# An account of the Whitebeams (*Sorbus* L., Rosaceae) of Cheddar Gorge, England, with description of three new species

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ABSTRACT

An account of the Whitebeams (*Sorbus* L., Rosaceae) of Cheddar Gorge, Somerset, England is given. *Sorbus aria* is abundant, and variable. *Sorbus anglica* and *S. eminens* are quite widespread, but *S. porrigentiformis* is rarer. Three new polyploid species endemic to the gorge are described supported by DNA analysis: *S. cheddarensis, S. eminentoides* and *S. rupicoloides*. The gorge is one of the most important sites for *Sorbus* in Britain. Browsing is affecting significant numbers of *Sorbus* trees, and grazing is affecting regeneration.

KEYWORDS: Endemic, goats, microsatellites, Somerset.

INTRODUCTION

Cheddar Gorge in the Mendips, Somerset, is Britain's largest gorge and one of its best known limestone features. The Carboniferous Limestone cliffs tower up to c. 120 m above the gorge bottom on the south side, with extensive screes, slopes and smaller cliffs on the north side. The gorge is part of the Cheddar Complex Site of Special Scientific Interest (SSSI) (which includes the former Cheddar Gorge SSSI), designated for a suite of rare plants, animals and communities and the geological interest. The north side is owned by the National Trust, the south side by the Longleat Estate.

Cheddar Gorge has been known for many years as a rich botanical site with nationally rare plants such as *Dianthus gratianopolitanus* Vill., *Galium fleurotii* Jord. and the Cheddar endemic *Hieracium stenolepiforme* (Pugsley) P. D. Sell & C. West, and other uncommon species such as *Geranium purpureum* Vill., *Cerastium pumilum* Curtis and *Sedum forsterianum* Sm. The gorge is also home to rare *Sorbus* species, but there is relatively little data on them compared to other Cheddar rare plants. In their review of the rare plants in Cheddar, FitzGerald & McDonnell (1997) pointed out that the gorge was of great importance for *Sorbus* and recommended a full audit of the species present.

The common and widespread *Sorbus aria* (L.) Crantz has been known in Cheddar Gorge for many years and is abundant. *Sorbus anglica* Hedl. was first recorded in 1901 by A. Ley (Roe 1981), and has always been regarded as rare. *Sorbus porrigentiformis* E. F. Warb. was first confirmed in 1966 from material collected by A. W. Gravestock, and is also rare (Green *et al*. 1997). Surprisingly, *S. eminens* E. F. Warb., now known to be the second commonest species in the gorge, was only first reported by Proctor & Groenhof (1992), though it had been previously collected without a name by E. C. Wallace in 1935 and by F. Rose in 1948. *Sorbus aucuparia* L. and *S. torminalis* (L.) Crantz are known in the Cheddar area, but neither has been recorded from the gorge itself (Roe 1981; Green *et al.* 1997).

Cheddar Gorge and the surrounding area were grazed for many centuries by cattle, sheep and goats, when trees and scrub were largely confined to the cliffs. After the Second World War, stock grazing decreased and scrub species such as *Cornus sanguinea* L., *Crataegus monogyna* Jacq., *Rhamnus cathartica* L., *Taxus baccata* L., *Viburnum lantana* L. and *Sorbus aria* began to invade the grasslands, the scrub eventually developing locally into secondary woodland. The whitebeams, especially *S. aria*, benefited during this time and spread into the grasslands. Scrub clearance has been carried out to maintain open grasslands for the rare herbaceous species, but as rare whitebeams

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were known to be present, few *Sorbus* trees were cleared, and soon small groves of whitebeams were quite frequent in the gorge. To enable some *S. aria* trees to be cleared without affecting the rare *Sorbus* species, L. Houston was commissioned to survey the rare whitebeams by the National Trust in 2005 and by the Longleat Estate in 2006. Full details are given in Houston (2006, 2009) and the results are summarized here with descriptions of three new species found during the surveys.

## METHODS

### DNA MICROSATELLITES

Bud samples were collected for DNA analysis from ten *S. aria,* six *S. anglica,* six *S. eminens* and ten *S. cheddarensis* during the autumn of 2005 and from a single *S. eminentoides* and a single *S. rupicoloides* in 2006. They were placed in separate bags that were sealed and stored at 4°C for four days after which they were transferred to a freezer and stored at -20°C until needed. DNA was extracted using Qiagen® DNeasy® Plant Mini Kit 2004 protocol. Four nuclear microsatellite loci were amplified using two sets of primers developed for *Malus* × *domestica* (Gianfranceschi *et al.* 1998) and two pairs developed for *Sorbus torminalis* (Oddou-Muratorio *et al*. 2001). Each of these primer-pairs were redesigned, from sequences deposited in Genbank, to facilitate amplification of a wide range of *Sorbus* taxa (Table 1). Forward primers were labelled with fluorescent dyes. Reverse primers were tailed with a non-target-specific sequence to overcome allele-sizing problems associated with the primer sequence dependant adenylation of PCR products by most *Taq* polymerases (Brownstein *et al*. 1996). PCR reaction mixtures (20µl total volume) contained the following components/concentrations: one unit of Hotstart Taq DNA polymerase (Qiagen), 2µl of 10× reaction buffer (Qiagen), 2 mM of each dNTP (Bioline), with 0·2µM of each forward and reverse primer and 20–50 ng of genomic DNA. PCR reactions were performed in a MJ-Research PTC-200 Peltier Thermal Cycler. The following programme was used: 1 step at 95°C for 15 minutes followed by 35 cycles of 1 minute at 94°C, 1 minute at 55°C, 1 minute and 30 seconds at 72°C, and a 10 minute extension step of 72°C. PCR amplification products from the labelled primers were separated on a laser based capillary electrophoresis instrument, the ABI 3730xl. Alleles were sized relative to an internal size standard and resulting electropherograms were analysed using GeneMarker genotyping software. Each individual electropherogram was scored manually.

### DATA ANALYSIS

The most appropriate measure to study genetic diversity for apomictic taxa is to compile and compare multilocus genetic phenotypes (Gornall 1999). Therefore, for each individual analysed in this study, microsatellite allele phenotypes were determined for each of the four amplified loci. These data were combined to construct the multilocus phenotypes of each sample. The numbers of individuals belonging to each multilocus phenotype were determined for each species. Ploidy level estimates were based on the maximum number of displayed alleles at a single locus. For example for *S. cheddarensis*, three alleles were displayed at

TABLE 1. NUCLEOTIDE SEQUENCES OF NUCLEAR AND CP DNA PRIMERS USED IN THIS STUDY

| Locus | Dye | Primers | Repeat | Na |
|---|---|---|---|---|
| CH01F02 [I] | 6-Fam | Forward CCACATTAGAGCAGTTGAGGATGA<br>Reverse ATAGGGTAGCAGCAGATGGTTGT | $(GA)_{22}$ | 9 |
| CH02D11 [I] | Vic | Forward AAATAAGCGTCCAGAGCAACAG<br>Reverse GGGACAAAATCTCACAAACAGA | $(AG)_{21}$ | 10 |
| MSS5 [II] | 6-Fam | Forward CCCCAACAACATTTTTCTCC<br>Reverse CCTCTCGCTCTTTGCCTCT | $(GA)_{19}$ | 12 |
| MSS16 [II] | Vic | Forward ATGTCACATCTCTCCCCTTGTGT<br>Reverse TTTTGCCCTCAAAGAATGCCTTA | $(GA)_{28}$ | 5 |

[I]Microsatellite Primers derived from *Malus* × *domestica* DNA (Gianfranceschi *et al.* 1998)
[II] Microsatellite Primers derived from *S. torminalis* (Oddou-Muratorio *et al.* 2001).
Na = the number of alleles amplified across all taxa.

locus F02 suggesting it is at least triploid. Each multilocus phenotype was transformed into binary code and metric distances were computed between them using Dice similarity coefficients (Dice 1945) with NTSYSPC version 2.11a software (Rohlf 2002). The relationships among the multilocus phenotypes were visualised using Principal Coordinate Analysis (PCO) with NTSYSPC software (Rohlf 2002).

MORPHOLOGY AND DESCRIPTIONS OF NEW SPECIES

Broad leaves from the short, vegetative shoots in sunlit situations, excluding the oldest and youngest leaf (Aas *et al.* 1994), were measured on herbarium material of the three new taxa in **NMW**. Fruits were measured on fresh material, and the colours matched against the Royal Horticultural Society colour charts (Royal Horticultural Society 1966).

POLLEN STAINABILITY

Pollen stainability, an estimate of potential pollen viability (Rich 2009), was investigated using Alexander's Stain (Alexander 1969) on the flowering collections available. Anthers were removed from herbarium specimens with tweezers under a low-power binocular microscope, and placed on a slide with a drop of Alexander's Stain, warmed briefly on the hotplate, then broken up with the tweezers. The preparation was then covered with a cover-slip and replaced on the hotplate to improve the uptake of the stain. The slides were then examined under a high-power compound microscope for areas of dense pollen grains. Potentially viable grains were counted as those which were large and rounded-triangular with cell walls which stained green and with cytoplasm inside which stained uniformly bright red. Small deformed grains or those staining green only with very little or no red staining inside (i.e. no cytoplasm) were considered infertile. The numbers of pollen grains counted are cited for individual trees.

