

Chapter (non-refereed)

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Within-species variation and its genetical control

20. *BETULA PUBESCENS*—THE AFFINITIES OF TYPES IN THE SCOTTISH HIGHLANDS WITH THOSE OF CONTINENTAL EUROPE: A STUDY OF LEAF MORPHOLOGY OR THE APPLICATION OF MORPHOMETRICS

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Of the 3 species of *Betula* L. native to Great Britain, one is the dwarf birch, *B. nana* L., whereas the other 2, *B. pendula* Roth, the silver birch, and *B. pubescens* Ehrh., the downy birch, form medium sized trees. *B. pubescens* is the more variable of the latter, it being current practice to subdivide it into 2 subspecies. Subspecies *pubescens* is believed to be more widely distributed in lowland habitats, whilst ssp *odorata* is associated with the Scottish highlands.

Instead of 2, 3 subspecies of *B. pubescens* are recognised in continental Europe—ssp *pubescens*, ssp *tortuosa* and ssp *carpatica*. It may appear at first glance that ssp *odorata* is unique to Britain, but a closer comparison of the various editions of the Flora of The British Isles with Flora Europaea shows that ssp *odorata* has been equated at different times with both ssp *carpatica* and ssp *tortuosa*.

Because of their variability ssp *carpatica* and ssp *tortuosa* have only been distinguished with difficulty. They are essentially shrub-like mountain or highland birches; ssp *tortuosa* has the more twisted appearance with many interlacing branches and ssp *carpatica* is the less hairy or pubescent. In an attempt to define these variable subspecies more clearly, Jentys-Szaferowa (1950) made a biometric study of their leaf sizes and shapes. On the basis of population means for a set of 13 continuous variables, she derived species means for *B. pendula* (*B. verrucosa*), *B. pubescens*, *B. carpatica*, *B. tortuosa*, *B. obscura* and *B. oycoviensis*, the subspecies already mentioned being given specific ranking within a broader concept, the collective species *B. alba* L.

Her variables included different characteristics that determine both leaf size and shape. Thirty to 40 years ago the analysis of the data was time-consuming and restricted, but, with the advent of electronic computers and more sophisticated statistical packages, the task has been made easier and

more searching, notably through the use of principal component analysis.

With these advances it was decided to (i) investigate the differences between mainly highland samples of *B. pubescens* and (ii) seek their affinities with their continental counterparts, remembering that British populations, which originally migrated from the continent, have now been isolated for thousands of years.

1. Objectives

- 1.1. To obtain the relevant portions of Jentys-Szaferowa's data so as to structure a comparison between British populations of *B. pubescens*, with special emphasis on those from the Scottish highlands, and their continental counterparts.
- 1.2. To determine if the observed differences among British populations are commensurate with a classification of 2 or 3 subspecies.
- 1.3. To detect if the patterns of variation among British subspecies are regionally distributed.
- 1.4. To study the range of variation of individuals within different populations. Do different discrete populations contain more than one subspecies?

2. Approach

Observations were made on leaves of (i) 23 mainly highland populations of *B. pubescens* identified and collected in 1953 by Dr F.W.J. England, (ii) 50 individual trees in Morrone National Nature Reserve and (iii) 15 trees from Sluie Wood—both Sluie and Morrone NNRs being located in Deeside, Scotland.

Although Jentys-Szaferowa used 13 continuous variables per leaf, this number was reduced to 6 by applying Jolliffe's method for discarding superfluous variables (Jolliffe, 1972, 1973). The composition of this set of 6 changed slightly with modifications to the comparative framework (described below); those selected for the 3 taxa level are illustrated in Figure 40.

