Multivariate analysis of the elms of northern France

II. Pooled analysis of the elm populations of northern France and England

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Summary

Biometrical foliar data from pooled sets of 655 French and of 1131 English samples, already described separately, were analysed by five different methods, the first three involving clustering, two based on data transformed to principal components and the third on untransformed data, and the second two on location of biometrical nearest neighbours of English elms in France, one using principal components and the other not.

Three major populations (two U. minor and one U. X hollandica) occur in northern France with no English counterpart, seven English populations (U. glabra, U. procera and five U. minor) are not derivable from northern France, while six English populations (five U. minor and one U. X hollandica) appear to have originated in northern France. Six main sources of the English elm flora are postulated. The first is spontaneous post-Glacial origin of U. glabra from Central Europe. The rest involve human introduction as follows: U. procera from Spain in the Bronze Age; the East Anglian and east Midland population of U. minor from Central Europe in the Bronze Age; the U. minor populations of coastal Essex and Kent from northern France in the Iron Age; Cornish U. minor from Brittany in the 1st millenium AD; and U. X hollandica (Dutch elm) from northern France via the Netherlands in the 17th century AD.

The first paper in this series (Richens and Jeffers, 1975) presented a biometrical analysis of the elm populations of the maritime departments of northern France from Nord to Loire-Atlantique. In the present paper, a pooled analysis is made of this French material merged with the English collection described earlier by Jeffers and Richens (1970). The results are used as a basis for considering the sources of the English elm flora.

Key words: ***Ulmus*** **minor** Mill., ***Ulmus*** glabra Huds., taxonomy, **principal-component** analysis, **migration, prehistory,** ethnobotany.

Zusammenfassung

Um die Taxonomie und Entstehung der englischen *Ulmus*-Population abzuklären, wurden 655 aus Frankreich und 1131 aus England stammende Blattproben mittels fünf unterschiedlicher biometrischer Methoden untersucht. Auf Grund der Untersuchungsergebnisise wird angenommen, daß sich diese Population in 7 Provenienzen aufteilen läßt. U. glabra ist aus Mitteleuropa eingewandert. Alle anderen Ulmen sind künstlich verbreitet worden, und zwar U. procera aus Spanien und zwei Populationen von U. minor aus Mitteleuropa während der Bronzezeit, zwei Populationen von U. minor aus dem nördlichen Frankreich während der Eisenzeit, die Ulme von Cornwall aus dem nördlichen Frankreich während des ersten Jahrtausends n. Chr. und U. X hollandica (Dutch elm) aus dem nördlichen Frankreich während des 16ten Jahrhunderts.

Material and Methods

The material was the combined set of 655 French and 1131 English samples decribed in the earlier papers. The foliar characters measured were: absolute length of the longer side of the lamina (AL); the breadth (TB), length (TL) and depth (TD) of the primary teeth on the shoulder of the leaf; relative breadth of the lamina (RB); relative petiole length (RP); relative asymmetry (RA); and number of secondary teeth (TN). Further details of these measurements are given in the previous paper.

Measurements of individual leaves or the modal values of groups are represented by the notation introduced in the previous paper, upper biometrical values of the characters cited above being represented by the respective capitals LBDWPAN and lower values by the corresponding lowercase letters lbdwpan. Tooth length is omitted as previously, being very strongly correlated with tooth breadth. The example quoted earlier was a specimen from Doullens *(So)* designated LbdwPN; this has upper-range values for AL, RB and TN, mid-range value for RA, and lower-range values for TB, TD and RB. Full details of this notation are given in the earlier paper.

Five analytic methods, MI, MII, MIII, MIV and MV, were used. They are as follows:

MI. The pooled samples were converted to principal components and clustered by a modification of the minimum spanning tree technique of Gower and Ross (1969). As previously, the relative measurements RB, RP and RA were converted to the respective absolute values AB, AP and AA. A different distance restriction was tried. Initial clustering was inhibited unless the members were within a distance of 1.00. First-order clusters were aggregated into second-order clusters with the distance restriction relaxed to 1.50, and successive higher-order clusters were made with the distance restriction relaxed by 0.50 per cycle. As before, second and higher-order clusters were disqualified if the component first-order clusters had both upper-range and lower-range values for any characters.

Bold letters (in capitals for principal components), prefixed to the biometrical designation, indicate the order of the cluster. Numerical subscripts are used to distinguish different clusters with the same biometrical designation. Subscripts attached to the cluster-order prefix indicate the population concerned: F, France; E, England; and J, the joint population. Superscripts attached to the cluster-order prefix indicate the method of clustering, h (hierarchical clustering) for the present method. Thus, $\mathbf{C}^{h}_{J}$.bPan$_{2}$ represents one of the third-order clusters of biometrical designation bPan generated by the present method from the pooled data.

MII. This method also utilized A clusters based on principal components, but instead of aggregating these by iterative clustering, second-order groups were constituted by all A clusters with the same biometrical designation. The superscript for this method is b (biometrically equivalent). Obviously, the A clusters in MI and MII are the same, so that, for example, $\mathbf{A}^{h}_{J}$.lbdwaN $\equiv$ $\mathbf{A}^{b}_{J}$.lbdwaN.

MIII. In this method, the biometrical data were not transformed to principal components. All samples with the same biometrical designation were allocated to a first-order cluster similarly designated. The cluster-order prefix is put in lower case to show that untransformed measurements rather than principal components are being used. Aggregation into second-order clusters was based on number of samples per **a** cluster. Any **a** cluster with more samples than any of its neighbours was treated as the frequency peak of a b cluster to which all its neighbours were

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attached. If an **a** cluster were attached to more than one frequency peak it was excluded from them all. The superscript for this method is f (frequency peak). For example, $\mathbf{a}^{f}_{J}$.lbdan has 15 members. It is bounded by $\mathbf{a}^{f}_{J}$.bdan, $\mathbf{a}^{f}_{J}$.ldan, $\mathbf{a}^{f}_{J}$.lban, $\mathbf{a}^{f}_{J}$.lbdWan, $\mathbf{a}^{f}_{J}$.lbdPan, $\mathbf{a}^{f}_{J}$.lbdn, $\mathbf{a}^{f}_{J}$.lbda, $\mathbf{a}^{f}_{J}$.lbdWan, $\mathbf{a}^{f}_{J}$.lbdwan, $\mathbf{a}^{f}_{J}$.lbdpan, none of which has more than 14 members. They are all attached to $\mathbf{a}^{f}_{J}$.lbdan, to constitute $\mathbf{b}^{f}_{J}$.lbdan. Occasionally, two neighbouring clusters have the same peak frequency; the neighbours of both were attached in this case to the two peak clusters.

MIV. This method utilized 13 well defined English elm populations, mainly the nuclei of those already described by Richens (1958, 1959, 1961 a, b, 1965, 1967). For each population, a list was made of all French samples which were nearest neighbours of any English specimen as shown by cluster analysis based on principal components. Each French nearest neighbour was then compared by visual inspection with its English equivalent plus four other samples from the same English population, taking into account also such additional characters as leaf and tooth-shape characteristics not represented by the eight biometrical characters, also type of indumentum and surface scabrosity. All French specimens lying within the range of variation of the English population in respect of all the characters recognizable by visual inspection were noted.