SOIL PH

Soil samples were collected from around the roots of a few trees in 2007, and air-dried. The pH was subsequently measured on a 50 soil:50 distilled water mixture with a calibrated pHep2 Hanna pocket-sized pH meter.

FIELD SURVEY

Field surveys were mainly carried out by L. Houston during the period 14 July to 10 August 2005, and 24 August to 27 October 2006, with extra visits with T. Rich during 2005, 2006 and 2007. Existing records were also used to direct surveys (e.g. M. C. F. Proctor unpublished 1989 data held at **NMW**; FitzGerald & McDonnell 1997; T. Rich unpublished data 2001–2004). Figure 1 shows the areas of the gorge searched;

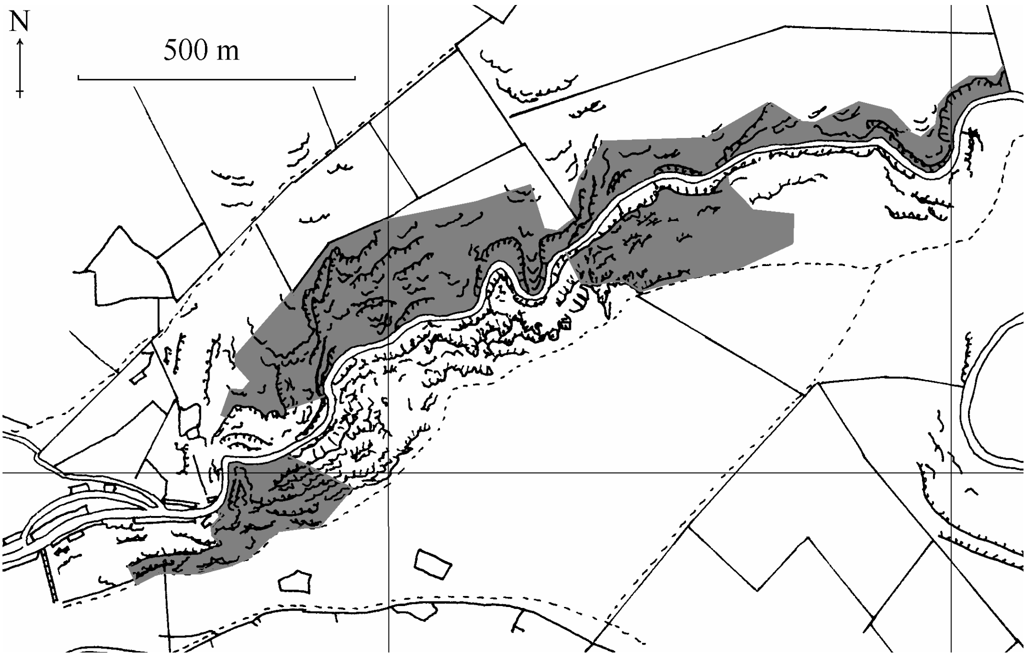


FIGURE 1. Areas of Cheddar Gorge surveyed for *Sorbus*.

the sheer size and scale of the gorge meant that it was not possible to survey it comprehensively, and thus the coverage shown in Figure 1 must be borne in mind when interpreting the distribution maps.

All locations and details of the rarer taxa were recorded, but for *S. aria* which is frequent throughout the site usually only brief details were noted. For the rarer trees, GPS grid references were recorded using a Garmin Etrex hand-held unit where possible. Tree height was estimated in metres, and the girth of accessible trees measured with a tape measure at 1·3 m. Notes were made on the growth form (maiden or coppice), and damage by goats, from conservation management work or from landscape work was noted. Numerous photographs were taken.

Most trees were named in the field. Trees on cliffs or with leaves high in the canopy were either sampled using a long-handled pruner or identified as far as possible with binoculars. No abseiling or climbing with or without ropes was undertaken. It was not possible to name with certainty many trees which were inaccessible on cliffs or trees which had lost leaves. Voucher specimens for some rarer trees or those requiring a second opinion were collected and named in consultation with T. Rich; the vouchers have been deposited in **NMW**.

## RESULTS

### NUCLEAR MICROSATELLITE ANALYSIS

In total, 36 alleles from four microsatellite loci were amplified from 34 adult *Sorbus* individuals. The number of alleles amplified at each locus across all taxa ranged from five at locus MSS16 to 12 at locus MSS5 (Table 1). The total number of different alleles displayed by each taxon ranged from nine for *S. cheddarensis* to 15 for *S. rupicoloides* (Tables 2 and 3). When data from all loci were combined, the total number of detectable multilocus phenotypes scored across all taxa was 15. *Sorbus anglica* and *S. eminens* each consisted of just a single multilocus phenotype, as would be expected of a clonally reproducing species (Table 3). Similarly each of the *S. cheddarensis* individuals shared the same multilocus phenotype, supporting the hypothesis that *S. cheddarensis* is a novel *Sorbus* species that, like *S. anglica* and *S. eminens*, reproduces apomictically (Table 3). In contrast, each *S. aria* individual had a unique

TABLE 2. GENETIC DIVERSITY MEASURES FOR THE CHEDDAR GORGE *SORBUS* TAXA

| Taxon | Ni | Xo | Xe | A' | Ng |
|---|---|---|---|---|---|
| *S. aria* | 10 | 2 | 2 | 14 | 10 |
| *S. anglica* | 6 | 3 | 4 | 12 | 1 |
| *S. cheddarensis* | 10 | 3 | | 9 | 1 |
| *S. eminens* | 6 | 4 | 4 | 12 | 1 |
| *S. eminentoides* | 1 | 4 | | 13 | |
| *S. rupicoloides* | 1 | 4 | | 15 | |

Ni = number of individuals sampled; Xo = observed ploidy, based on the maximum number of displayed alleles at a single locus; Xe = expected ploidy, based on published cytological work; A' = total number of different alleles seen across all loci; Ng = number of multilocus phenotypes detected.

TABLE 3. MULTILOCUS PHENOTYPES FOR THE CHEDDAR POLYPLOID *SORBUS* TAXA AND THE TOTAL ALLELE POPULATION FOUND AT EACH LOCUS FOR *S. ARIA*

| Taxon | Alleles at locus: | | | |
|---|---|---|---|---|
| | F02 | MSS5 | D11 | MSS16 |
| *S. aria* | 196,198,200,206 | 126,132,134,144,146 | 163,177,193 | 166,172 |
| *S. anglica* | 192,202,206 | 126,136,142 | 157,159,205 | 162,166,170 |
| *S. cheddarensis* | 196,206,208 | 132,140 | 159,193 | 166,178 |
| *S. eminens* | 196,202,206 | 120,126,140,142 | 159,163,169 | 166,178 |
| *S. eminentoides* | 196,202,208 | 120,132,136,140 | 159,161,205 | 166,168,178 |
| *S. rupicoloides* | 200,204,208,214 | 126,132,138,180 | 159,169,175,189 | 166,168,170 |

multilocus genotype, as would be expected of an obligate out-crossing diploid species. All individuals genotyped for *S. aria* displayed either one or two alleles at each locus, confirming them to be diploid. In contrast, each individual genotyped among *S. anglica*, *S. cheddarensis, S. eminens*, *S. eminentoides* and *S. rupicoloides* displayed more than two alleles (usually three or four) at a minimum of one locus, confirming that they were all polyploid (Table 3). The triploid ploidy level of *S. anglica* and the tetraploid ploidy level of *S. eminens* indicated by these alleles are supported by existing chromosome counts from Cheddar (Bailey *et al*. 2008). The alleles suggest that *S. cheddarensis* is at least triploid, and *S. eminentoides* and *S. rupicoloides* tetraploid, which require cytological confirmation.

Genetic similarity among the 15 multilocus phenotypes was calculated and the subsequent similarity matrix was used as the input for Principal Coordinate Analysis (PCO). In addition to the 15 multilocus phenotypes found during the current study the multilocus phenotypes of *S. porrigentiformis* and *S. rupicola*, found during a previous study of *Sorbus* taxa (Robertson *et al.* 2009), were included in the PCO analysis. These two taxa were included as they are possible putative parents of *S. cheddarensis*, *S. eminentoides* and *S. rupicoloides*, and samples of these two taxa were not readily available from the sampled area of the current study. The PCO analysis revealed that the 17 multilocus phenotypes were divided clearly into two groups, group 1 consisting of *S. aria* and group 2 consisting of *S. cheddarensis*, *S. eminentoides* and *S. rupicoloides* and the other four polyploid apomicts (Fig. 2). The widespread nature of the *S. aria* group shows clearly the genetic diversity found among the individuals while the close grouping of the seven polyploid taxa