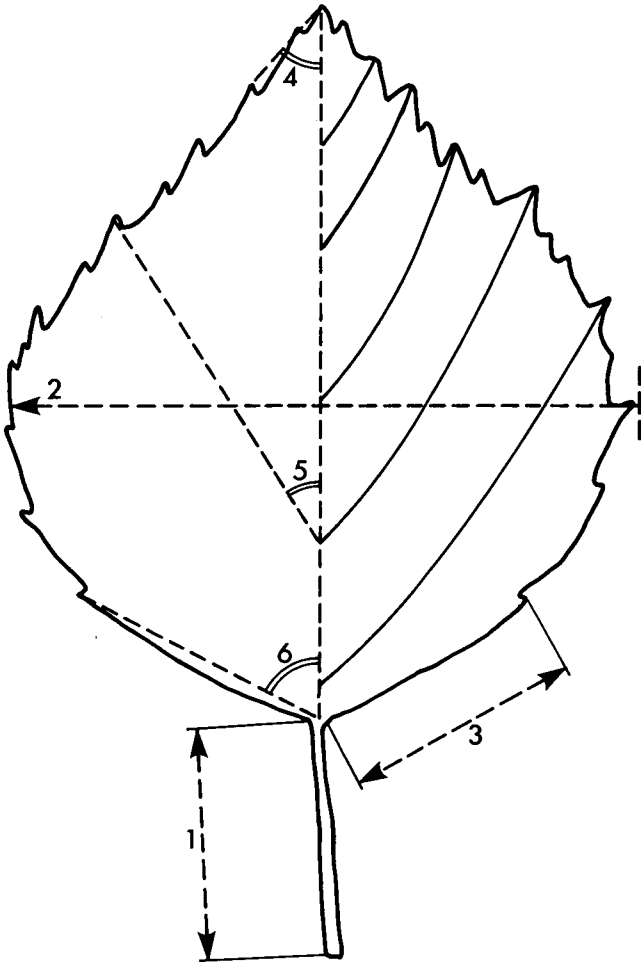


Fig. 40 Diagram showing the 6 variables (selected by Jolliffe's method for discarding superfluous variables) which characterise the leaf morphology of *Betula pubescens* spp *pubescens*, *tortuosa* and *carpatica*:
 1. petiole length
 2. broadest width
 3. distance of 1st tooth from join of lamina and petiole
 4. apex angle
 5. axil of second nerve
 6. angle at base of lamina.

The data were then subjected to principal component analysis, which indicated that the variation could be summarized by 2 significant axes or components. In the event, 3 principal component analyses were made—each preceded by a run of Jolliffe's procedure—in which numbers of taxa in the basic framework were reduced from 5 to 4 and, finally, 3. At the start, Jentys-Szaferowa's mean values for *B. pendula*, *B. pubescens*, *B. tortuosa*, *B. carpatica* and *B. oycoviensis* were included, *B. obscura* having been discarded as earlier work had shown it to be identical with *B. pendula* (Gardiner & Jeffers, 1962). In the second analysis, *B. pendula* was excluded as none of the 23 British populations showed a close affinity with this

species; for a similar reason *B. oycoviensis* was dropped from the third analysis. In the third analysis, the first component contrasted the apex angle with the other variables and the second component contrasted blade width, apex angle,

