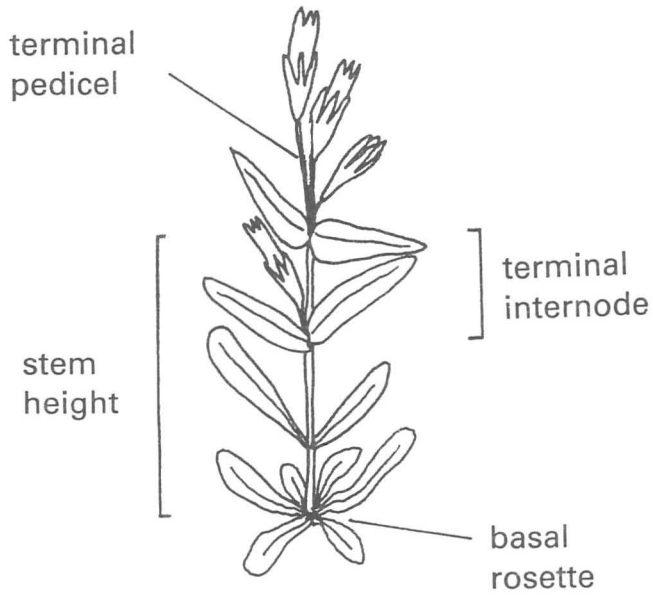

FIGURE 1. Stylised *Gentianella* plant showing measurements of stem height and the terminal internode.

may continue to grow slightly during flowering and while seed ripens. Some plants only had a basal rosette and thus had no height or terminal internode measurement. Characters 3 and 4 were used to calculate the percentage that the terminal internode contributes to the height of the stem; this is similar to Pritchard's (1959) "(log A/T Int.) + 1" character which also describes the contribution of terminal internode to the height.

For each character, the population mean and standard error were calculated.

RESULTS

The measurements from the populations investigated are summarised in Table 1 and detailed data for selected characters are plotted in Figs 2–5 for populations of *G. anglica* from eastern England and Cornwall, for *G. amarella* and for some mixed populations from England. Means for all populations are summarised in Figs 6 & 7.

As found previously by Pritchard (1959), *Gentianella* taxa are variable within populations and differ between populations. Some populations were clearly referable to *G. anglica* or *G. amarella*. There was considerably more variation in plants from Cornwall than was expected, and at least three intermediate populations were also found elsewhere in Britain. These three cases are described below.

CHARACTERS DISTINGUISHING *G. ANGLICA* AND *G. AMARELLA*

In general we agree with Pritchard (1959) on the characters used to distinguish *G. anglica* and *G. amarella*. We found that the best characters are the number of internodes, percentage of height of stem contributed by the terminal internode, and the flowering time.

G. anglica usually has distinctly fewer internodes than *G. amarella*. A population mean of less than 3 internodes is considered to be characteristic of *G. anglica* with the number ranging from 0 to 4 internodes for any one plant within a population (Figs 2 & 7). A mean of 5 or more internodes is accepted as characteristic of *G. amarella*, ranging from (4–) 5–11 internodes for individual plants in a population (e.g. Figs 4 & 7) as previously described for this taxon. Pritchard (1959) noted that the number of internodes in *G. amarella* varies quite markedly in different parts of Britain.

TABLE 1. POPULATION MEANS (± STANDARD ERROR) FOR MEASUREMENTS OF *GENTIANELLA ANGLICA*, *G. AMARELLA* AND HYBRID POPULATIONS