MV. The same 13 English populations were utilized as in MIV. Since a nearest-neighbour determination could not conveniently be made from the untransformed measurements, an analogue was devised as follows. The biometrical designation is a cell in a 7-dimensional hypercube with three values (lower range, mid-range and upper range) per dimension. The lower and upper ranges were now divided into subunits of equal size to the mid-range. Any French sample that fell into the same subunit as an English specimen was taken as one of its nearest neighbours. These were checked by visual inspection as in MIV. In order that the English analysis published earlier (Jeffers and Richens, 1970) should be comparable with the present joint analysis, the English material was reclustered under a more severe distance restriction (repeated clustering under distance restraints successively relaxed by 0.5) and under a cluster-range restriction similar to that used in the present paper. The resultant clusters are designated in the notation of the present paper.

The standard taxa are cited as before: *U. minor* Mill. sensu lato (Richens, 1968), *Um; U. procera* Salisb., *Up; U. glabra* Huds., *Ug;* and *U. glabra* × *U. minor* hybrids, *Umg.* The Channel Islands are treated as French for botanical purposes.

Results: (1) Methodology

The computational data used for clustering based on principal components are set out in *Tables 1, 2* and *3. Table 1* presents the minimum, mean and maximum values and standard deviations of the eight foliar characters for the pooled populations. *Table 2* gives the coefficients of correlation between the characters, while *Table 3* lists the first four principal components derived from these and used in the subsequent clustering.

By MI, the 1786 pooled samples aggregated into 524 $\mathbf{A}^{h}_{J}$ clusters, and these into 177 higher-order and residual $\mathbf{A}^{h}_{J}$

Table 1. — Minimum, mean and maximum values of the foliar characters.

Character	Minimum	Mean	Maximum	Standard Deviation
AL	26.2	59.70	138.0	12.09
TB	2.0	4.64	8.2	0.95
TL	2.5	4.79	9.6	0.94
TD	1.0	2.25	4.8	0.56
AB	17.3	38.54	68.04	8.42
AP	1.64	6.74	17.2	2.25
AA	0.4	5.20	16.56	2.36
TN	42.0	98.7	248.0	26.7

Table 2. — Coefficients of correlation.

TB	0.472						
TL	0.485	0.942					
TD	0.321	0.764	0.787				
AB	0.749	0.641	0.573	0.607			
AP	0.237	0.010	0.031	-0.132	0.057		
AA	0.512	0.390	0.333	0.286	0.609	0.374	
TN	0.675	0.118	0.172	0.103	0,492	0.158	0.454
	AL	TB	TL	TD	AB	AP	AA

Table 3. — First four principal components.

		1	2	3	4
Latent root		4.10	1.70	0.93	0.51
% total variance		51.3	21.3	11.6	6.4
Latent vector elements	AL	0.8908	0.6448	0.2824	0.4842
	TB	0.9575	-0.6946	-0.2347	0.1465
	TL	0.9466	-0. 872	-0.2201	0.3821
	TD	0.8460	-0.8453	-0.0286	-0.1422
	AB	1.000	0.1562	0.2483	-0.3145
	AP	0.1841	0.9565	-1.000	0.4028
	AA	0.7529	0.7095	-0.2773	-1.000
	TN	0.5898	1.000	0.5938	0.3054

Table 4. — Geographical distribution of the larger higher-order clusters.

Cluster	England	France (including Channel Islands)
MI		
$\mathbf{D}^{h}_{J}$.lbdan$_{1}$	K(2), Ex(4), Ht(3), Bd(2), Sf, Ha, Li(3)	Nd, Calv(2), Mche(14), Je, CN, Fin(7), Morb, LC(3), Lret
$\mathbf{B}^{h}_{J}$.lbda	K(7), Ex(4), Bd, Hu	Nd, PC, So(2), Eu, Mche(2), Je(2), Gu, Ald, IV, BR, Gers
$\mathbf{C}^{h}_{J}$.lbdPan	K(2), Ex(6), Ht(2), Bd(2), Hu(5)	So, SMar, Eu(2), Mche(2), IV, CN(2), Fin, Morb, ML, Gers(3), Lret, Sthe
$\mathbf{C}^{h}_{J}$.lban	K(12), Ex(5), Ht, Bd, Hu(5), Np	Mche(6), Je(6), Gu, CN(4), Fin(2), Morb, Gers(2)
$\mathbf{C}^{h}_{J}$.ba	K(4), Ex(3), Ht(3), Bd(4), Hu(5), Y	PC(3), Eu, Or(3), Je(5), Sk, IV, Fin(3), Morb(2), Gers(2)
$\mathbf{C}^{h}_{J}$.bPan$_{1}$	K(2), Ex(11), Ht(7), Bd(3), Hu(10), Li	So, SMar(3), Or(2), Mche(4), IV(4), CN(5). Fin(5), Morb(3), Latl, Oi, Sthe
$\mathbf{C}^{h}_{J}$.bPan$_{2}$	K(4), Ex(16), Ht(2), Bd, Hu(6)	So, Mche(4), Je(4), Ald, IV(3), CN(4), Fin(2), Morb(2), LAtl, LC
$\mathbf{C}^{h}_{J}$.bPn	Ex(11), Ht(3), Hu(3), Sf, Li, Nf	PC, Or, Mche, Gu, IV(3), CN, Morb, Sthe
$\mathbf{B}^{h}_{J}$.bP$_{2}$	K, Ex(9), Hu	PC, Eu(2), Calv(2), Mche, IV(2), Fin, Morb, LAtl, Gers
$\mathbf{B}^{h}_{J}$.DPn	Ex(7), Ht(2), Bd, Hu, Sf(8), Le, Nf	Mche, CN, Morb, EL
$\mathbf{C}^{h}_{J}$.DWpan	K(11), Ht(14), Bd(6), Sx	Calv, CN
$\mathbf{B}^{h}_{J}$.DWn	K(2), Ex(3), Ht(13), Bd(23), Hu, Sp	Je
$\mathbf{B}^{h}_{J}$.DW$_{1}$	K(12), Ex(8), Ht(10), Bd(7), Hu, Br, O	PC
$\mathbf{C}^{h}_{J}$.DWAn$_{1}$	Ex(16), Ht(24), Bd(33), Hu(3), Sf(7), Br, Bu, El(5), Li(4), Sr	PC, Sk
$\mathbf{B}^{h}_{J}$.DWA	Ex(13), Ht(2), Bd(2), El, Li	So, Mche(2), Je(2)
$\mathbf{B}^{h}_{J}$.BDW	Ex(9), Ht(4), Bd(15), El, Li(3), Ss	Ald
$\mathbf{C}^{h}_{J}$.LbwPa	Ex(11), Ht, Bd(3), Hu(8), Sf, El(4)	PC(2), So, SMar, Eu(2), Or, Mche(2), Morb, Gers, HRh, LC, Oi
$\mathbf{C}^{h}_{J}$.LbPAN	Ex(17), Ht, Bd(2), Hu, Sf, El, Li	So, Eu, Or(2), Calv(7), Mche(3), Je(2), LAtl, Lot, Oi
$\mathbf{C}^{h}_{J}$.LDwa	Ex, Ht, Bd, Hu, Sf(13), Le, Li(3)	Mche, IV, Fin, LAtl
$\mathbf{B}^{h}_{J}$.LDaN	Ex(5), Bd, Sf(8), El(2)	PC, So(2), Calv, Je(2), Fin, Gers, LC
$\mathbf{B}^{h}_{J}$.LDN	Ex(7), Bd(2), Sf, El(2), Li(2)	PC, So, Calv, Je(2), IV(2), CN, Dord
$\mathbf{B}^{h}_{J}$.LDWA	Ex(10), Ht, Sf	Eu, Calv, Mche, Je(3), Sk, AlpM
$\mathbf{C}^{h}_{J}$.LBDPAn	Ex(7), Sf(11), El(4), Le	Calv, Mche(2)
MIII		
$\mathbf{b}^{f}_{J}$.lbdan	K(15), Ex(7), Ht(2), Hu, Sf, Li	Nd, Eu, Calv(2), Mche(10), Je(2), Gu, Ald(2), CN(7), Fin(7), Morb(3), BR, Lret, ML, PyrO, Sthe
$\mathbf{b}^{f}_{J}$.bdwP	K(4), Ex(8), Hu(8)	PC, So, SMar, Calv(4), Mche, Je, IV, Fin, Morb
$\mathbf{b}^{f}_{J}$.bdPn	Ex(8), Ht(2)	So, SMar, Eu(2), Or, Calv(2), Mche, CN(6), Fin(2), Morb(4), LC, Lot
$\mathbf{b}^{f}_{J}$.bwan	K(4), Ex(12), Ht(11), Bd(3), Hu(10), Co	PC, SMar(2), Or(4), Mche(5), Je(4), IV(2), Fin(2), Morb, Gers(2)
$\mathbf{b}^{f}_{J}$.bP	K(4), Ex(18), Br(2), Sx	So(4), SMar(3), Eu(3), Or(2), Calv, Mche(3), Je(5), Gu(4), IV(4), CN, Fin, Morb(4), LAt(12)
$\mathbf{b}^{f}_{J}$.DWn	K(12), Ex(25), Ht(61), Bd(72), Hu(5), Br(2), Bu(2), Ha, Li, O, Sp, Sr, Sx, Wo	Je, Herm, CN, BAlp, EL
$\mathbf{b}^{f}_{J}$.LbdwPN	Ex(2), Hu(2), El, Li	PC(6), So(5), SMar(2), Eu(3), Se
$\mathbf{b}^{f}_{J}$.LbwaN	Ex(11), Bd(3), Hu(4), El, Le, Li(2)	PC, So, Eu(2), Mche, Dord
$\mathbf{b}^{f}_{J}$.LbPN	Ex(11), Hu	So, Or(3), Calv(3), Mche,Je, Cher, Oi, HRh
$\mathbf{b}^{f}_{J}$.LDpaN	Ex(6), Bd(5), Sf, Ch, La, Du, Li(2), Nb, Ss	So(2), Eu(3), Mche(2), Gu(4), IV, CN(2), Fin(2), Gers, LC
$\mathbf{b}^{f}_{J}$.LDPAN	Ex(19), Bd, Sf, El, Li, Nf	Calv(3), Mche(6), Je(11), Gu(3), Ald(6), CN, Morb
$\mathbf{b}^{f}_{J}$.LDWN	Ex(7), Ht, Bd(2), Sf(2), El(2), Li(3)	PC, So(3), Eu, Calv(5), Mche(5), Je(3), Ald, Herm, IV(2), CN, BR, Vau
$\mathbf{b}^{f}_{J}$.LBDn	Ex(2), Ht, Bd(2), Sf(13), El(2), Li(3)	PC, Mche, IV
$\mathbf{b}^{f}_{J}$.LBDPA	Ex, Sf(10), El(3)	Calv(2), Je(3)