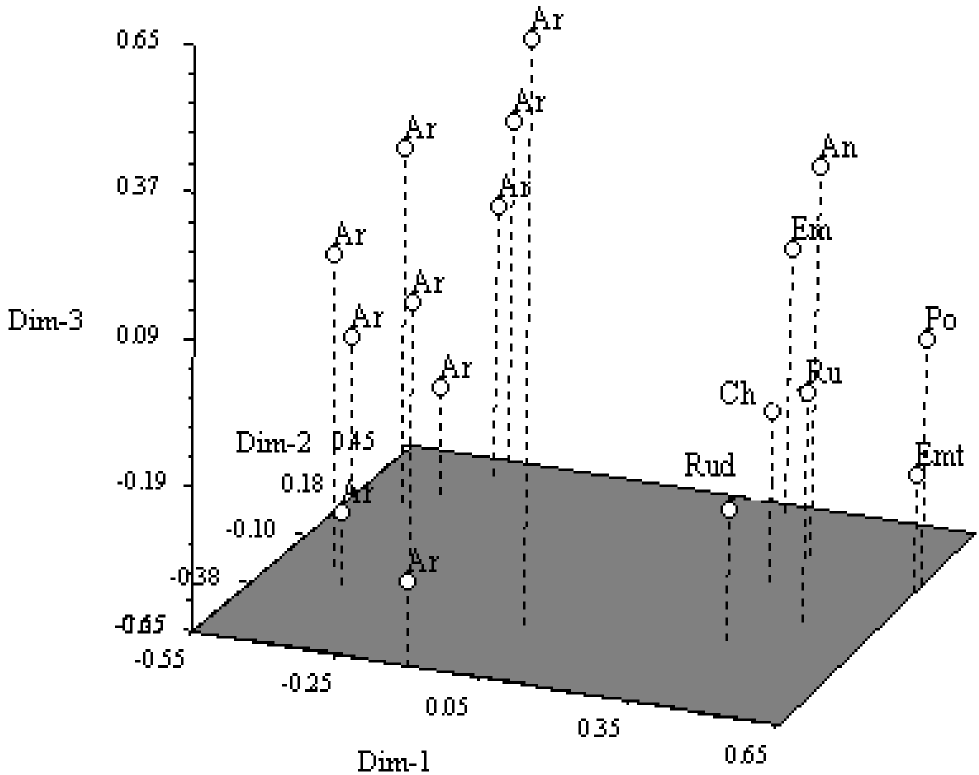


FIGURE 2. Principal Coordinate Analysis of the similarity relationships among the 15 Cheddar Gorge and two Avon Gorge *Sorbus* multilocus phenotypes, showing the first three dimensions. Two major groupings are easily identified; the grouping to the left of the figure consists solely of *S. aria*, and the grouping to the right consists solely of *Sorbus* polyploids. These three dimensions account for 57·44% of the total variation found among the phenotypes. Ar = *S. aria*, An = *S. anglica*, Ch = *S. cheddarensis*, Em = *S. eminens*, Emt = *S. eminentoides*, Po = *S. porrigentiformis*, Ru = *S. rupicola* and Rud = *S. rupicoloides.*

demonstrates how closely related they are and how likely it is that they share similar origins. Further sampling is required to determine the exact parentage of the new taxa.

## DESCRIPTIONS OF NEW SPECIES

***Sorbus cheddarensis*** L. Houston & Ashley Robertson, **sp. nov**.

HOLOTYPUS: Cheddar Gorge, v.c. 6, North Somerset, England, ST472544, 19 September 2007, T. C. G. Rich & L. Houston, Cheddar survey number 601 (**NMW**, accession number V.2007.1.130).

Vernacular name: Cheddar Whitebeam

Frutex vel arbor parva ad 7 m ut minimum. Gemmae ovoideae, virides, ad apicem pilis albidis pilosae. Folia lata brachyblastorum (8·5–)9·0–12·0(–12·5) × 6·0–8·0 cm, (1·35–)1·4–1·7(–1·8)plo longiora quam latiora, elliptica, ad longitudinis suae 48–58(–60) partes centensimas latissima, apice acuto vel obtuso, basi cuneata, in centro laminae (0–)2–11(–13) partibus centensimis ad costam plerumque leniter lobata, marginibus uniserratis dentes parvos acutos prorsum projectos ferentibus vel leniter biserratis, sed 1–2 centimetris infimis prope petiolum fere integris; pagina superior viridis glabra; pagina inferior viridula tomentosa, venis (19–)20–24 ad angulum (24–)27–37° a costa tentis. Petioli 13–24 mm. Inflorescentia ad 8 cm lata, ramulis viridialbis tomentosis instructa. Flores 15–17 mm lati, fragrantes. Sepala anguste triangularia, viridula sed ad basin tomentosa, in marginibus glandibus nullis vel paucis. Petala 7–10 × 5–7 mm, anguste elliptica, cupulata, alba. Antherae cremeae, nonnunquam dilutissime roseotinctae. Styli 2, in triente infimo colligati, virides, basi pilosa. Fructus maximi (10–)10·5–13·5(–14) × (10–)11–13 mm, 0·9–1·1(–1·2)plo longiores quam latiores, plerumque aspectu globosi, in medio latissimi, in maturitate rubri, lenticellis paucis parvis vel mediocribus praediti.

Shrub or small tree to at least 7 m. Buds ovoid, green, pilose at tip with whitish hairs. Broad leaves of short shoots (8·5–)9·0–12·0(–12·5) × 6·0–8·0 cm, (1·35–)1·4–1·7(–1·8) times as long as wide, elliptic, widest at 48–58(–60)% along leaf length, with apex acute to obtuse and base cuneate, usually shallowly lobed (0–)2–11(–13)% of way to midrib at centre of leaf; margins uniserrate with small acute, forwardly-directed teeth to weakly biserrate, but with the lowest *c.* 1–2 cm near the petiole nearly entire; upper surface green, glabrous; lower surface greenish tomentose, with (19–)20–24 veins held at an angle of (24–)27–37° to the midrib. Petioles 13–24 mm. Inflorescence to 8 cm across, with branchlets greenish-white tomentose. Flowers 15–17 mm across, fragrant. Sepals narrowly triangular, greenish but tomentose at base, without or with a few glands on margins. Petals 7–10 × 5–7 mm, narrowly elliptic, cupped, white. Anthers cream, sometimes with vaguest hint of pink. Styles 2, joined for the lowest third, green, hairy at base. Largest fruits (10–)10·5–13·5(–14) × (10–)11–13 mm, 0·9–1·1(–1·2) times as long as wide and usually looking globose, widest at the middle, red at maturity (RHS colour 42A, 44A, 45B), with a few small to medium-sized lenticels.

*Sorbus cheddarensis* is a difficult species to characterize in words, but is distinct in the field once known. It has elliptic leaves which are widest just above the middle (but not enough to be regarded as obovate), which curve to the base and apex symmetrically in the shape of an eye, with the shallow lobes on the margins cutting in to join the lamina at right angles, small, neat, acute, forward-directed teeth, and greenish-tomentose underneath with the prominent, parallel, whitish veins standing out noticeably (Fig. 3). It is a member of *Sorbus* subgenus *Aria* Pers.

*Sorbus cheddarensis* differs from *S. aria* in the greener underside to the leaves, the regular, neat toothing, and globose fruits (white undersides to the leaves with variable teeth and lobing, and fruits usually longer than wide in the very variable *S. aria*). *Sorbus porrigentiformis* differs in having obovate leaves and fruits wider than long. *Sorbus cheddarensis* is readily separated from all other Cheddar taxa; *S. anglica* and *S. intermedia* have deeply lobed leaves, *S. eminentoides* has broadly elliptic leaves with large, coarse toothing, and *S. rupicoloides* has much narrower leaves.

Two plants collected in 2001 by T. Rich and reported as *S. aria* and *S. porrigentiformis*, now redetermined as *S. cheddarensis*, had the widespread *Aria* group 'A' chloroplast type (Chester *et al.* 2006). The pollen stainability of the type tree was 71% (82 grains counted;