Population	n	Corolla length (mm)	Number of internodes	Stem height (mm)	Length of terminal internode (mm)	Percentage of height contributed by terminal internode (%)
G. anglica						
1. Braunton, 3	1	11	1	2	2	100
2. Braunton, 1	15	16·7±0·75	2·4±0·3	10·5±2·1	4·2±0·63	48·7±5·3
3. Ivinghoe, 1	15	13·1±0·11	1·3±0·11	2·7±0·47	2·4±0·43	90·4±4·8
4. Ivinghoe, 2	15	15·7±0·55	1·4±0·12	10·1±1·4	8·5±0·96	88·4±3·5
5. Trottiscliffe	5	18 ±0·4	3·0±0	24·2±1·2	10·8±2·2	45·9±10
6. Barnstead	6	17 ±0·23	2 ±0·23	19·8±7·2	11 ±3·2	66·3±7·9
7. Beachy Head	15	15 ±0·6	2·7±0·22	19·3±2·95	8·9±1·6	45·1±4·8
8. Freshwater	15	15·9±0·5	2·3±0·12	19·9±2·2	13·3±1·8	67·1±3·7
9. Edlington	15	16·1±0·4	1·5±0·21	11·3±2·6	8·3±1·4	87·1±4·9
10. Durlston Head	12	15·9±0·34	1·5±0·19	21·5±2·4	16·9±1·4	82·4±4·3
11. Ventnor	9	13·8±0·3	2·7±0·16	26·3±2·37	13·9±1·5	54·4±4·7
12. Steephill (type)	8	16·1±0·21	2·9±0·28	23·4±3·6	16·6±3·0	70·2±5·5
G. anglica, Cornwall						
13. Porthtowan, 1	14	16·9±0·33	2·8±0·2	21·9±1·9	6·8±0·78	34·3±4·4
14. Porthtowan, 2	15	14·6±0·61	1·6±0·2	6·5±1·3	3·8±0·94	68·2±7·52
15. Gear Sands, 1	15	16·3±0·5	2·5±0·16	8·3±1·12	4·7±0·65	58·6±4·1
16. Gear Sands, 2	15	13·8±0·7	2·1±0·19	4·4±0·56	2·1±0·27	56·9±6·8
17. Perranporth	15	13·6±0·5	1·5±0·3	8·7±1·5	4·5±0·62	68·0±9·3
18. Perranzabuloe	1	20	4·0	55	19	34.5
19. Perranporth	10	16 ±0·32	4·7±0·53	34·4±4·3	10·6±1·2	36·6±5·8
G. × *davidiana*						
20a. St Boniface Downs	1	15	5	67	23	34
20b. St Boniface Downs	9	16·33±0·72	4·11±0·43	53 ±6.2	27 ±2.7	56 ±5.9
21. Beachy Head	15	14·7±0·42	4·1±0·22	26·5±3·5	2·3±0·51	12·1±3·1
22. Braunton	15	17·3±0·43	3·9±0·22	24·8±2·6	7·4±0·98	33·6±4·4
23. Gear, 2	15	16·9±0·6	3·7±0·2	16·3±1·8	3·5±0·8	21·5±3·6
24. Gear 2 (DTH)	30	9·4±0·3	4·1±0·21	12·3±1·5	2·7±0·38	27·1±3·5
25. Mount	15	16·2±0·4	2·9±0·2	20 ±2·2	9·5±1·3	49·3±4·4
26. Trottiscliffe	15	17·5±0·42	4·8±0·17	40·4±3·8	4·2±0·74	11·6±1·6
G. amarella						
27. Arundel	12	13·8±0·6	6·8±0·26	31·8±4·0	5·7±1·41	17·8±2·72
28. Banstead	15	13·3±0·28	7·3±0·33	85·7±8·1	6·2±1·3	7·7±1·4
29. Braunton, 1	15	12·3±0·3	8·4±0·2	50·1±4·3	1·9±0·19	3·9±0·41
30. Braunton, 3	12	17 ±1·25	5·3±0·17	73·7±11·9	5·9±1·1	8·7±0·93
31. Gear Sands, 2	15	–	5·5±0·13	28·1±2·0	1·8±0·27	6·3±0·75
32. Noar Hill	15	15 ±0·41	8·0±0·3	88·9±7·7	8·3±1·5	9·4±1·6
33. Watergate	15	13·7±0·3	6·9±0·26	21·6±2	2·9±0·3	14·9±2
34. Beachy Head	15	16·8±0·2	6·7±0·15	25·9±1·74	3·8±0·53	14·74±1·5
35. Whitford	8	15·9±0·3	8·2±0·23	101·9±7·3	4·0±0·3	4·1±0·38

The sources are as follows: 1. Braunton, Raven Slack, Devon, 12 June 1995, T. C. G. Rich, P. A. Smith & J. Breeds. 2. Braunton, Old Met Slack, Devon, 12 June 1995, T. C. G. Rich, P. A. Smith & J. Breeds. 3. Ivinghoe top, Buckinghamshire, 20 June 1995, T. C. G. Rich & R. Maycock. 4. Ivinghoe west, Buckinghamshire, 20 June 1995, T. C. G. Rich & R. Maycock. 5. Trottiscliffe, Kent, 18 June 1995, T. C. G. Rich & E. Philp. 6. Banstead, Surrey, 17 June 1995, T. C. G. Rich & Mrs P. Livermore. 7. Beachy Head, Sussex, June 1995, T. C. G. Rich & P. G. Angold. 8. Freshwater, chalk downs, Isle of Wight, June 1910, *H. E. Fox* (**BM**). 9. Edlington, downs, Wiltshire, 1 June 1903, *E. S. Marshall* (**BM**). 10. Durlston Head, Dorset, 24 May 1889, *E. F. Linton* (**BM**). 11. Ventnor Downs, Isle of Wight, May 1891, *J. H. A. Stuart* (**BM**). 12. Steephill, chalk down, Isle of Wight, 27 May 1878, *F. Stratton* (**OXF**; isotype). 13. Porthtowan, Cornwall, 21 June 1905, *F. H. Davey* (**BM**). 14. Porthtowan,