Abbreviations:

ENGLAND. Bd, Bedfordshire; Br, Berkshire; Bu, Buckinghamshire; Ca, Cambridgeshire; Ch, Cheshire; Co, Cornwall; Du, Co. Durham; El, Isle of Ely; Ex, Essex; G, Gloucestershire; Ha, Hampshire; Ht, Hertfordshire; Hu, Huntingdonshire; K, Kent; La, Lancashire; Le, Leicestershire; Li, Lincolnshire; Mx, Middlesex; Nb, Northumberland; Nf, Norfolk; Np, Northamptonshire; Nt, Nottinghamshire; O, Oxfordshire; Sf, Suffolk; Sp, Shropshire; Sr, Surrey; Ss, Somerset; Sx, Sussex; Wa, Warwickshire; We, Westmorland; Wo, Worcestershire; Y, Yorkshire.

FRANCE. Ald, Alderney; AlpM, Alpes-Maritimes; Aube; BALp, Basses-Alpes; BR, Bouches-de-Rhône; Calv, Calvados; Ch, Cher; CN, Côtes-du-Nord; Dord, Dordogne; EL, Eure-et-Loir; Eu, Eure; Fin, Finistère; Gers; Gu, Guernsey; Herm; HRh, Haut-Rhin; HSne, Haute-Saône; IV, Ille-et-Villaine; Je, Jersey; LAtl, Loire-Atlantique; LC, Loire-et-Cher; Lot; Lret, Loiret; Mche, Manche; ML, Maine-et-Loire; Morb, Morbihan; Nd, Nord; Oi, Oise; PyrO, Pyrénées-Orientales; Se, (Seine); Sk, Sark; SL, Saône-et-Loire; SMar, Seine-Maritime; So, Somme; Sthe, Sarthe; Vau, Vaucluse.

clusters. Of the initial $\mathbf{A}^{h}_{J}$ clusters, 77 were exclusively French, 204 were English and 234 mixed, a ratio of 15 : 39 : 46. The larger higher-order clusters (20+ members) and their geographical distribution are set out in the first part of *Table 4*. The parallel results for MII are not tabulated for reason of brevity but are used hereafter concurrently with those of MI.

By MIII, the 1786 samples aggregated into 842 $\mathbf{a}^{f}_{J}$ clusters and these into 419 $\mathbf{b}^{f}_{J} + \mathbf{a}^{f}_{J}$ clusters. Of the initial $\mathbf{a}^{f}_{J}$ clusters, 153 were exclusively French, 229 were English and 160 mixed, a ratio of 34 : 41 : 35. The larger MIII clusters (20+ members) are set out in the second part of *Table 4*.

Table 5. — Enumeration of larger higher-order clusters contributing to the Englsih local populations. The number of representatives from each cluster is added in brackets. Clusters contribution one representative only are omitted.