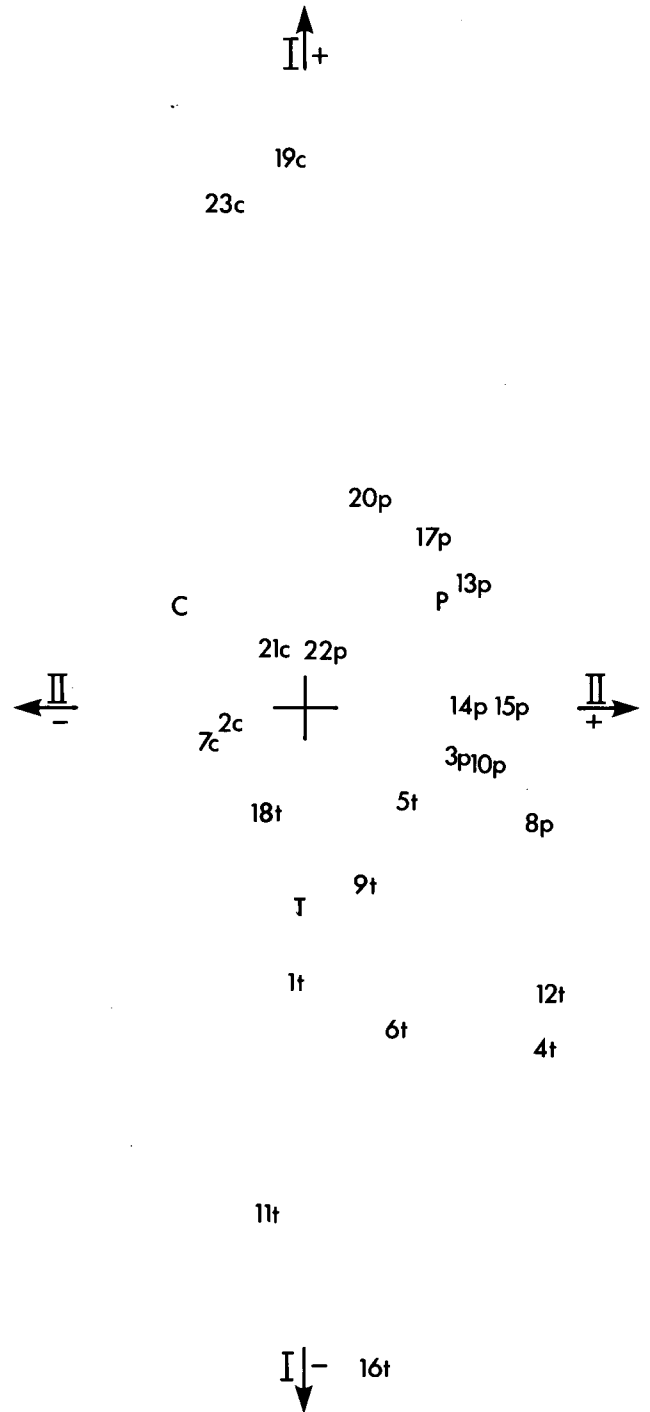


Fig. 41 Distribution of 23 populations of predominantly Scottish *Betula pubescens* when the first (I) and (II) components of a principal component analysis, including details of continental spp *pubescens* (P), *tortuosa* (T) and *carpatica* (C), were arranged 2-dimensionally. c, p and t indicate affinities of the British populations (1-23).

TABLE 30 Subspecies affinities of 23 British populations of *B. pubescens* when compared with (i) *B. pendula*, *B. pubescens*, *B. tortuosa*, *B. carpatica*, *B. oycoviensis* - 5 taxa; (ii) 4 taxa (*B. pendula* excluded); and (iii) 3 taxa (*B. pendula*, and *B. oycoviensis* excluded).

Sample No.	Location of British populations	Levels of comparison		
		5 taxa	4 taxa	3 taxa
1	Skye	carpatica	carpatica	tortuosa
2	Skye	pubescens	pubescens	carpatica
3	Loch Carron	pubescens	pubescens	pubescens
4	Achnasheen	tortuosa	carpatica	tortuosa
5	Achanalt	pubescens	pubescens	tortuosa
6	Tomatin	tortuosa	carpatica	tortuosa
7	Tomich	pubescens	pubescens	carpatica
8	Invergarry	pubescens	pubescens	pubescens
9	Glen Shiel	pubescens	pubescens	tortuosa
10	Bridge of Brown	pubescens	pubescens	pubescens
11	Cluanie	tortuosa	tortuosa	tortuosa
12	Newtonmore	oycoviensis	pubescens	tortuosa
13	Arisaig	pubescens	pubescens	pubescens
14	Kinlochleven	pubescens	pubescens	pubescens
15	Crianlarich	pubescens	pubescens	pubescens
16	Aberfeldy	tortuosa	tortuosa	tortuosa
17	Callander	pubescens	pubescens	pubescens
18	Penicuik	carpatica	carpatica	tortuosa
19	Houghton	carpatica	pubescens	carpatica
20	Hackness	carpatica	pubescens	pubescens
21	Ling Gill	carpatica	carpatica	carpatica
22	Borden	carpatica	carpatica	pubescens
23	Okehampton	pubescens	pubescens	carpatica

base angle and the axil of the second nerve with the remaining linear variables. These contrasts effectively separated *B. tortuosa* from *B. carpatica* and *B. pubescens* on the first (I) axis and *B. carpatica* from *B. pubescens* on the second (II) (Figure 41).

3. Outcome

When the 23 populations of *B. pubescens* were related (shortest Euclidean distance) to progress-

pubescens to *B. carpatica*. The analyses suggest that the 23 populations should be divided, as on the continent, into 3 subspecies *pubescens*, *carpatica* and *tortuosa*, the graphical representation of their distinctiveness, based on leaf characteristics (Figure 41), suggesting that the variation is continuous. Surprisingly, the 3 types do not seem to have disparate patterns of geographical distribution, there being a marked overlap between ssp *pubescens* and ssp *tortuosa* in the Scottish highlands (Figure 42).