cliff, Cornwall, 8 June 1995, T. C. G. Rich, D. T. Holyoak, J. Clitherow & R. J. Murphy. 15. Gear Sands, top, Cornwall, 9 June 1995, T. C. G. Rich, D. T. Holyoak, C. French & R. J. Murphy. 16. Gear Sands by large dune, Cornwall, 9 June 1995, T. C. G. Rich, D. T. Holyoak, C. French & R. J. Murphy. 17. Perranporth, heathland by roadside, Cornwall, 20 June 1919, *F. Robinson* (**BM**). 18. Penhale, Perranzabuloe, Cornwall, 26 March 1907, *J. F. P[ickard?]* (**BM**; type specimen of *G. anglica* subsp. *cornubiensis*). 19. Perranporth sand hills, 13 August 1915, *F. Rilstone* (**NMW**). 20. St Boniface Downs, 26 June 1925, *R. Melville* (**NMW**); 20a holotype. 20b complete sheet. 21. Beachy Head, Sussex, June 1995, T. C. G. Rich & P. G. Angold. 22. Braunton, north of Vennor's Pond, Devon, 12 June 1995, T. C. G. Rich, P. Smith & J. Breeds. 23. Gear Sands, by large dune, Cornwall, 9 June 1995, T. C. G. Rich, D. T. Holyoak, C. French & R. J. Murphy. 24. Gear Sands, Cornwall, 9 July 1995, D. T. Holyoak. 25. Mount, Cornwall 9 June 1995, T. C. G. Rich, D. T. Holyoak, C. French & R. J. Murphy. 26. Trottiscliffe, Kent, 18 June 1995, T. C. G. Rich & E. Phillip. 27. Arundel Park, Sussex, 21 July 1995, T. C. G. Rich. 28. Banstead, Surrey, 28 August 1995, T. C. G. Rich. 29. Braunton, Old Met Slack, Devon, 20 September 1995, T. C. G. Rich. 30. Braunton, Raven Slack, Devon, 20 September 1995, T. C. G. Rich. 31. Gear Sands by large dune, Cornwall, 9 June 1995, T. C. G. Rich, D. T. Holyoak, C. French & R. J. Murphy. 32. Noar Hill, Hampshire, 17 August 1995, T. C. G. Rich. 33. Watergate near Newquay, 30 August and 26 September 1901, *A. O. Hume* (**SLBI**). 34. Beachy Head, 21 August 1907, *A. O. Hume* (**SLBI**). 35. Whitford Burrows, Glamorgan, 5 August 1995, T. C. G. Rich, M. Kitchen & Q. O. N. Kay.
n: number of plants.

In *G. anglica*, the terminal internode is generally longer than the other internodes and when present contributes a mean of 40–100% of the height of the stem, ranging from (20%–) 30%–100% for individual plants (Figs 2 & 7). In *G. amarella* the terminal internode is usually shorter than the other internodes; it usually contributes a mean of less than c. 20% to the height of the stem, ranging from 1%–c. 35% in individual plants, the latter exceptionally (Figs 2 & 7).

There is a strong negative relationship between the number of internodes and the percentage of the stem height contributed by the terminal internode (Fig. 7).

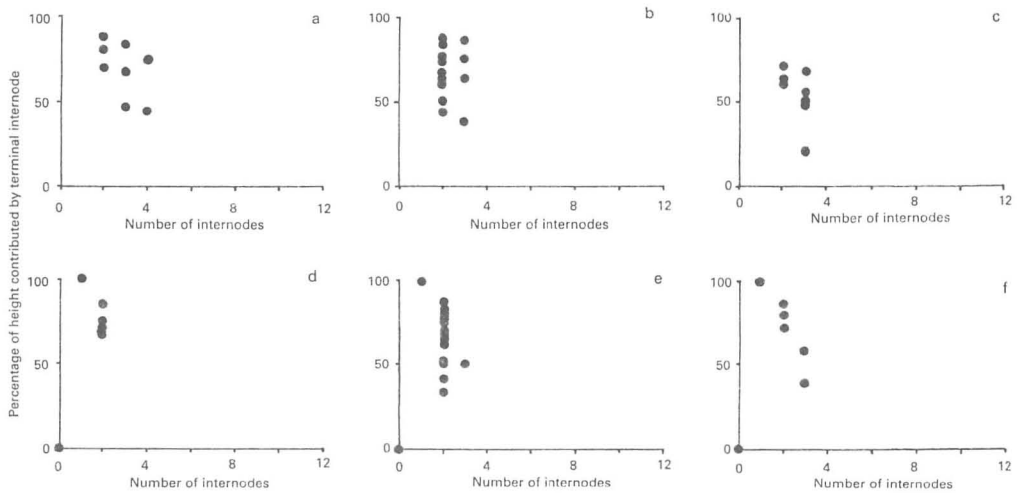

FIGURE 2. Number of internodes plotted against percentage of height contributed by the terminal internode to the height of the stem for populations of *Gentianella anglica*. a. Steephill, chalk down, Isle of Wight, 27 May 1878, *F. Stratton* (**OXF**; lectotype). b. Freshwater, chalk downs, Isle of Wight, June 1910, *H. E. Fox* (**BM**). c. Ventnor Downs, Isle of Wight, May 1891, *J. H. A. Stuart* (**BM**). d. Durlston Head, Dorset, 24 May 1889, *E. F. Linton* (**BM**). e. Ivinghoe, Buckinghamshire, 20 June 1995. f. Edlington, downs, Wiltshire, 1 June 1903, *E. S. Marshall* (**BM**).