English local population	Method	Clusters
Up	MI	**C**$^{h}_{J}$.DWpan(12), **B**$^{h}_{J}$.DWn(43), **B**$^{h}_{J}$.DW$_1$(40), **C**$^{h}_{J}$.DWAn$_1$(77), **B**$^{h}_{J}$.DWA(20), **B**$^{h}_{J}$.BDW(23)
	MIII	**b**$^{f}_{J}$.Dwn(184),, **b**$^{f}_{J}$.LDWN(7), **b**$^{f}_{J}$.LDPAN(3), **b**$^{f}_{J}$.LBDn(2)
East Anglia	MI	**B**$^{h}_{J}$.DPn(10), **C**$^{h}_{J}$.DWAn(8), **C**$^{h}_{J}$.LDwa(13), **B**$^{h}_{J}$.LDaN(8), **C**$^{h}_{J}$.LBDPAn(11)
	MIII	**b**$^{f}_{J}$.LBDn(14), **b**$^{f}_{J}$.LBDPA(9)
Godmanchester (includes Dean)	MI	**B**$^{h}_{J}$.lbda(3), **C**$^{h}_{J}$.lbdPan(6), **C**$^{h}_{J}$.lban(6), **C**$^{h}_{J}$.ba(6), **C**$^{h}_{J}$.bPan$_1$(12), **C**$^{h}_{J}$.bPan$_2$(6), **C**$^{h}_{J}$.LbwPa(9)
	MIII	**b**$^{f}_{J}$.bdwP(9), **b**$^{f}_{J}$.bwan(12), **b**$^{f}_{J}$LbdwPN(2), **b**$^{f}_{J}$.LbwaN(4)
Kent	MI	**D**$^{h}_{J}$.lbdan$_1$(2), **B**$^{h}_{J}$.lbda(7), **C**$^{h}_{J}$.lbdPan(2), **C**$^{h}_{J}$.lban(12), **C**$^{h}_{J}$.ba(4), **C**$^{h}_{J}$.bPan$_1$(2), **C**$^{h}_{J}$bPan$_2$(4)
	MIII	**b**$^{f}_{J}$.lbdan(15), **b**$^{f}_{J}$.bwan(3), **b**$^{f}_{J}$.bP(4)
Ug	MI	—
	MIII	**b**$^{f}_{J}$.LDpaN(13)
Colchester (includes Layer)	MI	**C**$^{h}_{J}$.LbwPa(2)
	MIII	**b**$^{f}_{J}$.bP(3)
Clacton	MI	**C**$^{h}_{J}$.lban(2), **C**$^{h}_{J}$.bPan$_2$(3)
	MIII	**b**$^{f}_{J}$.bdwP(2), **b**$^{f}_{J}$.bdPn(2)
Epping	MI	**C**$^{h}_{J}$.bPan$_1$(2), **C**$^{h}_{J}$.bPan$_2$(2), **B**$^{h}_{J}$.bP$_2$(2)
	MIII	**b**$^{f}_{J}$.bdwP(2), **b**$^{f}_{J}$.bdPn(2), **b**$^{f}_{J}$.bP(2)
Hundon (includes Tewin)	MI	**C**$^{h}_{J}$.ba(2), **C**$^{h}_{J}$.bPan$_1$(3)
	MIII	**b**$^{f}_{J}$.bwan(4)
Dengie	MI	**C**$^{h}_{J}$.bPan$_2$(2), **B**$^{h}_{J}$.bP$_2$(2)
	MIII	**b**$^{f}_{J}$.bdPn(3), **b**$^{f}_{J}$.bP(6)
Dutch elm	MI	**B**$^{h}_{J}$.LDaN(2), **B**$^{h}_{J}$.LDN(2)
	MIII	**b**$^{f}_{J}$.LDpaN(4), **b**$^{f}_{J}$.LDWN(5)
Carlton	MI	—
	MIII	—
Braughing	MI	**C**$^{h}_{J}$.bPan$_1$(2)
	MIII	—

Table 6. — Geographical distribution of the French nearest neighbours of the English local populations.

English local population	Method	French nearest neighbours
Up	MIV	PC, So, Eu, Mche(2), Gu(3)†, Ald*, Herm(2)**††, IV†, Fin, Morb
	MV	Eu, Calv, Mche(2), Gu(2)†, Herm(2)**††, IV(3)†, CN, AlpM, Balp, EL
East Anglia	MIV	So, SMar(2), Calv, Mche(2), Je(4), Sk, IV, Morb, LAtl, Sthe
	MV	—
Godmanchester	MIV	Nd, PC, SMar†, Eu, Or(4), Calv(3)†, Mche(2), Je(4), Gu, IV(2)†, CN(2)†, Fin(4), Morb, LAtl, Gers, HSne, ML, Sthe
	MV	So, SMar†, Eu, Or(3)*, Calv(2)†, Mche, Je(2), IV(2)†, CN(2)†, Fin*, Gers, Sthe
Kent	MIV	PC, So(2), Calv, Mche(2)*, Gu, CN, Fin†, Aube, EL, LC
	MV	Nd(2)*, Eu(4), Or, Calv(4), Mche(3), Je(2), IV(2), Fin(3)*†, Morb(2), EL, Gers, Oi, PyrO
Ug	MIV	PC*, So, Eu, Calv, Mche(3)**, Gu*, IV, Fin
	MV	—
Colchester	MIV	IV
	MV	PC, Eu, Or, Calv, Mche(2)*, Je, Gu(2), Fin, Morb
Clacton	MIV	So, SMar, Je†, CN(3), Fin, Morb(3)*†, LAtl*†
	MV	Je†, Morb(2)††, LAtl*†
Epping	MIV	SMar, Mche, IV, CN(2), Morb, LAtl
	MV	IV, Morb, ML, Sthe
Hundon	MIV	PC†, Mche, CN(2), Fin, Morb, Gers
	MV	PC(2)*†, So, Eu, Mche, Je, IV, CN(2), Fin**, Morb
Dengie	MIV	PC*, Eu†, Or*, Calv*†, Mche, Je(2)*, IV*, CN
	MV	So, SMar, Eu(4)†, Calv*†, Mche(3), Je(2)**, Gu, IV, CN(3), Fin(2), Morb (3)
Dutch elm	MIV	So*, Eu, Mche(3), Je(2), IV, CN(2), Fin
	MV	—
Carlton	MIV	Je
	MV	—
Braughing	MIV	Morb
	MV	—

Abbreviations: as in Table 4
* nearest neighbour match confirmed by visual inspection
† nearest neighbour common to MIV and MV

The composition of the 13 English populations used in MIV and MV in terms of the larger higher-order clusters is set out in *Table 5*. Again, for brevity, the results from MII are not tabulated. The geographical distribution of nearest-neighbour specimens as derived by MIV and MV is shown in *Table 6*.

A point requiring early consideration is the stability of the clustering before and after pooling the data.

The 525 $\mathbf{A}^{h}_{J}$ clusters can be divided into eleven categories in respect of their relations to the $\mathbf{A}^{h}_{E}$ clusters of the previous English analysis and the $\mathbf{A}^{h}_{F}$ clusters of the previous French analysis. The first two categories include clusters completely unaffected by pooling; 98 $\mathbf{A}^{h}_{J}$ clusters are identical with $\mathbf{A}^{h}_{E}$ clusters and 43 $\mathbf{A}^{h}_{J}$ clusters are identical with $\mathbf{A}^{h}_{F}$ clusters. Thus 141 clusters, just over one quarter, have been totally unaffected by pooling. Somewhat surprisingly, 84 $\mathbf{A}^{h}_{J}$ clusters are parts of single $\mathbf{A}^{h}_{E}$ clusters and 21 parts of single $\mathbf{A}^{h}_{F}$ clusters, so a further 105 $\mathbf{A}^{h}_{J}$ clusters represent parts of unpooled clusters but without rearrangement. Six $\mathbf{A}^{h}_{J}$ clusters only were formed by simple juncture of a single $\mathbf{A}^{h}_{E}$ cluster with a single $\mathbf{A}^{h}_{F}$ cluster, but 24 $\mathbf{A}^{h}_{J}$ clusters resulted from juncture between a whole $\mathbf{A}^{h}_{F}$ cluster and part of an $\mathbf{A}^{h}_{E}$ cluster, and 35 $\mathbf{A}^{h}_{J}$ clusters arose from juncture between a whole $\mathbf{A}^{h}_{E}$ clusster and part of an $\mathbf{A}^{h}_{F}$ cluster. However 92 $\mathbf{A}^{h}_{J}$ clusters were formed from part of an $\mathbf{A}^{h}_{F}$ cluster attached to part of an $\mathbf{A}^{h}_{E}$ cluster. So 157 $\mathbf{A}^{h}_{J}$clusters are constituted of two portions with no interchange between $\mathbf{A}^{h}_{F}$ clusters or between $\mathbf{A}^{h}_{E}$ clusters.

The remaining $\mathbf{A}^{h}_{J}$ clusters are in more complex relation to the unpooled clusters; 6 are composed of parts of two or more $\mathbf{A}^{h}_{F}$ clusters, 21 of parts of two or more $\mathbf{A}^{h}_{E}$ clusters, and 83 from parts of three or more of the unpooled clusters, some French and some English. Thus, this last complex category comprises 110 $\mathbf{A}^{h}_{J}$ clusters.