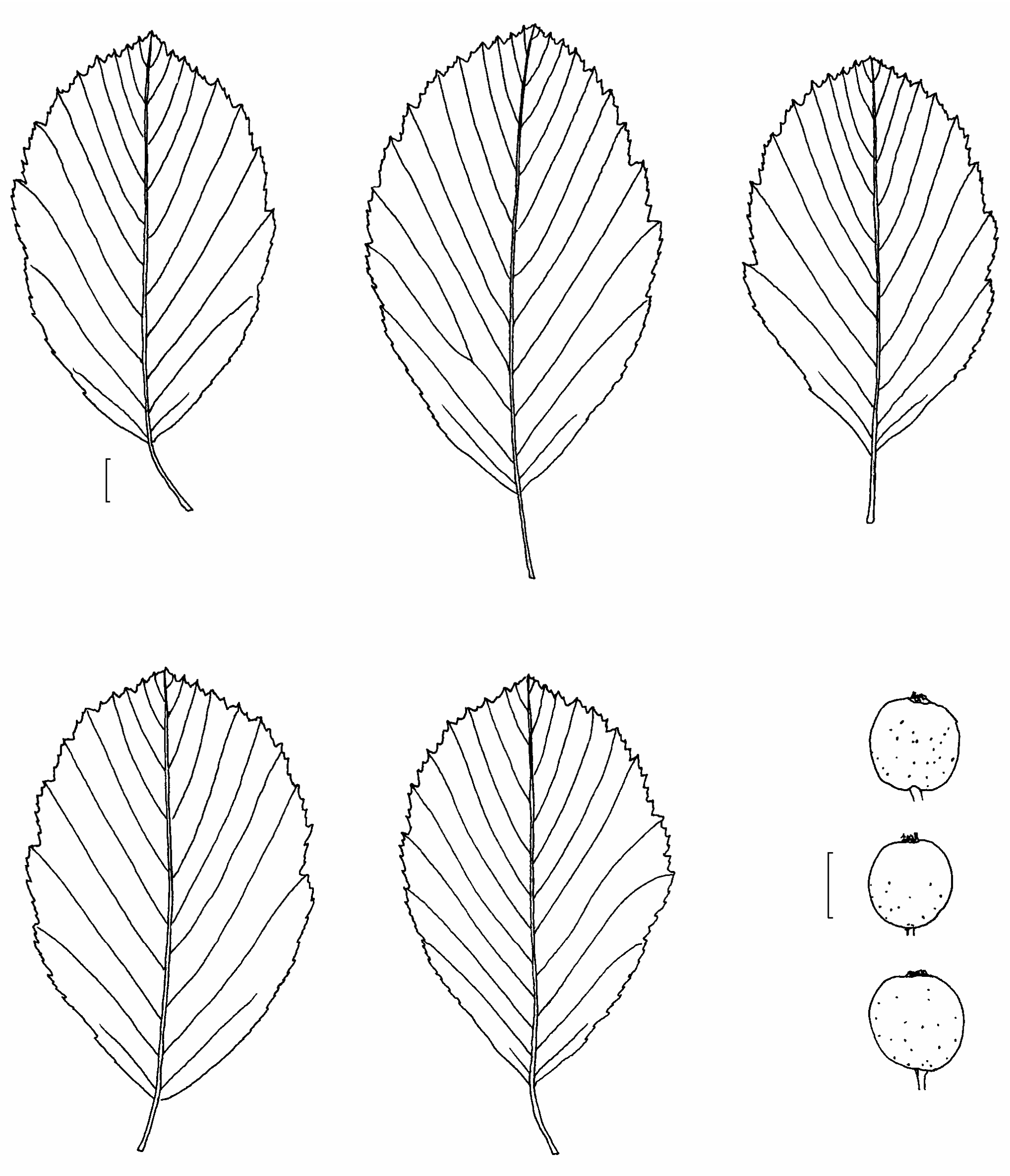

FIGURE 3. Leaves and fruits of *Sorbus cheddarensis*. Scale bars 1 cm.

A. Patto, pers. comm. 2007). Fruit set in 2006 varied between trees. Acute leaf lobes in *S. aria* may be a sign of introgression from *S. torminalis* in the Wye Valley (Price & Rich 2007), but there is no evidence of *S. torminalis* in this species.

*Sorbus cheddarensis* occurs on Carboniferous Limestone slopes and rocks in Cheddar Gorge, Somerset (v.c. 6), England. Soil from under the type tree was pH 7·2. It was first recognised as a distinct taxon by L. Houston in 2005 whilst surveying the whitebeams, and was given the nickname 'Pinstripe' on account of the prominent parallel veins as seen against the greenish lower surface of the leaf. It mainly grows associated with *S. aria*.

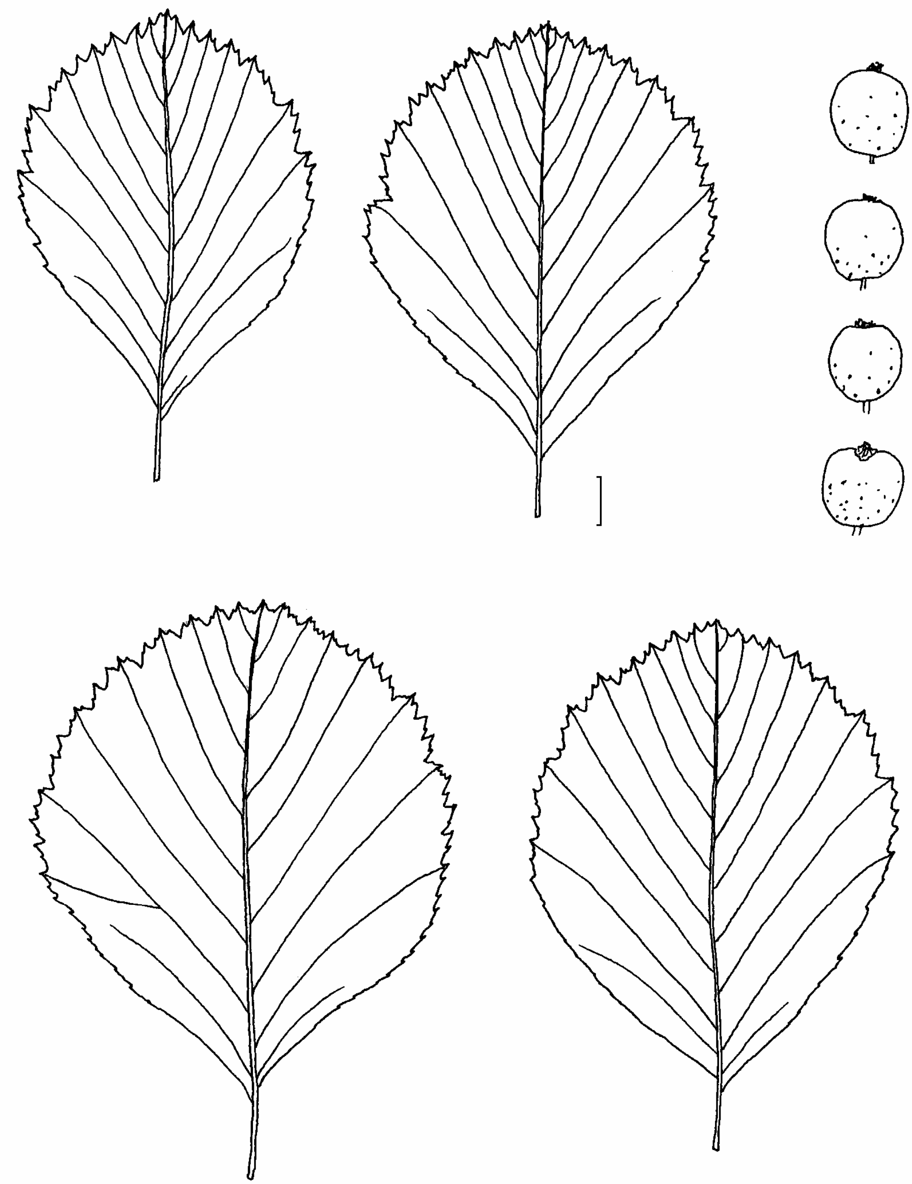

FIGURE 4. Leaves and fruits of *Sorbus eminentoides*. Scale bars 1 cm.

***Sorbus eminentoides*** L. Houston, **sp. nov**.

HOLOTYPUS: Cheddar Gorge, v.c. 6, North Somerset, England, ST466539, 19 September 2007, T. C. G. Rich & L. Houston, Cheddar survey number 261 (**NMW**, accession number V.2007.1.127).

ISOTYPUS: **BM**, **CGE**, **E**, **OXF**.

Vernacular name: Twin Cliffs Whitebeam

Frutex vel arbor parva ad 9(–15) m ut minimum; cortex cinereobrunneus. Gemmae ovoideoconicae, virides, ad apicem pilis albidis pilosae. Folia lata brachyblastorum (7·0–)8·0–11·0(–11·5) × 5·5–8·5(–9·0) cm, (1·1–)1·2–1·4 (–1·5)plo longiora quam latiora, late elliptica, raro late ovata, ad longitudinis suae (35–)41–58(–68) partes centensimas latissima, apice acuto vel raro acuminato, basi cuneata vel raro margine extrorsus arcuato, 11 partibus centensimis ad costam leniter lobata vel dentibus longis (*c.* 2–3 mm) latis acuminatis exstantibus valde biserrata, sed 2–3 centimetris infimis prope petiolum fere integris; pagina superior viridis glabra; pagina inferior cinereoviridis tomentosa, venis 16–24 ad angulum 30–40(–41)º a costa tentis. Petioli 10–19 mm. Inflorescentia ad 8 cm lata, aggregata, leniter tholiformis, ramulis viridialbis tomentosis instructa. Flores 16–20 mm lati, fragrantes. Sepala anguste triangularia, viridula sed ad basin tomentosa, in marginibus sine glandibus. Petala 8–10 × 6·5–8 mm, late elliptica, cupulata, alba. Antherae cremeae, lenissime roseotinctae. Styli 2(–3), usque ad basin discreti, virides, basi pilosa. Fructus maximi (11·5–)12–14·5(–15) × 12–15(–15·5) mm, 0·9–1·1plo longiores quam latiores, plerumque aspectu globosi vel longiores quam latiores, in maturitate rubri, lenticellis paucis parvis vel mediocribus praediti.