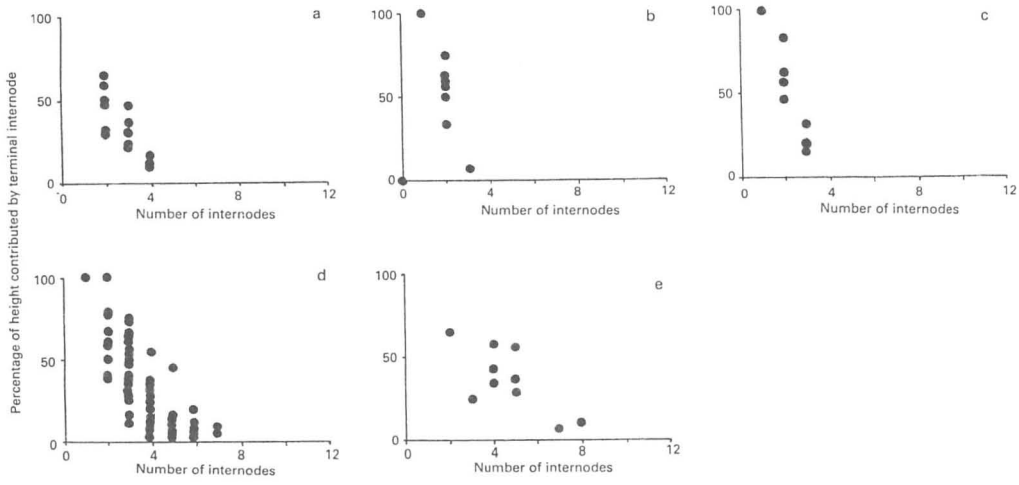

FIGURE 3. Number of internodes plotted against percentage of height contributed by the terminal internode to the height of the stem for populations of *Gentianella anglica* from Cornwall. a. Porthtowan, Cornwall, 21 June 1905, *F. H. Davey* (**BM**). b. Porthtowan, cliff, Cornwall, 8 June 1995. c. Perranporth, heathland by roadside, Cornwall, 20 June 1919, *F. Robinson* (**BM**). d. Perranporth, Cornwall, 9 June and 9 July 1995. e. Perranporth, Cornwall, 13 August 1915, *F. Rilstone* (**NMW**).

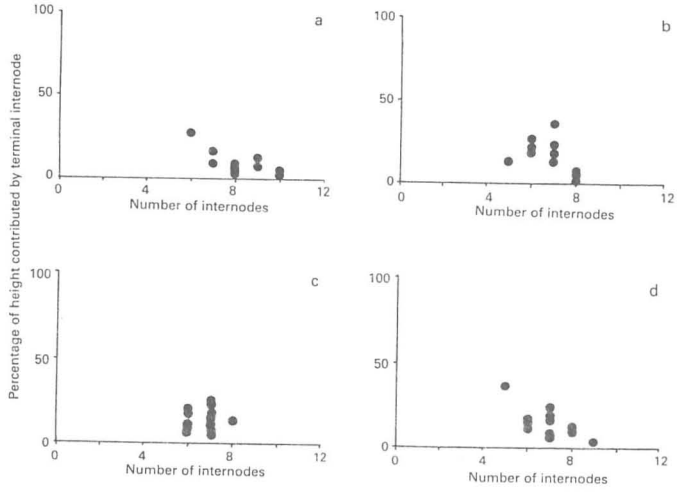

FIGURE 4. Number of internodes plotted against percentage of height contributed by the terminal internode to the height of the stem for populations of *Gentianella amarella*. a. Noar Hill, Hampshire, 17 August 1995. b. Arundel Park Sussex, 21 July 1995. c. Beachy Head, 21 August 1907, *A. O. Hume* (**SLBI**). d. Watergate near Newquay, 30 August and 26 September 1901, *A. O. Hume* (**SLBI**).

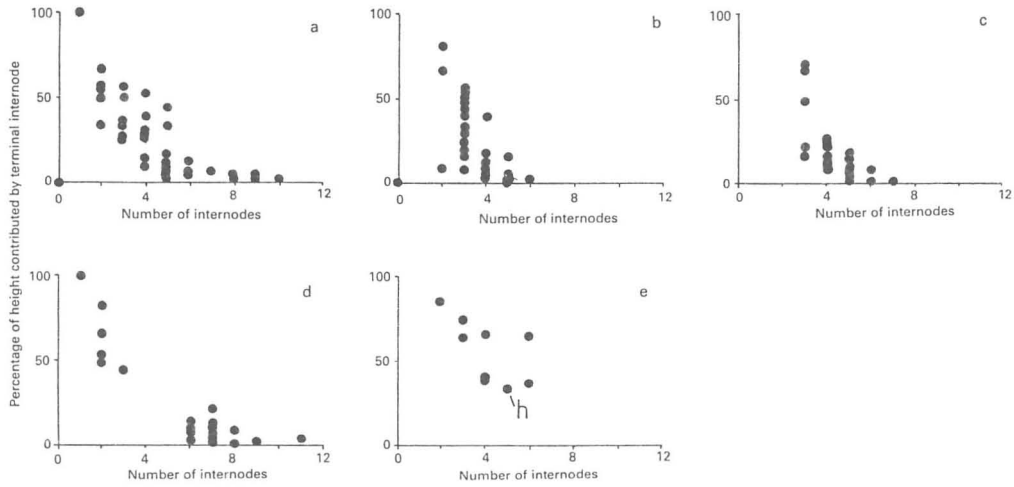

FIGURE 5. Number of internodes plotted against percentage of height contributed by the terminal internode to the height of the stem for populations of *Gentianella* from elsewhere in southern England. a. Braunton, Devon, 12 June and 20 September 1995. b. Beachy Head, Sussex, June 1995. c. Trottiscliffe, Kent, 18 June 1995. d. Banstead, Surrey, 17 June and 28 August 1995. e. St Boniface Downs, Isle of Wight, 26 June 1925, *R. Melville* (**NMW**); h = holotype of *G.* × *davidiana*.

