Species with statistically greater numbers of diseased specimens than expected based on binomial distribution probabilities included *Silene saxifraga* (32 diseased specimens among 491 specimens), *Lychnis fulgens* (13 among 116 specimens), and *Silene parryi* (21 among 373 specimens).

Analysis of the host phylogeny revealed that perennials with high disease frequencies were found together in multiple well-supported clades either with perennials having low or no disease, or with annual species (Fig. 1). There was no statistically significant evidence for a phylogenetic signal for either annual vs perennial life-span or presence or absence of disease; that is, the estimated number of state transition steps in the host phylogeny (n = 11) was not lower than expected by chance, indicating that these characters are highly labile during the evolution of the *Sileneae*. The association of life-span (annual vs perennial) and disease status was found to be statistically significant while controlling for the plant phylogeny (P-value from 1000 simulations = 0.001; independent log likelihood = 51.1985; correlated log likelihood = 43.5713).

No significant correlation of disease rates was found with flower size (correlation coefficient = −0.057, P = 0.476, n = 156) or with darkness of flower color (correlation coefficient = 0.083, P = 0.247, n = 195). Because these correlations were nonsignificant, they were not tested further by controlling for the plant phylogeny.

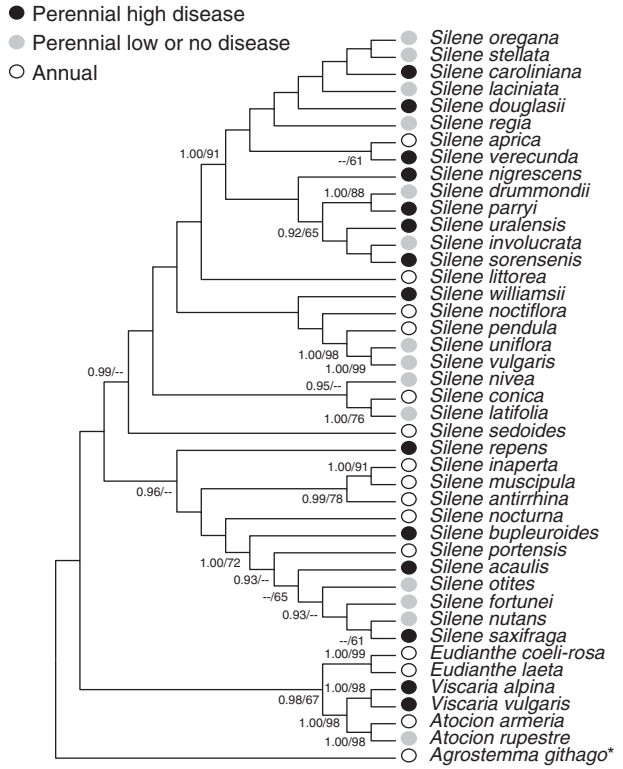

Fig. 1 Phylogeny of plant species of the tribe *Sileneae* based upon maximum parsimony analysis of ribosomal protein *rps16* DNA sequences. Support values for tree topology are shown when they had values of Bayesian posterior probabilities/maximum parsimony bootstraps at least equal to 0.9/60, respectively. DNA sequences were obtained from GenBank National Centre for Biotechnology Information (NCBI) for an equal number of plant species in the categories of annuals (open circles), perennials with high disease frequencies (closed circles), and perennials with low or no disease (gray circles). Perennial species were chosen as those with the most significant binomial distribution probabilities for positive or negative deviations from overall disease frequencies among perennials. Annuals were chosen as those with the largest numbers of specimens examined. **Agrostemma githago* was chosen as the outgroup to the remainder of the *Sileneae* based on Oxelman *et al.* (2001). Accession numbers are available in Table S2.

Host and pathogen distributions

The known geographical distribution of anther smuts (Fig. 2) was greatly expanded to include the presence of the pathogen in species of *Sileneae* from the Southern Hemisphere, both in South America (on *Silene chilensis* and *Silene magellanica*) and in southern regions of Africa (on *Silene burchellii*, *Silene ornata*, and *Silene undulata*). The difference between continents in the proportion of diseased perennial *Sileneae* specimens approached significance (χ^2 = 8.41, df = 4, P = 0.078), and the trend was toward the least disease in the Southern Hemisphere and the most disease in Asia (Table 3).

Within Europe, compiled distribution maps for perennial *Silene* species from the Atlas Florae Europaeae showed the highest species richness in southern mountain regions. Heavily diseased *Silene* species also appeared to be distributed in these regions (Fig. 3). By contrast, the most examined perennial species having no disease were more broadly distributed in regions of low *Silene* species richness. Annual *Silene* species exhibited a southern European distribution similar to that of perennial species, with each of the 10 annual species with the largest numbers of examined specimens overlapping in geographical distribution with the 10 most diseased perennial species (see Supporting Information Fig. S1). The geographical range size of perennial *Silene* in Europe was negatively correlated with the disease rates within species (Spearman's rank correlation coefficient for all examined perennial species in the AFE database = −0.195, P = 0.048, n = 104; rank correlation coefficient including only diseased species = −0.456, P = 0.013, n = 29).

Analysis of DNA sequence data from herbarium samples confirms that the lineage of *Microbotryum* causing anther smut on the Caryophyllaceae has representatives infecting other plant families (Le Gac *et al.*, 2007; but see Vánky, 1998, 2001). Samples collected from two species of South American *Calandrinia* (Fig. 2) group along with samples collected from species in the Caryophyllaceae rather than