In general, it appears that the clusters are stable under pooling though with a tendency to fragment. The average sizes of the French, English and pooled $\mathbf{A}^{h}$ clusters are 3.0, 3.3 and 3.4, respectively.

Having assured oneself of the relative stability of the $\mathbf{A}^{h}$ clusters, it is necessary to consider the more fundamental point of the value of transforming the original measurements to principal components.

The range of the $\mathbf{A}^{h}_{J}$ clusters based on principal components can be conveniently examined by an analogous method to that used to restrain higher-order clustering, i.e. by identifying any $\mathbf{A}^{h}_{J}$ cluster that has both upper and lower range values for any of the seven characters in the biometrical designation. Out of the 525 $\mathbf{A}^{h}_{J}$ clusters, 421 do not include both upper and lower range values for any character and these can be regarded as satisfactorily compact. In the remainder, the number of clusters that include upper and lower range values for each character are as follows: AL, 14; TB, 0; TD, 6; RB, 57; RP, 5; RA, 10; and TN, 27. The characters that are conspicuously most variable within clusters are thus relative breadth, followed by tooth number.

A few $\mathbf{A}^{h}_{J}$ clusters are completely invariant in the biometrical designation of their components. For example, $\mathbf{C}^{h}_{J}$.DWAn$_1$ includes three $\mathbf{A}^{h}_{J}$ clusters whose components are exclusively DWn, and one each exclusively DW, DWAn and BDWn. At the other extreme, $\mathbf{A}^{h}_{J}$.bPa$_2$ comprises three specimens, lbDWPn, bdwPaN and LbdwPan, which between them show upper and lower range values for four characters, AL, TD, RB and TN. While, therefore, most of the $\mathbf{A}^{h}_{J}$ clusters are compact, roughly one fifth are more diffuse than one would have wished.

A comparison between the $\mathbf{A}^{h}_{J}$ and $\mathbf{a}^{f}_{J}$ clusters can be made in respect of the independent criterion of geographical distribution. It was stated above that while the ratio of French : English : mixed $\mathbf{A}^{h}_{J}$ clusters was 15 : 39 : 46, the corresponding ratio for the $\mathbf{a}^{f}_{J}$ clusters was 34 : 41 : 35. The proportion of English clusters is nearly the same in both, but transformation to principal components has reduced the number of exclusively French clusters considerably. Average cluster size is almost the same in the two cases, 3.4 for $\mathbf{A}^{h}_{J}$ and 3.3 for $\mathbf{a}^{f}_{J}$.

Turning now to MIV, the usefulness of converting the data to principal components was tested by using the nearest-neighbour relations of two of the English populations : Kent and Godmanchester. Each English population plus the French samples in nearest-neighbour relationship to any of the members can be regarded as a single aggregate population of which the English and French populations are subsets. The expectation, if the aggregate population is homogeneous, is that the English and French subsets are not biometrically divergent.

The expectation was realized for the Kent population which had 11 French nearest neighbours. The modal biometrical designation of the 11 members of the English subset was bdP and of the corresponding French subset ba. The frequencies of the characters whose modes did not correspond were: (TD) d, 7; mid-value 4; D, zero, for England; d, 4; mid-value 6; D, 1, for France; (RP) p, zero; mid-value, 5; P, 6, for England; p, 1; mid-value, 6; P, 4, for France; and (RA) a, 5; mid-value, 5; A, 1, for England; and a, 7; mid-value, 3; A, 1, for France. The differences between the English and French subsets are too slight to suggest an overall disparity.

The Godmanchester population had 32 French nearest neighbours. The modal biometrical designation of the 32 members of the English subset was bwPa and of the corresponding French subset bPa. Only one character, relative breadth, is divergent, but its frequency distribution was as follows : (RB) w, 31; mid-value 1; W, zero, for England; w, 10; mid-value 17; W, 5, for France. This is a very marked difference, presumably associated with the fact recorded above that RB is the most variable character within $\mathbf{A}^{h}_{J}$ clusters based on principal components.

It is not immediately apparent why conversion to principal components involves a loss of diagnostic information in respect of relative breadth. However, as JEFFERS and RICHENS (1970) have pointed out earlier, there is very considerable heterogeneity of variance within the all-England population, several correlations becoming reversed in sign between subsets. It is also the case that the untransformed measurements used here were chosen to be as independent as possible, which is confirmed by the fact that every combination of upper, mid-range and lower values for each pair of characters occurs. Possibly, under these circumstances, the usual benefits of conversion to principal components no longer avail.

Detailed correspondences in geographical distribution between the largest higher-order clusters contributing to the local English populations, as generated by MI, MII and MIII, are rather few. Two examples must suffice. The largest higher-order clusters contributing to the Kent populations are $\mathbf{C}^{h}_{J}$.lban *(Fig. 1 a)*, $\mathbf{B}^{b}_{J}$.lbdan *(Fig. 1 b)* and $\mathbf{b}^{f}_{J}$.lbdan *(Fig. 1 c)* by the three methods respectively. The corresponding clusters comprise 47, 22 and 74 members. $\mathbf{C}^{h}_{J}$.lban agrees with $\mathbf{B}^{b}_{J}$.lbdan in having concentrations of members in Kent and the Cotentin — North Brittany area;

it differs in also having concentrations of members in Essex and Huntingdonshire. $\mathbf{C}^{h}_{J}$.lban agrees with $\mathbf{b}^{f}_{J}$.lbdan in its distribution in Kent and Cotentin — North Brittany; it is more frequent than $\mathbf{b}^{f}_{J}$.lbdan in Huntingdonshire, but $\mathbf{b}^{f}_{J}$.lbdan is more frequent in Finistère. $\mathbf{B}^{b}_{J}$.lban resembles $\mathbf{b}^{f}_{J}$.lbdan in its concentration of samples in Kent and Cotentin — North Brittany but lacks the representation in Essex and Finistère of the latter. Only two samples, from