Both species can flower together and have been observed doing so. *G. anglica* flowers earlier in the year than *G. amarella*, usually from late April to June, but extending from early March to the middle of July. *G. amarella* usually flowers from early July, though an early-flowering form is known in south Wales and south-west England (Pritchard 1959; observations by L. J. Margetts).

Of the characters not investigated in detail, *G. anglica* is usually smaller and more branched from the base than *G. amarella*. *G. anglica* tends to have narrower leaves; though it is a very variable character with much overlap, the vegetative plants cannot be determined with certainty using this character. The terminal pedicel of *G. anglica* contributes more to the plant height than in *G. amarella*, its calyx teeth are shorter than the tube (this character is of no use in distinguishing the taxa), and it usually has more unequal calyx teeth than in *G. amarella* though the variation in *G. amarella* means that this is also of little practical use in distinguishing the species. There is also a subtle colour difference in the flowers which is difficult to describe in words; *G. anglica* tends to have flowers towards the blue end of violet, whilst in *G. amarella* they tend to be towards the purple end of violet.

CHARACTERS DISTINGUISHING *G. ANGLICA* SUBSP. *ANGLICA* AND SUBSP. *CORNUBIENSIS*

The main characters used by Pritchard (1959) to distinguish *G. anglica* subsp. *cornubiensis* from subsp. *anglica* were its higher average number of internodes, its relatively shorter terminal internodes, its longer corollas, the presence of axillary flowers, and its plants seldom being branched from the base.

However, plants morphologically indistinguishable from subsp. *anglica* elsewhere in England were found near Porthtowan and Perranporth, Cornwall (Fig. 7). Some populations near Perranporth were mixed with more variable plants, some of which agreed with the description of subsp. *cornubiensis*, while others agreed with *G. amarella* (otherwise a rare plant in Cornwall) (Fig. 3d). There is almost complete overlap between the corolla lengths, number of internodes and percentage of height contributed by the terminal internode of *G. anglica* plants from Cornwall (Porthtowan, Perranporth, Gear Sands, Mount) and *G. anglica* and intermediates from elsewhere (Table 1).

The length of the corolla does not correlate with other characters or with the place of origin of plants, and there is much overlap between the different populations (Fig. 6). The type specimen of

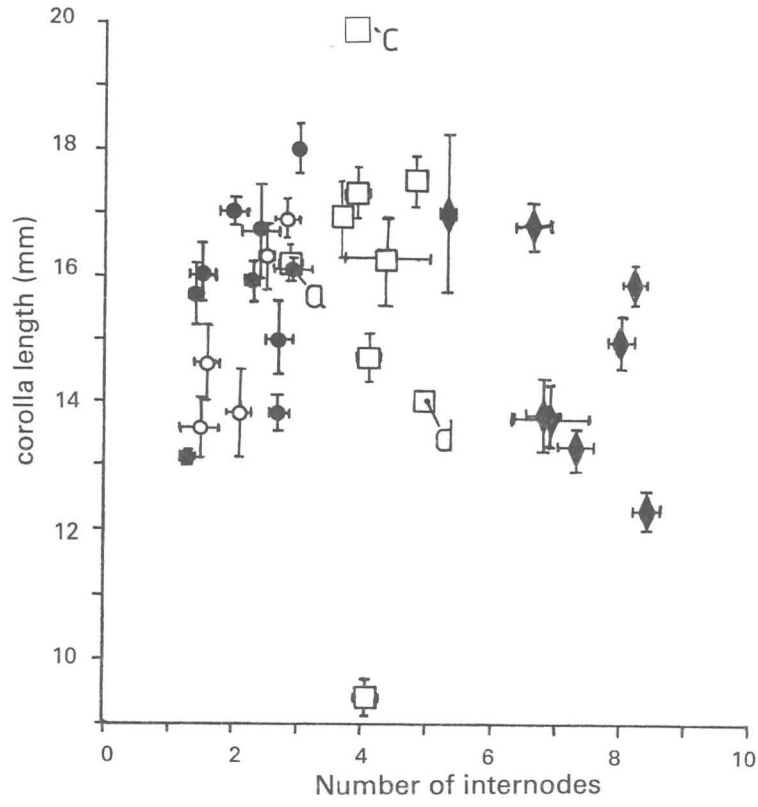

FIGURE 6. Number of internodes plotted against corolla length (mm) for populations of *Gentianella*. Points are population means and standard errors (see Table 1). ○ *G. anglica* from Cornwall; ● *G. anglica* from elsewhere in Britain; ◆ *G. amarella*; □ intermediates between *G. anglica* and *G. amarella*; a, lectotype of *G. anglica*; c, holotype of subsp. *cornubiensis*; d, holotype of *G.* × *davidiana*.

subsp. *cornubiensis* has one of the longest corollas seen and is not representative of other Cornish plants. Another set of corolla measurements from Gear Sands on 9 July 1995 were much shorter than normal, probably due to the effects of drought.