Shrub or small tree to at least 9(–15) m; bark greyish–brown. Buds ovoid-conical, green, pilose at tip with whitish hairs. Broad leaves of short shoots (7·0–)8·0–11·0(–11·5) × 5·5–8·5(–9·0) cm, (1·1–)1·2–1·4(–1·5) times as long as wide, broadly elliptic, rarely broadly ovate, widest at (35–)41–58(–68)% along leaf length, with apex obtuse or rarely acuminate and base cuneate or rarely with its margin arching outwards, weakly lobed to 11% of way to midrib or strongly biserrate with long (*c.* 2–3 mm) broad acuminate teeth directed outwards, but with the lowest *c.* 2–3 cm near the petiole nearly entire; upper surface green, glabrous; lower surface greyish-green tomentose, with 16–24 veins held at an angle of 30–40(–41)º to the midrib. Petioles 10–19 mm. Inflorescence to 8 cm across, crowded, weakly domed, with branchlets greenish-white tomentose. Flowers 16–20 mm across, fragrant. Sepals narrowly triangular, greenish but tomentose at base, without glands on margins. Petals 8–10 × 6·5–8 mm, broadly elliptic, cupped, white. Anthers cream with a hint of pink. Styles 2(–3), split to base, green, hairy at base. Largest fruits (11·5–)12–14·5(–15) × 12–15(–15·5) mm, 0·9–1·1 times as long as wide and usually looking globose or longer than wide, red at maturity (RHS colour 44A, 45A, 46B), with a few small to medium-sized lenticels.

*Sorbus eminentoides* is characterised by the large, broadly elliptic to roundish leaves with large teeth or weak lobes (the point at which strongly biserrate becomes weak lobing is debatable) and the large fruits which are about as long as wide (Fig. 4). It is a member of *Sorbus* subgenus *Aria*.

The broadly elliptic leaves separate it from most other British taxa with the exception of *S. eminens* and *S. aria*. It most closely resembles *S. eminens* in leaf shape (hence the specific epithet) but has large, coarse toothing whereas in *S. eminens* the teeth are fine and regular. *Sorbus aria* differs in having narrower, often ovate leaves with whitish undersides and fruits usually longer than wide. *Sorbus eminentoides* is readily separated from all other Cheddar taxa; *S. anglica* and *S. intermedia* have deeply lobed leaves, *S. cheddarensis* has elliptic leaves with fine toothing, *S. porrigentiformis* has obovate leaves and fruits wider than long, and *S. rupicoloides* has much narrower leaves.

*Sorbus eminentoides* occurs on Carboniferous Limestone cliffs at the south-west end of Cheddar Gorge, Somerset (v.c. 6), England. It was first found and collected in 2006 by L. Houston whilst surveying the Whitebeams. It grows associated with *S. anglica*, *S. aria*, *S. eminens*, *S. porrigentiformis* sensu lato and *S. rupicoloides*. The soil under the type tree had pH 7·6. The pollen fertility of the type tree assessed using Alexander's Stain was 94% (54 grains counted) and of another tree, no. 138, 88% (77 grains counted).

***Sorbus rupicoloides*** L. Houston & T. C. G. Rich, **sp. nov.**

HOLOTYPUS: Cheddar Gorge, v.c. 6, North Somerset, England, ST467539, 19 September 2007, T. C. G. Rich & L. Houston, Cheddar survey number 254 (**NMW**, accession number V.2007.1.131).

ISOTYPUS: **BM**.

Vernacular name: Gough's Rock Whitebeam

Frutex vel arbor parva ad 7 m ut minimum, ramis saepe deorsum arcuatis; cortex cinereobrunneus. Gemmae ovoideoconicae, virides, ad apicem pilis albidis pilosae. Folia lata brachyblastorum (6·5–)7·0–12·0(–12·5) × (4·0–)4·5–7·5(–8·5) cm, (1·5–)1·6–1·8plo longiora quam latiora, obovata, ad longitudinis suae 55–65 partes centensimas latissima, apice acuto vel acuminato, basi cuneata, plerumque non lobata, marginibus apicem versus leniter biserratis

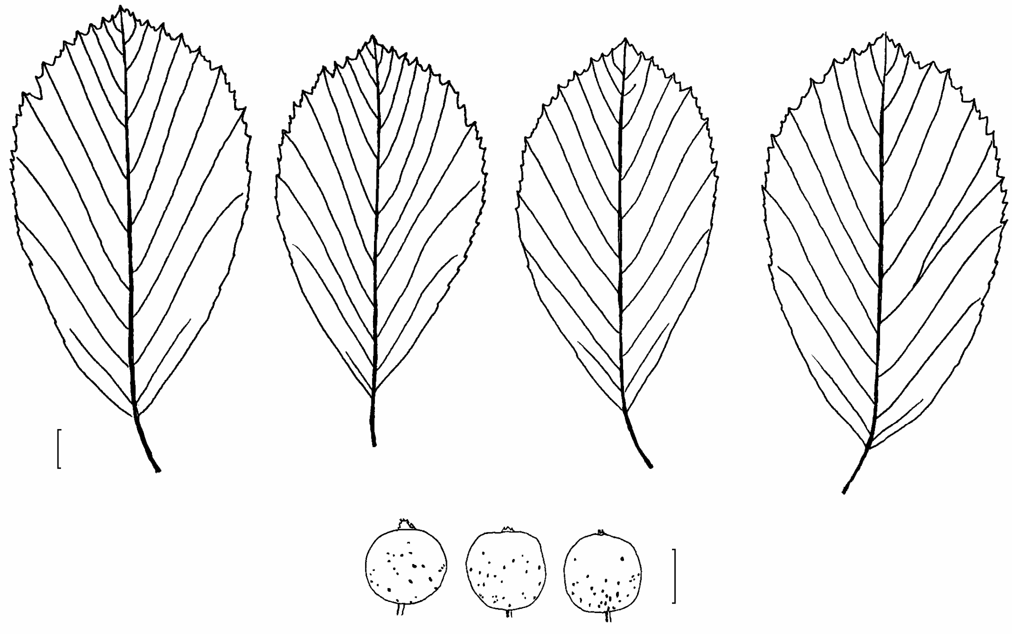

FIGURE 5. Leaves and fruits of *Sorbus rupicoloides*. Scale bars 1 cm.

dentes exstantes ferentibus, sed triente infimo fere integro; pagina superior atroviridis glabra, grosse rugosa, convexa; pagina inferior cinereoviridis tomentosa, venis 16–21 ad angulum 25–35° a costa tentis. Petioli 10–21 mm, crassi. Inflorescentia aggregata, leniter tholiformis, ramulis albis tomentosis, ubi fructiferis glabrescentibus, instructa. Flores 15–18 mm lati, fragrantes. Sepala anguste triangularia, tomentosa, in marginibus sine glandibus. Petala 8–10 × 6–8 mm, late elliptica vel magis minusve orbicularia, cupulata, alba. Antherae dilutissime roseae. Styli 2, in triente infimo colligati, virides, basi pilosa. Fructus maximi 11–14(–15) × (12–)13–17(–18) mm, 0·73–0·97plo longiores quam latiores, plerumque aspectu latiores quam longiores, in medio latissimi, in maturitate rubri sed inaequaliter maturescentes, lenticellis paucis vel aliquot parvis vel magnis praediti, lenticellis magnis praecipue fructus basin versus locatis.

Shrub or small tree to at least 7 m, with branches often arching downwards; bark greyish-brown. Buds ovoid-conical, green, pilose at tip with whitish hairs. Broad leaves of short shoots (6·5–)7·0–12·0(–12·5) × (4·0–)4·5–7·5(–8·5) cm, (1·5–)1·6–1·8 times as long as wide, obovate, widest at 55–65% along leaf length, with apex acute to acuminate and base cuneate, usually unlobed, with the margins towards the apex weakly biserrate with teeth directed outwards, but with the lowest third nearly entire; upper surface dark green, glabrous, coarsely rugose, convex; lower surface greyish-green tomentose, with 16–21 veins held at an angle of 25–35° to the midrib. Petioles 10–21 mm, stout. Inflorescence crowded, weakly domed, with branchlets white tomentose, glabrescent in fruit. Flowers 15–18 mm across, fragrant. Sepals narrowly triangular, tomentose, without glands on margins. Petals 8–10 × 6–8 mm, broadly elliptic to more or less orbicular, cupped, white. Anthers very pale pink. Styles 2, joined for lowest third, green, hairy at base. Largest fruits 11–14(–15) × (12–)13–17(–18) mm, 0·73–0·97 times as long as wide and usually looking wider than long, widest at the middle, red at maturity (RHS colour 44A, 45A, 46A) but ripening unevenly, with a few to a moderate number of small to large lenticels, the large lenticels mainly towards the base of the fruit.

*Sorbus rupicoloides* is characterized by the narrow, obovate, acute leaves which are greenish-white underneath and the large, broad fruits (Fig. 5), which distinguish it from most other British taxa with the exception of the narrow-leaved *S. rupicola* (Syme) Hedlund, *S. vexans* E. F. Warb. and *S. margaretae* M. C. F. Proctor (Taxon D sensu Proctor *et al.* 1989). It is a member of *Sorbus* subgenus *Aria*.

At first glance, *S. rupicoloides* looks like *S. rupicola* (hence our epithet) but differs in having acute leaves with biserrate toothing (obtuse, oblong-obovate and with more or less uniserrate teeth which curve towards the leaf apex in *S. rupicola*), and has generally larger fruits (average 12·8 × 15 mm in *S. rupicoloides,* and 12·1 × 13·6 mm in *S. rupicola*) though there is much variation in *S. rupicola. Sorbus rupicoloides* differs from *S. vexans* in having larger fruits and obovate, acute leaves (obovate-oblong, obtuse leaves in *S. vexans*), and from *S. margaretae* in having fruits usually more or less globose (markedly wider than long in *S. margaretae*).