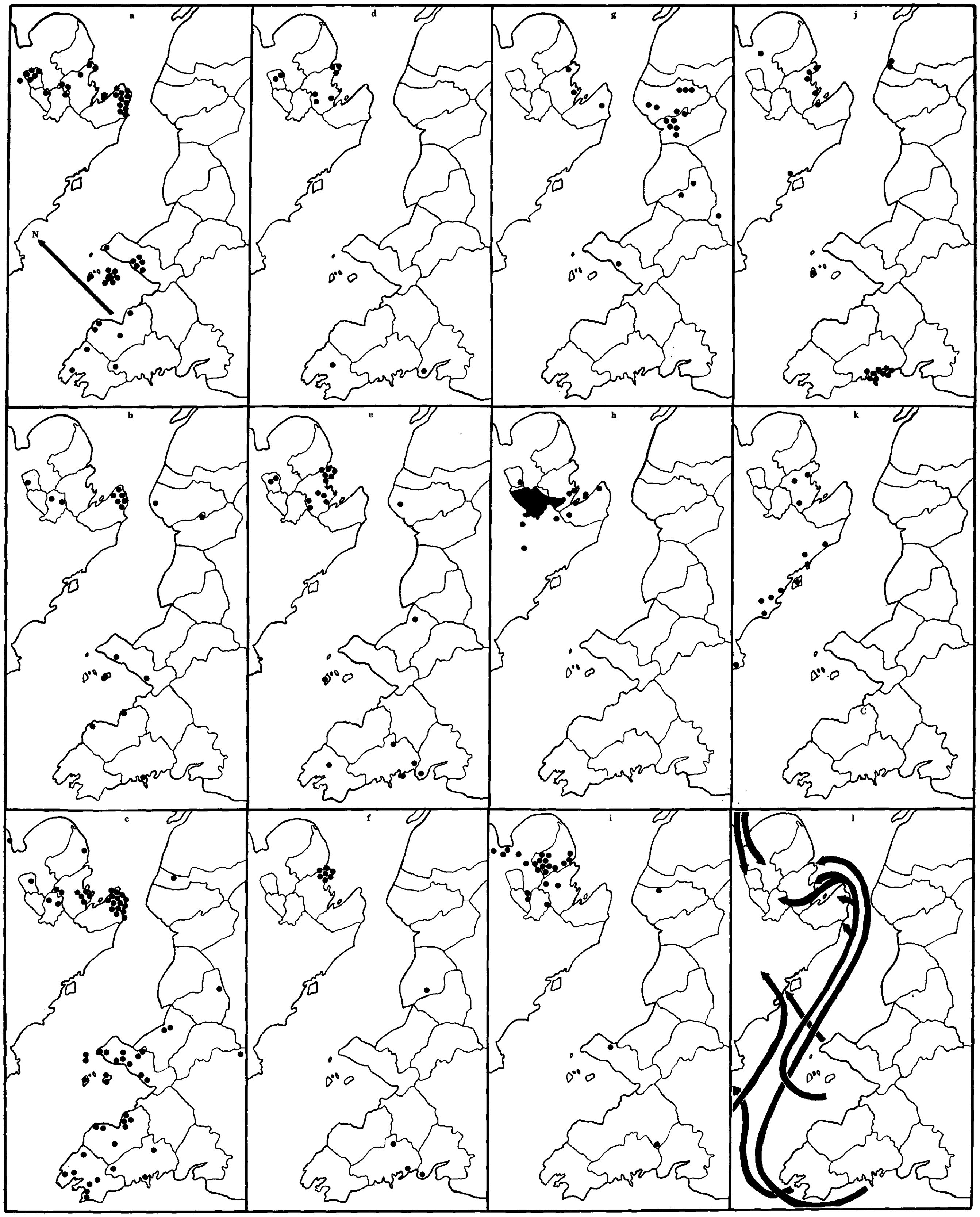

Figure 1. — *a.* $\mathbf{C}^{h}_{J}$.lban. *b.* $\mathbf{B}^{b}_{J}$.lbdan. *c.* $\mathbf{b}^{f}_{J}$.lbdan. *d.* $\mathbf{A}^{h}_{J}$.bdwPn. *e.* $\mathbf{B}^{b}_{J}$.bdwPn. *f.* $\mathbf{a}^{f}_{J}$.bdwPn. *g.* $\mathbf{C}^{h}_{J}$.bdwN. *h.* $\mathbf{B}^{b}_{J}$.DWn. *i.* $\mathbf{b}^{f}_{J}$.LBDn. *j.* Distribution of prehistoric salt pans, based on NENQUIN (1961), *k.* Site of *Coriosolis (C) and distribution of coins of the Coriosolites in England, based on ALLEN (1958). *l.* Putative immigration routes.

Bekesbourne and Seasalter in Kent, were common to all three clusters. A total of 17 samples from Kent, Hertfordshire, Essex, Jersey, Cotentin and Brittany, were common to $\mathbf{C}^{h}_{J}$.lban and $\mathbf{b}^{f}_{J}$.lbdan; 3 were common to $\mathbf{C}^{h}_{J}$.lban and $\mathbf{B}^{b}_{J}$.lbdan; and 8 were common to $\mathbf{B}^{b}_{J}$.lbdan and $\mathbf{b}^{f}_{J}$.lbdan. Of samples confined to one of the clusters only, 23 pertained to $\mathbf{C}^{h}_{J}$.lban, 7 to $\mathbf{B}^{b}_{J}$.lbdan and 41 to $\mathbf{b}^{f}_{J}$.lbdan.

The second example is based on the Clacton population. The largest higher-order clusters (not in the tables) contributing to this by the three respective methods are $\mathbf{A}^{h}_{J}$.bdwPn *(Fig. 1 d)*, $\mathbf{B}^{b}_{J}$.bdwPn *(Fig. 1 e)* and $\mathbf{a}^{f}_{J}$.bdwPn *(Fig. 1 f)*. The corresponding cluster sizes are 10, 21 and 11. The general distributions of the three clusters are similar, a concentration in north-east Essex and another in south Brittany. There are three samples common to all three clusters: Great Oakley and Frinton from Essex, and St. André-des-Eaux from Loire-Atlantique. In contrast to the previous comparison, no samples were common only to the clusters generated by MI and MIII; 6 were common to $\mathbf{A}^{h}_{J}$.bdwPn and $\mathbf{B}^{b}_{J}$.bdwPn; and 3 were common to $\mathbf{B}^{b}_{J}$.bdwPn and $\mathbf{a}^{f}_{J}$.bdwPn. Of the samples confined to one of the clusters only, 1 was peculiar to $\mathbf{A}^{h}_{J}$.bdwPn, 7 to $\mathbf{B}^{b}_{J}$.bdwPn, and 5 to $\mathbf{a}^{f}_{J}$.bdwPn.

Thus, though the three methods generate clusters with rather general correspondences, the detailed correspondences are few. MI and MIII produced most overlap for the Kent comparison, MI and MII for the Clacton comparison.

The results of these methodological comparisons can be summarized as follows. MI has the great advantage of disposing the material in the smallest number of higher-order clusters. However, the clusters generated by MIII tended to be less variable and more geographically homogeneous than the clusters of MI and MIII and they were not subject to the loss in diagnostic information that particularly affected RB in MI. To these theoretical advantages one could add the practical points that MIII is a desk method and stable through updating.

Possibly the optimum method for this material would retain the clustering technique of MI but be applied to Euclidean or city-block distances in the 7-dimensional hyperspace of the untransformed measurements rather than the 4-dimensional hyperspace of the first four principal components.

In the ensuing discussion, no method is given preference and all are utilized in analysing each population.

Results: (2) French populations

Three substantial French populations appear to be unrepresented by any derived population north of the English Channel. They are as follows:

(1) A *Um* population with leaves of medium breadth, medium to higher tooth number and long petiole. It is principally represented By $\mathbf{B}^{h}_{J}$.bP$_3$ (not in table) and $\mathbf{C}^{h}_{J}$.LbPAN by MI and $\mathbf{b}^{f}_{J}$.LbPN by MIII. Only small clusters covering this assemblage were generated by MII. Elms of this type are frequent in Normandy and southern Picardy. In the previous French analysis, this assemblage was chiefly represented by $\mathbf{B}^{h}_{F}$.LbPN$_2$ and $\mathbf{C}^{h}_{F}$.LbPAN.

(2) The narrow-leaved *Um* population of Picardy. This aggregated mainly under $\mathbf{C}^{h}_{J}$.bdwN *(Fig. 1 g)* (not in table) by MI and $\mathbf{b}^{f}_{J}$.LbdwPN by MIII, these clusters corresponding to $\mathbf{C}^{h}_{J}$.LbdwPN of the earlier analysis. This is one of the principal elms over much of Picardy.