Thus Cornish *G. anglica* populations cannot be distinguished satisfactorily from *G. anglica* from elsewhere using the characters investigated. Indeed, the population from the cliffs at Porthtowan (Table 1, no. 14), regarded by Pritchard (1972) as "the pure facies of *cornubiensis*", has fewer internodes and a smaller corolla than plants from the type locality of subsp. *anglica* from Steephill on the Isle of Wight (Table 1, no. 12) (Fig. 6).

MIXED POPULATIONS

Data from four mixed populations some of which have intermediate plants are given in Table 1 and Fig. 5.

The populations at Braunton were quite variable and included individual plants which agreed well with *G. anglica* and *G. amarella*, but there was complete intergradation between them and with many intermediates (Fig. 5a). The populations at Beachy Head, Sussex were predominantly *G. anglica* and intermediates (Fig. 5b) but were not sampled later in the season. The Trottiscliffe, Kent population was similarly sampled only once but contained predominantly intermediate plants with a few which could be regarded as *G. anglica* (Fig. 5c). No intermediates were present at Banstead, Surrey where plants typical of good *G. anglica* and *G. amarella* occur (Fig. 5d).

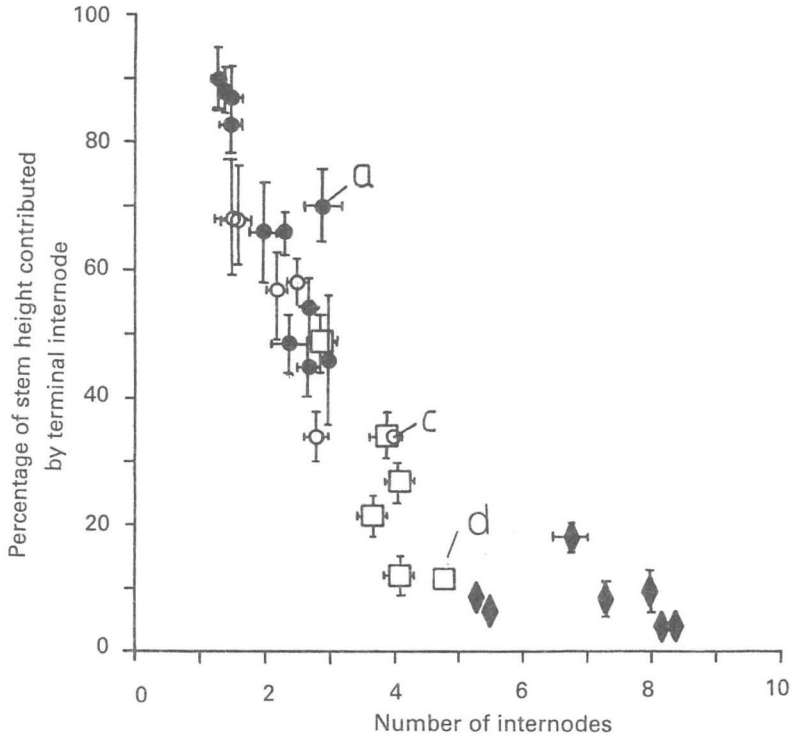

FIGURE 7. Number of internodes plotted against percentage of height contributed by the terminal internode to the height of the stem for populations of *Gentianella*. Points are population means and standard deviations (see Table 1). ○ *G. anglica* from Cornwall; ● *G. anglica* from elsewhere in Britain; ◆ *G. amarella*; □ intermediates between *G. anglica* and *G. amarella*; a, lectotype of *G. anglica*; c, holotype of subsp. *cornubiensis*; d, holotype of *G.* × *davidiana*.

The pattern of variation was similar in these populations to that observed near Perranporth (Fig. 3d).

DISCUSSION

GENTIANELLA ANGLICA

We agree with previous authors (Pugsley 1936; Pritchard 1959) that *Gentianella anglica* is a distinct species from *G. amarella*: plants which flower early have few internodes and an elongated terminal internode (Table 2).

Other authors have regarded *G. anglica* as an early-flowering form of *G. amarella* (e.g. McClintock 1972). Early-flowering forms of *G. campestris*, *G. germanica* and *G. uliginosa* have been noted (Briggs 1870; Trimen 1878; Zopfi 1991), and early-flowering plants could also occur occasionally in *G. amarella*. Indeed, one early-flowering plant of a *Gentianella* was found by E. Philp at Eccles, Kent in 1994 (Rich & Philp 1995); this had a contracted terminal internode, and could have simply been an odd *G. amarella*. Hence it cannot be assumed that all early-flowering plants are *G. anglica*. Seasonal-flowering variants of *G. amarella* are recorded for Europe by Pritchard & Tutin (1972) and Zopfi (1991) but have not been reported in Britain. Further investigation and observation of this phenomenon is required.