*Sorbus rupicoloides* occurs on and below a Carboniferous Limestone cliff on the south side at the west end of Cheddar Gorge, Somerset (v.c. 6), England. It was first found and collected in 2006 whilst L. Houston was carrying out a survey of the whitebeams. It grows associated with *S. anglica*, *S. aria*, *S. eminens* and *S. eminentoides*.

## FIELD SURVEY

A total of 3622 *Sorbus* trees belonging to at least eight taxa were recorded in the areas surveyed. 71 trees were dead, or probably dead, but still recognizable to genus. 256 living plants could not be identified to species, mainly either because they were inaccessible, had lost their leaves or been so eaten by goats that they were not recognizable.

### *SORBUS ANGLICA*

112 *S. anglica* trees were recorded (Table 4), with another six possible trees, scattered throughout the site but especially concentrated at the west end (Fig. 6). Given that *S. anglica* had been regarded as rare, the number of trees found was very pleasing. It is the most widespread of the polyploids in the gorge.

Two puzzling trees with leaves somewhat intermediate between *S. aria* and *S. anglica* were noted, which might be hybrids; hybrids of this parentage have not been recorded before, and these trees merit further investigation.

### *SORBUS ARIA*

*Sorbus aria* trees were noted throughout the site (data not presented), with 2803 positively

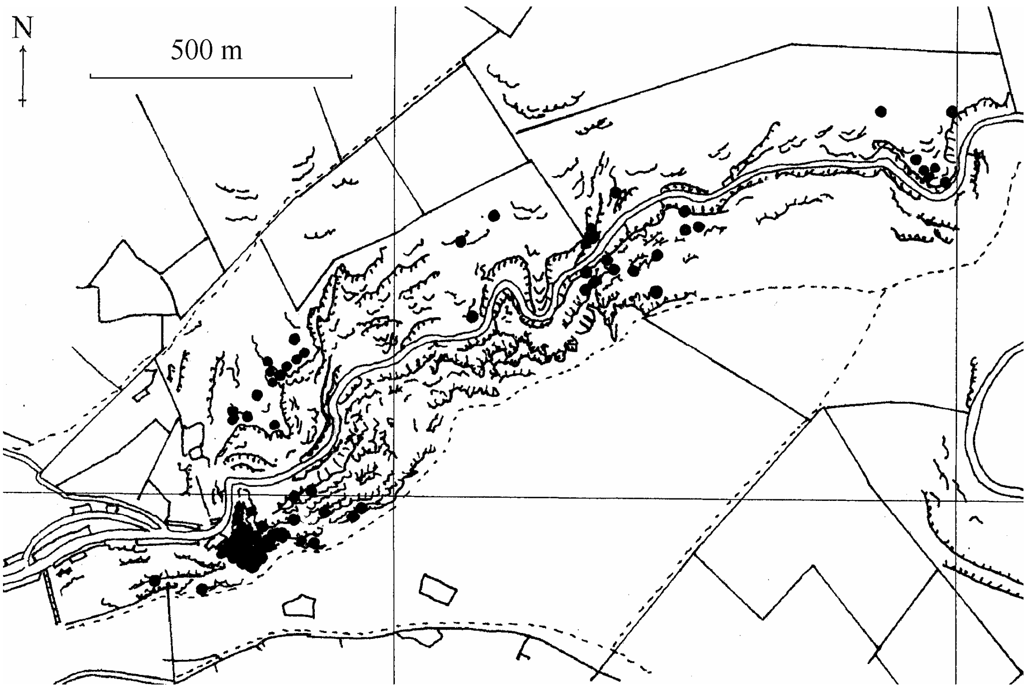


FIGURE 6. Distribution of *Sorbus anglica* at Cheddar Gorge in areas surveyed.

TABLE 4. NUMBERS OF *SORBUS* INDIVIDUALS RECORDED WITH DAMAGE TO TREES BY BROWSING

| Species | Total no. trees | No. trees recorded for goat damage | Trees damaged | % damaged |
|---|---|---|---|---|
| *S. anglica* | 112 | 99 | 31 | 31% |
| *S. aria* | 2803 | 1785 | 175 | 10% |
| *S. cheddarensis* | 19 | 13 | 6 | 46% |
| *S. eminens* | 200 | 152 | 62 | 41% |
| *S. eminentoides* | 15 | 14 | 2 | 14% |
| *S. intermedia* | 1 | 1 | 0 | 0% |
| *S. porrigentiformis* | 32 | 29 | 7 | 24% |
| *S. rupicoloides* | 12 | 12 | 3 | 25% |
| *Sorbus* of uncertain identity | 355 | 315 | 188 | 60% |
| | | | Overall average | 20% |

identified trees recorded (Table 4) and another 15 probably best attributed to *S. aria.* The total Cheddar Gorge population including unsurveyed areas is likely to be closer to 10,000.

*Sorbus aria* is very variable in Cheddar, possibly second only to the Avon Gorge in diversity of forms, and there are many trees with leaves varying towards those of other taxa.

Two *S. aria* trees were noted with acute lobes to the leaves which might be introgressed hybrids with *S. torminalis* (L.) Crantz (cf. Price & Rich 2007). The only sample of *S. aria* with a *torminalis* chloroplast type recorded by Chester *et al*. (2007) was from Cheddar, possibly a result in chloroplast capture as reported for France by Oddou-Muratorio *et al*. (2001).

*SORBUS CHEDDARENSIS*

19 trees of this new taxon were noted with 15 trees which may also be this species (Table 4). These occur mainly around the centre of the site above the horseshoe bend on the northern side (Fig. 7).

*SORBUS EMINENS*

200 *S. eminens* trees were recorded with another possible 42 whose identification requires confirmation (Table 4). These were concentrated at the western end of the gorge on the larger cliffs (Fig. 8).

Seven trees with leaves intermediate between *S. aria* and *S. eminens* were found which could be the hybrid *S.* × *robertsonii* T. C. G. Rich; these require confirmation from DNA.

*SORBUS EMINENTOIDES*

15 trees of *S. eminentoides* were noted (Table 4), with another four possible trees, all in the area of cliffs above Gough's Cave at the west end of the gorge (Fig. 9).

*SORBUS INTERMEDIA*

One 5 m tree was noted towards the east end of the gorge on the south side (Table 4). *Sorbus intermedia* has presumably spread from the mature trees planted in Cheddar village, but it is perhaps surprising that this species, which naturalizes readily on limestone soils elsewhere, is not more widespread in the gorge.

*SORBUS PORRIGENTIFORMIS*

This species was surprisingly rare and often difficult to separate from the variation in the other taxa. Only 18 trees were regarded as *S. porrigentiformis* sensu stricto (Table 4), with another 14 as *S. porrigentiformis* sensu lato and another eight possible trees. These occurred scattered along the gorge (Fig. 10).

One plant seen may have been referable to *S. aria* × *S. porrigentiformis* = S. × *avonensis* T. C. G. Rich but requires confirmation by DNA analysis.

*SORBUS RUPICOLOIDES*

Twelve trees of this new taxon were recorded (Table 4), all within a small area of the cliffs around Gough's Cave (Fig. 11).

## EFFECTS OF GOATS

Damage by goats is used in a general way here to include browsing of leaves, shoots and twigs, and barking of small trees. Some damage may have been caused by Soay sheep, deer or other mammals which occur at Cheddar, but the bulk of the damage was clearly attributable to, and is in areas frequented by, goats.

The damage caused by goats was recorded for all the *Sorbus* species (Table 4). The large number of trees damaged by goats to one

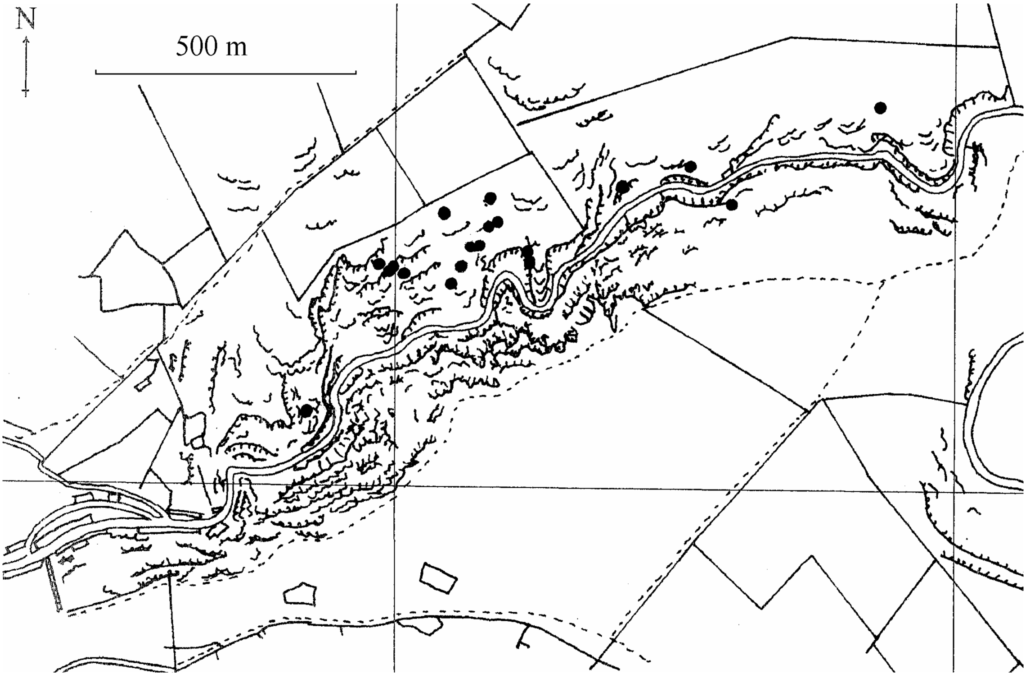


FIGURE 7. Distribution of *Sorbus cheddarensis* at Cheddar Gorge in areas surveyed.