TABLE 31 Affinities with *B. pubescens* ssp *pubescens*, *tortuosa* and *carpatica* of individual trees sampled in Morrone and Sluie Woods, Deeside, Scotland, when data were subjected to principal component analysis using reference data from these 3 subspecies.

	ssp. <i>pubescens</i>	ssp. <i>tortuosa</i>	ssp. <i>carpatica</i>	Number in sample
Morrone		50		50
Sluie	3	7	5	15

ively fewer of the taxa, as defined by Jentys-Szaferowa, it was found that the affinities of some of them changed (Table 30). Thus, for example, the Skye population No. 1 seemed more like the continental *B. carpatica* when data for *B. pubescens*, *B. tortuosa*, *B. carpatica* and *B. oycoviensis* were included; when *B. oycoviensis* was excluded, the 3 taxa analysis suggested *B. tortuosa*. With the Skye population No. 2 there was a change from *B.*

As with the populations, the affinities of the different collections of individual trees changed to some extent as numbers of European taxa used in the principal component analyses were progressively decreased. In 3 taxa comparisons (ssp *pubescens*, *tortuosa* and *carpatica*) all 50 trees in the Morrone NNR sample were most closely related to ssp *tortuosa*, but specimens of the other 2 subspecies, in addition to ssp *tortuosa*,

were identified at the lower altitude Sluie Wood, some 30 miles along the River Dee from Morrone (Table 31 and Figure 43). It seems therefore that the 3 subspecies may occur in the same region, but their occurrence may differ locally with changes of habitat and altitude. In some locations the additional presence of *B. pendula* may, through the ease of inter-specific hybridization, give rise to further variants.

The analyses have indicated that samples of pubescent birch, mainly from the Scottish highlands and, by implication, representatives of ssp *odorata*, have close affinities with the continental ssp *pubescens*, *tortuosa*, and *carpatica*. While these similarities suggest that a re-examination of their taxonomic status might be rewarding, there is little doubt that they refute the idea of regionally distinct subspecies.

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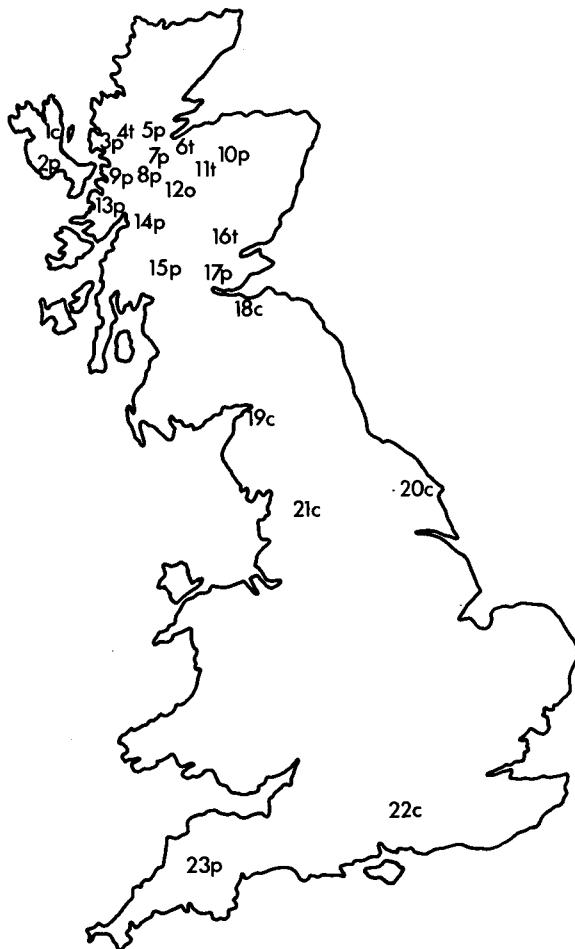


Fig. 42 Geographical locations of 23 British populations of *B. pubescens* with their affinities at the "5-taxa level" (*pendula*, *pubescens*, *tortuosa*, *carpatica*, *oycoviensis*). (*p* = *pubescens*, *t* = *tortuosa*, *c* = *carpatica*, *o* = *oycoviensis*).