(3) The *Umg* population of Cotentin and the Channel Islands. This aggregated mainly under $\mathbf{B}^{h}_{J}$.LDWPN and $\mathbf{B}^{h}_{J}$.LDWPN (neither in table) by MI, $\mathbf{B}^{b}_{J}$.LDN and $\mathbf{B}^{h}_{J}$.LDWAN by MII and $\mathbf{b}^{f}_{J}$.LDPAN by MIII. This population corresponds to hybrid III of the previous paper (Richens and Jeffers, 1975) in which it aggregated chiefly under $\mathbf{B}^{h}_{F}$.LDPN$_1$, $\mathbf{B}^{h}_{F}$.LDPN$_2$, $\mathbf{C}^{h}_{F}$.LDPAN and $\mathbf{B}^{h}_{F}$.LDWPAN.

It may be significant that the two *Um* populations are amongst those which, it was previously suggested, had reached northern France via the interior, and not by sea. The *Umg* population was thought to have arisen *in situ* by hybridization between immigrant *Um* and relict *Ug*.

Results: (3) English populations

The following English populations appear to have no corresponding population in northern France from which a derivation could be inferred:

(1) *Up*. This is the most widespread population in central, south and west England. It aggregated chiefly under $\mathbf{B}^{h}_{J}$.Dwn, $\mathbf{B}^{h}_{J}$.DW$_1$ and $\mathbf{C}^{h}_{J}$.DWAn, by MI, $\mathbf{B}^{b}_{J}$.DWn *(Fig. 1 h)* by MII and $\mathbf{b}^{f}_{J}$.DWn by MIII. The only French nearest-neighbour specimens which were confirmed on visual inspection were from Alderney and Herm, whither they were presumably taken from England by English immigrants. In the previous English analysis, the main aggregations were under $\mathbf{B}^{h}_{E}$.BDWn, $\mathbf{C}^{h}_{E}$.DW and $\mathbf{B}^{h}_{E}$DW$_2$.

(2) East Anglia. This *Um* group, a major constituent of the elmscape of East Anglia and the eastern Midlands, mainly aggregated under $\mathbf{B}^{h}_{J}$.DPn, $\mathbf{C}^{h}_{J}$.LDwa, $\mathbf{B}^{h}_{J}$.LDaN and $\mathbf{C}^{h}_{J}$.LBDPAn by MI, and $\mathbf{b}^{f}_{J}$.LBDn *(Fig. 1 i)* and $\mathbf{b}^{f}_{J}$.LBDPA by MIII. No salient clusters emerged by MII. No nearest-neighbour French specimens were found by MV and those identified by MIV were not confirmed by visual inspection. The corresponding clusters in the English analysis were $\mathbf{D}^{h}_{E}$.LBDPan and $\mathbf{D}^{h}_{E}$.LBDPA.

(3) Godmanchester. This *Um* group occupies the whole of Huntingdonshire and the northern part of Bedfordshire. It aggregated principally under $\mathbf{C}^{h}_{J}$.lbdPan, $\mathbf{C}^{h}_{J}$lban, $\mathbf{C}^{h}_{J}$.ba, $\mathbf{C}^{h}_{J}$.bPan$_1$, $\mathbf{C}^{h}_{J}$.bPan$_2$ and $\mathbf{C}^{h}_{J}$.LbwPa by MI. With MII, the largest cluster relating to this population was $\mathbf{B}^{b}_{J}$.bwP. With MIII, the main clusters were $\mathbf{b}^{f}_{J}$.bdwP, $\mathbf{b}^{f}_{J}$.bwan and $\mathbf{b}^{f}_{J}$bwPN (not in tables). A considerable number of French nearest neighbours were generated by MIV and MV but none was confirmed by visual inspection. This population was dispersed widely in the English analysis; the principal clusters comprising it were $\mathbf{C}^{h}_{E}$.bwP$_1$ and $\mathbf{C}^{h}_{E}$.ban$_1$.

(4) *Ug*. This population, the characteristic elm of northern England and of higher ground in the south and west, is treated in this section since, although the English specimens can be matched with French ones, it is not considered likely that the English population is of French origin. This is the only population regarded as indigenous to England. It is relatively uniform over wide areas of Europe, and Richens (1963), on the basis of monophage analysis, concluded that it had immigrated to England over the North Sea from Central Europe in the Boreal period. The samples aggregated under $\mathbf{B}^{h}_{J}$.LbpN and $\mathbf{C}^{h}_{J}$.LDwpaN (neither in tables) by MI and $\mathbf{b}^{f}_{J}$.LbwpN (not in table) and $\mathbf{b}^{f}_{J}$.LDpaN by MIII. No salient clusters for this population were generated by MII. In the French analysis, *Ug* most frequently appeared as $\mathbf{C}^{h}_{F}$.LbDpaN or $\mathbf{C}^{h}_{F}$.LbDpaN$_2$; in the English analysis, the principal cluster was $\mathbf{D}^{h}_{E}$.LbDpaN.

(5) Colchester. This *Um* population, principally found behind midcoastal Essex, does not emerge satisfactorily by any method, the greatest number of components in a single cluster being three under $\mathbf{b}^{f}_{J}$.bP by MIII. Only one nearest neighbour was picked up by MV, and of the several indicated by MIV, only one, Fontenay-sur-Mer (Mche), was

confirmed by visual inspection. Since this was a solitary example of a type not collected elsewhere in France, it is regarded as unlikely to have represented the source population of the English population. In the English analysis, the Colchester elms mainly aggregated under $\mathbf{C}^{\mathbf{h}}_{E}$.LDPN.

(6) Carlton. This small *Um* population is confined to north Bedfordshire and adjoining parts of Northamptonshire. The only method which picked it up satisfactorily was MI where it aggregated principally under $\mathbf{B}^{\mathbf{h}}_{J}$.LwP (not in table). No French nearest neighbour was identified by MV, and only one, discounted by visual inspection, by MIV. In the English analysis, this population mainly aggregated under $\mathbf{C}^{\mathbf{h}}_{E}$.LwP$_1$.

(7) Braughing. This highly distinctive *Um* population is confined to a small area in north-east Hertfordshire. It was not satisfactorily aggregated by any method. It had no French nearest neighbours by MV and only one, discounted by visual inspection, by MIV. The English analysis mainly aggregated this population under $\mathbf{D}^{\mathbf{h}}_{E}$.lbDPan or $\mathbf{A}^{\mathbf{h}}_{E}$.bDwPan.

Results: (4) Anglo-French populations

In this section, populations existing in either side of the English Channel are listed, the presumption being that the English segment is derived from the French.

(1) Kent. The English part of this *Um* population is confined to eastern Kent. It aggregated mainly under $\mathbf{B}^{\mathbf{h}}_{J}$.lbda and $\mathbf{C}^{\mathbf{h}}_{J}$.lban *(Fig. 1 a)* by MI, $\mathbf{B}^{\mathbf{b}}_{J}$.lbdan *(Fig. 1 b)* and $\mathbf{B}^{\mathbf{b}}_{J}$.ba by MII, and $\mathbf{b}^{\mathbf{f}}_{J}$.lbdan *(Fig. 1 c)* by MIII. $\mathbf{B}^{\mathbf{h}}_{J}$.lbda occurs in Picardy, Cotentin and the Channel Islands, with one outlier in northern Brittany. $\mathbf{C}^{\mathbf{h}}_{J}$.lban is entirely western, being mainly found in Cotentin, the Channel Islands and northern Brittany. $\mathbf{B}^{\mathbf{b}}_{J}$.lbdan occurs in Picardy, Cotentin and the Channel Islands, with two samples from northern and one from southern Brittany. $\mathbf{b}^{\mathbf{f}}_{J}$.lbdan has a single representative in Picardy and a few in central Normandy; it is abundant in Cotentin, the Channel Islands and north and south Brittany.