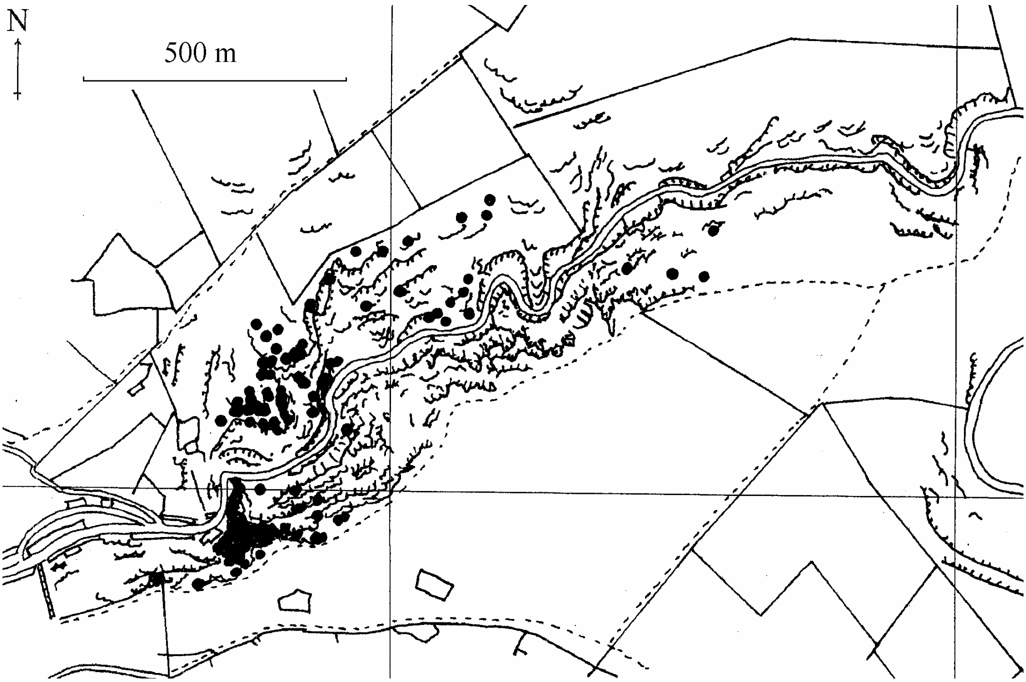


FIGURE 8. Distribution of *Sorbus eminens* at Cheddar Gorge in areas surveyed.

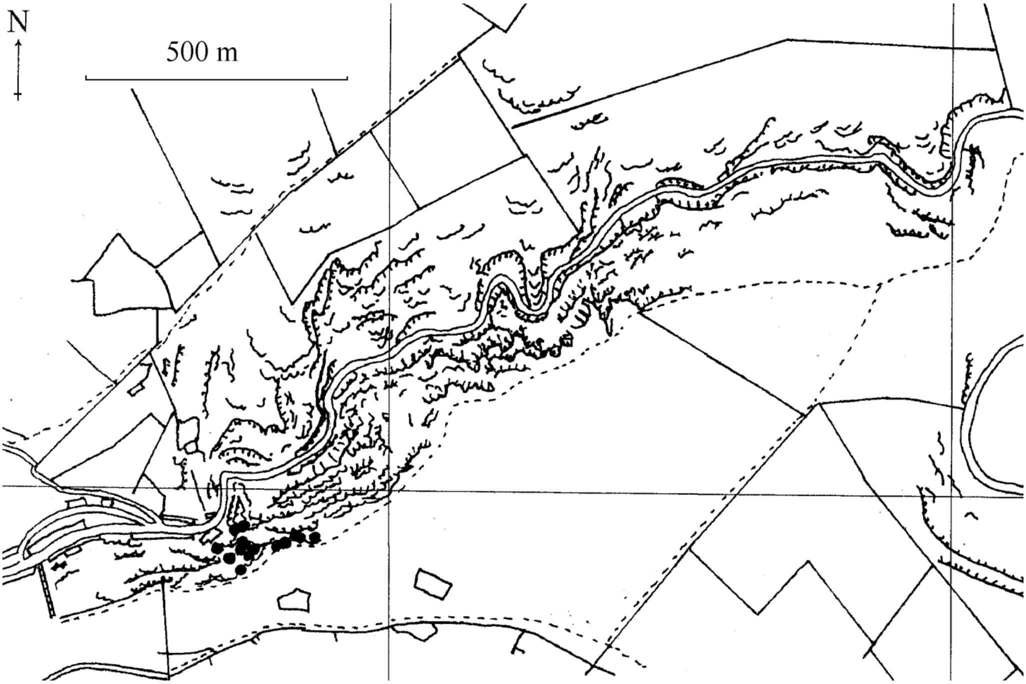


FIGURE 9. Distribution of *Sorbus eminentoides* at Cheddar Gorge in areas surveyed.

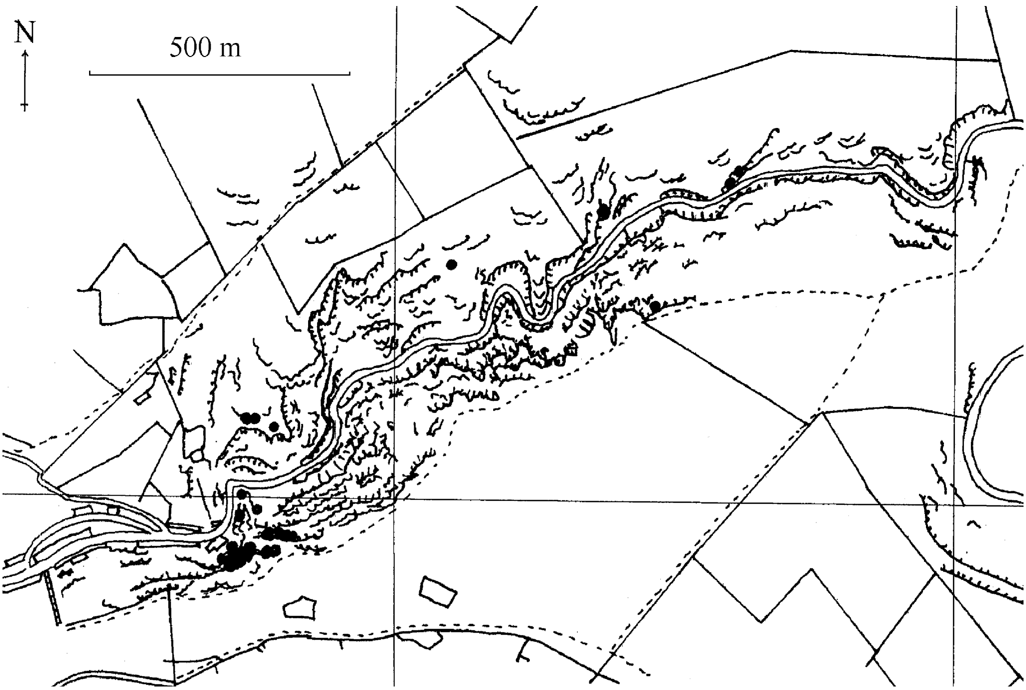


FIGURE 10. Distribution of *Sorbus porrigentiformis* sensu lato at Cheddar Gorge in areas surveyed.