TABLE 2. CHARACTERS DISTINGUISHING *GENTIANELLA AMARELLA*, *G. ANGLICA* AND *G. × DAVIDIANA* (FIGURES ARE POPULATION MEANS)

	G. amarella	*G. × davidiana*	*G. anglica*
Number of internodes	5–11	3–5	0–3
Percentage of height contributed by terminal internode	1–20%	10%–40%	40–100%
Main flowering time	July–October	May–July (–? August)	March–July
Terminal pedicel	Short	Intermediate	Long

GENTIANELLA ANGLICA SUBSP. *CORNUBIENSIS* AND OTHER MIXED POPULATIONS

The investigations of Cornish and other populations has two main conclusions.

First, there is more variation present in Cornish populations than has previously been recognised. Some populations investigated in the field in 1995 are morphologically similar to *G. anglica* from other parts of England. It is therefore impossible to maintain the concept that the Cornish plants are morphologically and ecologically different or disjunct in distribution from other *G. anglica* populations. Surprisingly few sheets of typical, small plants of *G. anglica* from Cornwall have been seen in the limited number of herbarium collections available, but they are present. Collectors may have gathered the larger, more obvious, later-flowering plants; these are more likely to be hybrids and may not be representative of the populations as a whole. Pritchard (1959) appears to have investigated the specimens available but saw few plants in the wild.

Second, there are plants intermediate between *G. anglica* and *G. amarella* near Perranporth in Cornwall (the type locality of subsp. *cornubiensis*) and elsewhere in England. The simplest explanation of the intermediates is that they are hybrids between *G. anglica* and *G. amarella*. Some of these populations show continuous variation from one species to the other. Intermediate plants at Gear Sands near Perranporth in 1995 were highly fertile, and the populations show signs of introgression, a phenomenon also known in other *Gentianella* populations (Pritchard 1959, 1961).

Cornish plants may therefore either be *G. anglica* or the hybrid, and cannot be referred to a distinct subspecies. The type specimen of *G. anglica* subsp. *cornubiensis* is, with the exception of its long corolla which is not typical of Cornish plants, indistinguishable from other intermediates between *G. anglica* and *G. amarella* and is regarded by us as hybrid.

Given the importance of conservation of *G. anglica* and the need to distinguish between pure *G. anglica* and the hybrids, a name for the intermediates is desirable.

Gentianella amarella (L.) Boerner × **G. anglica** (Pugsley) E. F. Warb. = **G. × davidiana** T. C. G. Rich, **hybr. nov.**

HOLOTYPUS: The lower right hand specimen above the label is selected as the holotype on the sheet collected from St Boniface Downs, Isle of Wight (v.c. 10), 26 June 1925, *R. Melville* (**NMW**). The holotype has five internodes and the terminal internode contributes 34% to the height of the stem. The other eight specimens on the sheet show the typical range of variation present in mixed flowering populations.

SYNONYMS

Gentianella anglica (Pugsley) E. F. Warb. subsp. *cornubiensis* Pritchard (Pritchard 1959). *G. cornubiensis* (Pritchard) Pritchard (Pritchard 1972), **nomen. inval.**

DESCRIPTION

Hybrida fertilis inter *Gentianella amarella* (L.) Boerner et *G. anglica* (Pugsley) E. F. Warb. inter parentes media. Internodia 3–5. Internodium terminale c. 10–40% totius longitudinis caulis. Corolla (9·4–) 14–18 (–20) mm.

A fertile hybrid between *Gentianella amarella* and *G. anglica* intermediate between the parents. Internodes 3–5. Terminal internode forming c. 10–40% of total stem length. Corolla length of (9·4–) 14–18 (–20) mm.

Named in honour of R. (Dick) W. David (1912–93) who did much to champion the cause of plant conservation in Britain and botanised extensively in Cornwall for many years (Davies 1994).

DISTRIBUTION

Currently known only from England; see Fig. 8. V.c. 1, West Cornwall. Perranporth sand hills, 13 August 1915, *F. Rilstone* (**NMW**). Penhale Sands, huge hybrid swarm, 1966, L. J. Margetts (Margetts & David 1981). Gear Sands and Mount, 1995, T. C. G. Rich, D. T. Holyoak, C. French & R. J. Murphy. V.c. 4, North Devon. Braunton Burrows, 1986, L. J. Margetts & W. H. Tucker (Margetts 1987); 1995, T. C. G. Rich, P. A. Smith & J. Breeds. V.c. 10, Wight. St Boniface Downs, 26 June 1925, *R. Melville* (**NMW**). V.c. 14, East Sussex. Castle Hill N.N.R., 1994, T. C. G. Rich & S. A. Richardson. Beachy Head, 1995, T. C. G. Rich & P. G. Angold. V.c. 16, West Kent, Trottiscliffe, 1995, T. C. G. Rich & E. G. Philp.

In addition it is possible that plants at Stackpole, Pembrokeshire (v.c. 45) and Scottesthorpe Quarry, Lincolnshire (v.c. 53) are this hybrid but they require further investigation from a larger sample size than hitherto available.