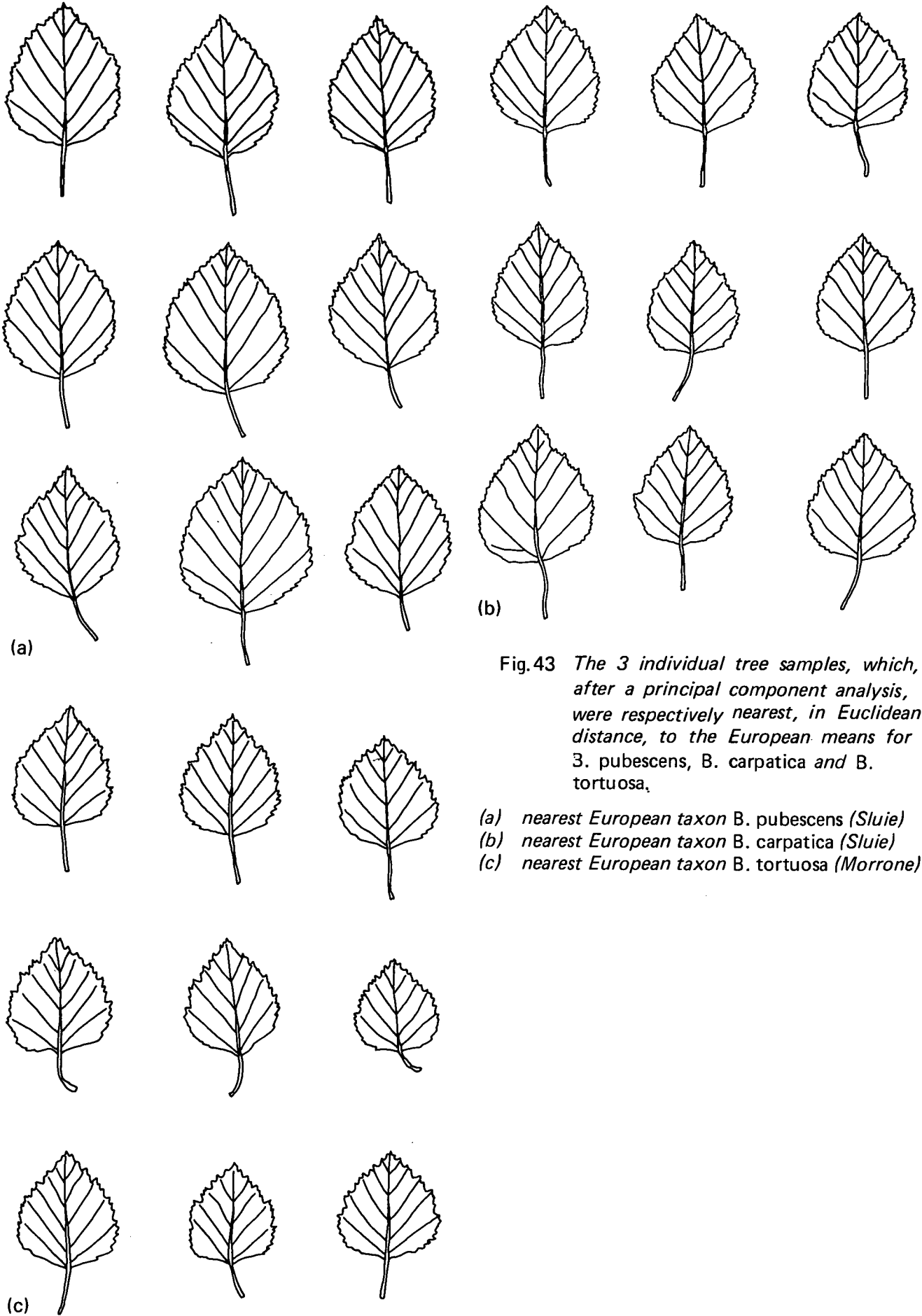


Fig.43 *The 3 individual tree samples, which, after a principal component analysis, were respectively nearest, in Euclidean distance, to the European means for B. pubescens, B. carpatica and B. tortuosa,*

- (a) *nearest European taxon B. pubescens (Sluie)*
 (b) *nearest European taxon B. carpatica (Sluie)*
 (c) *nearest European taxon B. tortuosa (Morrone)*