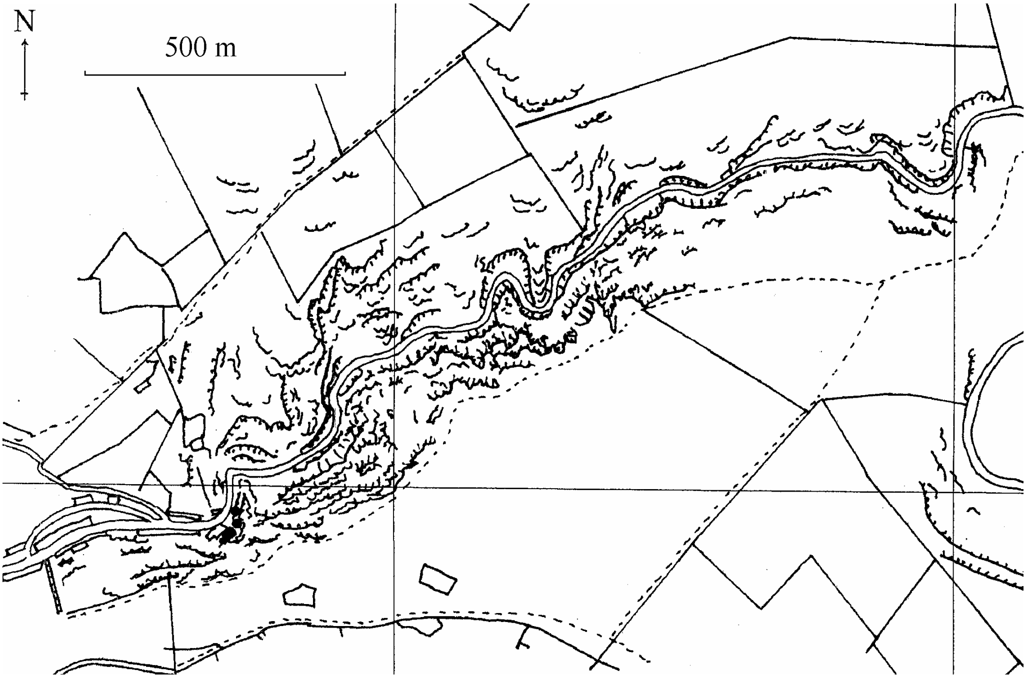


FIGURE 11. Distribution of *Sorbus rupicoloides* at Cheddar Gorge in areas surveyed.

extent or another (20% overall), and the high proportion of dead trees recorded on the National Trust side which were due to goat browsing (7 out of 9 trees), indicate the scale of the problem. It is not certain if the relatively high damage to *S. cheddarensis* and *S. eminens* (Table 4) is due to selective browsing of these species, or is related to their occurrence in areas the goats frequent; a specific study is required. Trees particularly affected are those beside the paths regularly used by goats, and the effects are most marked on the sunnier, more open slopes on the National Trust side, at Commoners' Spur and Heart Leaf Bluff, where the goats prefer to reside. The main impact of animals on the Longleat side appears to be prevention of regeneration, which may be due to a combination of goats and Soay sheep.

The goats have proved capable of destroying some small trees altogether, in a gradual process, by breaking off branches and crown to leave the remains of the stem as a moribund stick. Young shoots produced at the base have then been vulnerable to selective browsing. Smith (2005) reported that goats will browse to a height of up to 2 m in woodland, and we noted that in more open areas trees with slender stems up to 3 m tall were vulnerable to being pulled or broken down. Some goats were even observed climbing in trees. One *S. anglica* tree at Horseshoe Bend cut down during conservation work in 2002 did survive initially by re-sprouting from the base, but the young shoots were selectively browsed and it was dead by 2005. In a few cases, photographs taken by T. Rich in 2001 provide clear evidence of damage to individual trees (e.g. *S. anglica* no. 76), and other trees watched between 2005 and 2007 were seen to become progressively more damaged.

## DISCUSSION

Eight *Sorbus* species were recorded in Cheddar Gorge, of which the three new taxa *S. cheddarensis, S. eminentoides* and *S. rupicoloides* are endemic to the gorge, and *S. eminens* and *S. porrigentiformis* are endemic to Britain. This is clearly a nationally important site for *Sorbus*, ranking with the Avon Gorge, Wye Valley, Craig-y-Cilau and the north Devon-Somerset coast as centres of diversity. It is perhaps surprising that the importance of Cheddar for *Sorbus* has been so relatively poorly known, though this reflects the difficulties both of surveying the gorge and of identifying *Sorbus*

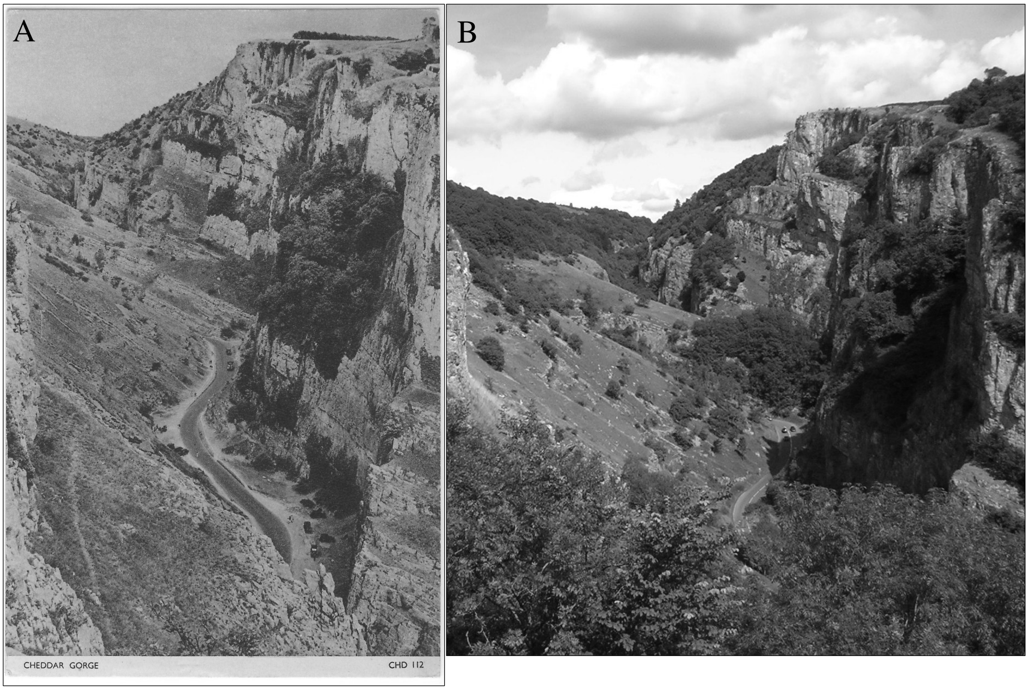


FIGURE 12. Photographs showing scrub invasion and woodland development at Cheddar. A. Old postcard, pre-Second World War. B, Approximate same view, 2005.

(the recognition of the new taxa here aided by DNA), but it is possible that the post-war removal of grazing has allowed the rarer taxa to spread onto the screes and slopes so that they are now more easily found in accessible places. The survey has also shown many more individuals of the rarer species than had previously been known. Many of the rarer trees are also concentrated around the massive cliffs and slopes at the west end of the gorge, but not exclusively so. The conservation statuses of *S. cheddarensis, S. eminentoides* and *S. rupicoloides* are 'Critically Endangered' following the IUCN (2001) guidelines.

The diversity in Cheddar, as in the Avon Gorge (cf. Robertson *et al.* 2009), is partly attributed to presence of *S. aria* and the ease with which it hybridizes with *S. porrigentiformis*. The genetic and morphological diversity within *S. aria* is also important, this site containing one of the more morphologically variable populations of *S. aria* seen by T. Rich.

Our survey data show that there is damage to the *Sorbus* populations by goats and other animals. Goats were introduced to Cheddar to control scrub, at which they are very effective and an important conservation tool (Smith & Bullock 1993). The National Trust herd is currently five, free-ranging, neutered males whose preference is for the north side of the gorge at the west end. The goats were initially confined to an enclosure, but soon escaped and continued to do so when corralled back into the enclosure. On the Longleat Estate side of the gorge, a large breeding herd has been introduced recently to an extensive enclosure, but these have also escaped. While some goats have been reported from as far away as Hutton, near Weston-super-Mare 20 km to the west (D. Bullock, pers. comm. 2008), others have crossed to the sunnier north side of the gorge; there were 25 feral goats in the gorge by 2007 (D. Bullock, pers. comm., 2008). Smith & Bullock (1993) found that goats selectively targeted *Sorbus* species in summer, and Smith (2005) noted that it may be the bark stripping during the winter which actually kills the trees. Goats tend to prefer sheltered, sunny, open areas, and will browse in some areas more than others, locally affecting the vegetation; this may cause problems where it coincides with the occurrence of rare species. The herd of feral Soay sheep have been in the gorge since 1992; their population has varied between 34 and 124 between 2000 and 2007 (D. Bullock, pers. comm. 2008). The sheep also browse saplings, and have an impact on the *Sorbus* species. A recent study of the impact of sheep and goats in Cheddar by Wheatley (2009) has confirmed that significant damage to the whitebeams is taking place.

There is a nature conservation dilemma at Cheddar Gorge. On the one hand, it is important to maintain the open grassland for rarities such as *Dianthus gratianopolitanus*; on the other hand, it is important to conserve the *Sorbus* which prefers the intermediate stages of scrub succession to woodland. A comparison of modern day views with those shown in old photographs shows the extent of scrub recolonization in the gorge (Fig. 12). Allowing further development to closed woodland will not be acceptable for either rare grassland species or *Sorbus*, but continued heavy grazing would probably result in restriction of most of the *Sorbus* species to cliffs or places inaccessible to animals. Quite how all these conflicting priorities can be resolved remains to be seen, but clearly both need accommodating perhaps by compartmentalization of parts of the gorge.

Finally, we strongly advise anyone wishing to see these whitebeams to take extreme care due to the number of loose rocks on the slopes and cliffs, and the large number of people who visit the gorge. Many of the *Sorbus* taxa can be seen safely from the public paths, but permission must be obtained to access the area of Gough's Cave where *S. rupicoloides* occurs as it is above buildings in an area with restricted public access.

## ACKNOWLEDGMENTS

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