TYPIFICATION OF *GENTIANA AMARELLA* L. VAR. *PRAECOX* TOWNSEND

The basionym for *Gentianella anglica* is *Gentiana amarella* var. *praecox* Townsend (1883) as described by Pritchard (1959).

Townsend (1883) cites a pre-Linnaean polynomial *Gentianella fugax verna seu praecox*, *Ray Synop.*, ed. 3, 275 (Ray 1724) as the source of his epithet var. *praecox*. This third edition of Ray's *Synopsis* was edited by J. Dillenius at Oxford. There are no specimens in **herb. Dillenius** at **OXF**, but there is a specimen in **herb. C. Du Bois** (also in **OXF**) labelled "*Gentianella fugax verna seu praecox* accepi a D. Fitz-Roberts" which corresponds to the reference of plants found by Fitz-Roberts near Kendal, Cumbria (Ray 1724) and which would probably have been seen by Dillenius; this specimen is *G. campestris* (L.) Boerner.

Townsend also cites four localities for his var. *praecox* on the Isle of Wight, and for one of them, Steephill, refers to specimens collected by F. Stratton, noting "I have lately received dried specimens in flower gathered May 27, 1878". Townsend's main herbarium is in **SLBI** with other parts in **K**, **OXF**, **NMW** and **WAR** (Kent & Allen 1984). There are no corresponding specimens in **SLBI**, **NMW** or **WAR** but **OXF** and **K** contain sheets collected by F. Stratton from Steephill on 27 May 1878. Stratton (1878) stated "I have dried a good number of specimens for distribution through the Botanical Exchange Club" and duplicates are also held in **BM** and **CGE** and possibly elsewhere.

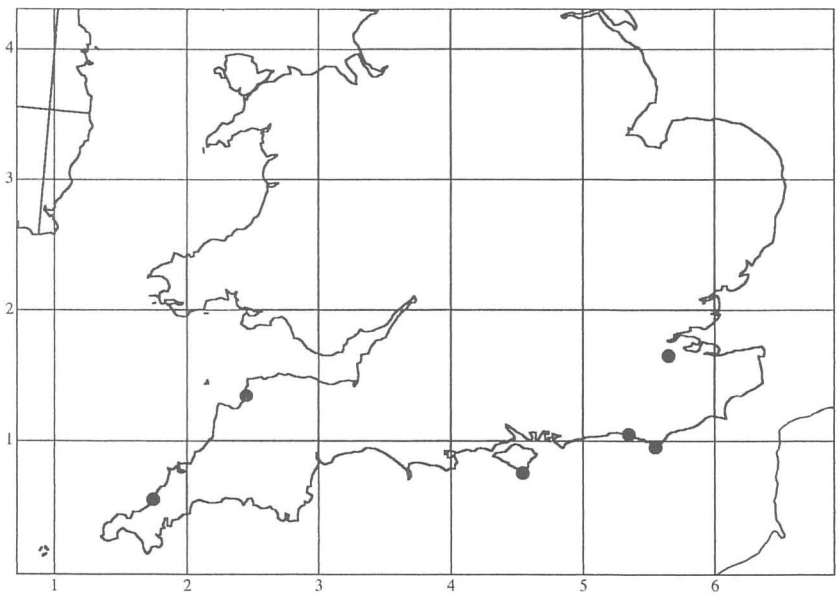

FIGURE 8. Distribution of *Gentianella* × *davidiana* in southern England.

A lectotype has been selected from the two sheets held in **OXF**. One has three specimens collected by Stratton on 27 May 1878 and two on 17 August 1878, but also has many specimens from different localities added by G. C. Druce; it is not clearly labelled and is rejected. The second sheet has eight specimens collected by Stratton on 27 May 1878, and five in fruit on 17 August 1878, and is more clearly labelled. The specimen on the left hand side immediately above the label numbered '163' in pencil by N. M. Pritchard is here selected as the lectotype of *Gentiana amarella* var. *praecox* Townsend (1883).

The lectotype is a typical example of *G. anglica* with a corolla 16 mm long, 3 internodes, a stem 37 mm tall and an upper internode 25 mm long forming 76% of the stem height.

IS HYBRIDISATION A THREAT TO CONSERVATION OF *G. ANGLICA*?

As hybridisation is believed to be responsible for the loss of range in *G. germanica* (Pritchard 1961) and the Bristol Channel race of *G. amarella* may indicate some past introgression from *G. uliginosa* (Pritchard 1959), hybridisation could also be a threat to survival of pure *G. anglica* colonies.

With the exception of some Cornish sites, all populations of *G. anglica* seen occur with *G. amarella*, either intermixed or nearby. Some populations observed in 1995 seem to be largely hybrid swarms (e.g. Trottiscliffe and Beachy Head). Typical *G. anglica* still occurs near Perranporth despite evidence from the herbarium specimens of hybridisation for nearly 100 years. Although there would seem to be considerable potential for hybridisation it has only been observed in a few populations to date. The species seem to be maintained as distinct by their different flowering times, despite the short period of overlap.

Thus the current evidence indicates hybridisation may be a threat to survival of some but not all populations of *G. anglica*. Further monitoring of the proportion of hybrids in populations and studies on the pollination ecology would be valuable.

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