MIV identified French nearest-neighbour samples mainly in Picardy, Cotentin and Brittany, and MV in the same areas and also in central Normandy and the Channel Islands. A nearest-neighbour specimen whose affinity was confirmed from visual inspection was collected at Plouguin (Fin), but it was not frequent here nor were similar forms collected elsewhere in western Brittany.

The Picard elm population is composed principally of French population (2) above, which has not been found north of the English Channel, and the Dutch elm, Anglo-French population (6) below, which was only introduced into England in the 17th century. The total Picard elm population is thus very different from that of Kent. The simplest explanation to account for the affinities between the Kent population and its analogues is Picardy and Cotentin — North Brittany is that the last area is the source for the other two.

The Kent population was mainly represented by $\mathbf{C}^{\mathbf{h}}_{E}$.ban$_1$ in the English analysis and its Continental analogues by $\mathbf{B}^{\mathbf{h}}_{F}$.lban$_1$ and $\mathbf{B}^{\mathbf{h}}_{F}$.ba$_1$ in the French analysis.

(2) Clacton. This homogeneous English *Um* population did not aggregate satisfactory with MI. It was principally represented by $\mathbf{B}^{\mathbf{b}}_{J}$.bdwPn by MII *(Fig. 1e)* and $\mathbf{a}^{\mathbf{f}}_{J}$.bdwPn (not in table) by MIII *(Fig. 1 f)*. The principal Continental distributions of both of these groups is in southern Brittany. Both MIV and MV also located nearest neighbours in south Brittany, in particular at Néant-s-Yvel (Morb) and St. André-des-Eaux (LAtl).

In the English analysis, the Clacton population was mainly represented by $\mathbf{B}^{\mathbf{h}}_{E}$.bwPan$_1$, $\mathbf{A}^{\mathbf{h}}_{E}$.bwPn$_1$ and $\mathbf{C}^{\mathbf{h}}_{E}$.ban$_1$. The Continental analogues were not clearly characterized in the French analysis, though other French populations, such as $\mathbf{B}^{\mathbf{h}}_{F}$.bdP, with a marked south Breton distribution were noted.

(3) Epping. Neither MI nor MIII provided a satisfactory aggregation for this *Um* population. MII was somewhat better, three members aggregating with $\mathbf{B}^{\mathbf{b}}_{J}$.bdP and three under $\mathbf{B}^{\mathbf{b}}_{J}$.bPa. No nearest-neighbour matches confirmed by visual inspection were obtained by either MIV or MV. However since the closest analogues were in Brittany and since $\mathbf{B}^{\mathbf{b}}_{J}$.bPa in particular is most frequent in Brittany, this may be the source of the Epping population.

In the English analysis, the Epping population was mainly represented by $\mathbf{A}^{\mathbf{h}}_{E}$.bdPn, $\mathbf{B}^{\mathbf{h}}_{E}$.bwPan$_2$ or $\mathbf{C}^{\mathbf{h}}_{E}$.bwP$_1$; the closest French analogues were in $\mathbf{B}^{\mathbf{h}}_{F}$.bPa.

(4) Hundon. This *Um* population did not aggregate very satisfactorily by either MI or MII, though MI provided a three-member grouping under $\mathbf{C}^{\mathbf{h}}_{J}$.bPan$_1$. MIII did rather better with a four-member grouping in $\mathbf{b}^{\mathbf{f}}_{J}$.bwan. Both these groups are widespread throughout northern France outside of Picardy, and especially in Cotentin and Brittany. Nearest neighbours confirmed by visual inspection were obtained by MV in Picardy and Brittany. An origin of this population from Picardy seems unlikely on grounds similar to those used to discount a Picardy origin of the Kent population. This leaves the Cotentin — Brittany area as the most likely source on present evidence.

The Hundon population was represented mainly by $\mathbf{C}^{\mathbf{h}}_{E}$.ban$_1$ in the English analysis; the Continental analogues in the French analysis were principally located under $\mathbf{B}^{\mathbf{h}}_{F}$.bPn$_1$ and $\mathbf{B}^{\mathbf{h}}_{F}$.bPn$_2$.

(5) Dengie. This *Um* population chiefly aggregated under $\mathbf{C}^{\mathbf{h}}_{J}$.bP$_1$ (not in table), $\mathbf{B}^{\mathbf{b}}_{J}$.bP and $\mathbf{b}^{\mathbf{f}}_{J}$.bP by MI, MII and MIII, respectively. All these groups are frequent in central Normandy and north and south Brittany; they are infrequent or lacking in Cotentin and Picardy. The nearest neighbours produced by MIV and MV are dispersed over the whole of northern France. It seems reasonable to conclude that the Dengie population derives from northern France but a narrower localization of its source requires more evidence than is at present available.

The English analysis placed the Dengie population mainly under $\mathbf{D}^{\mathbf{h}}_{E}$.bdPn$_1$, $\mathbf{C}^{\mathbf{h}}_{E}$.ban and $\mathbf{A}^{\mathbf{h}}_{E}$.bP; the Continental analogues in the French analysis were principally in $\mathbf{B}^{\mathbf{h}}_{F}$.bdP and $\mathbf{B}^{\mathbf{h}}_{F}$.bPn$_2$.

(6) Dutch elm. This *Umg* hybrid presents us with a different situation from the other Anglo-French populations since its date of introduction into England, as shown below, is relatively late (17th century) and well documented. Its ultimate source has long been obscure, since, though present in such Netherland localities as the Hague and Nordwijk, it is infrequent in both, and very rare in the Netherlands as a whole. The English representatives of this clone did not aggregate well with MI. With MII they mostly came into $\mathbf{B}^{\mathbf{b}}_{J}$.LDN, while with MIII they principally came under $\mathbf{b}^{\mathbf{f}}_{J}$.LDpaN or $\mathbf{b}^{\mathbf{f}}_{J}$.LDWN. Both $\mathbf{B}^{\mathbf{b}}_{J}$.LDN and $\mathbf{b}^{\mathbf{f}}_{J}$.LDWN have two Continental foci, one in Picardy and the other in the Cotentin — Channel Islands area. No French nearest neighbour resulted from MV, but of the various nearest neighbours called up by MIV one, at Ligescourt (So), was confirmed by visual inspection and this match was very close indeed. It had already been surmised in the previous paper that the Picardy population designated Hybrid I (locally *ypereau* or *ypereau)* was, in fact, the Dutch elm, and the detailed biometrical comparison fully supports this.

Presumably, this hybrid arose in Picardy, was taken into horticultural use by nurserymen in the Netherlands, and was introduced by them into England where knowledge of its previous history was lacking. Later, new clones, notably Belgica, replaced the Dutch elm in the Netherlands so that the latter is now only frequent in Picardy, its place of origin, many places in England, where it has been extensively planted, and other countries, such as Ireland, whither it has been taken by the English.

The English Dutch elm samples aggregated in the English analysis mainly under $\mathbf{D}^{h}_{E}$.LDN$_1$. The Continental analogues chiefly came under $\mathbf{B}^{h}_{F}$.LDW and $\mathbf{B}^{h}_{F}$.LDWN.

Results: (5) Small populations

In addition to the populations described above from which copious material was collected, four extra populations were represented by only a few samples and must accordingly be treated more tentatively. They are as follows:

(1) Unilateral elm. This characteristic *Um* elm of the north English midlands, frequently referred to in the literature as *U. plotii* Druce, is represented by three samples. The only clustering method that aggregated any of them was MI, by which two samples entered $\mathbf{D}^{h}_{J}$.lbdan$_1$, a population whose Continental distribution centres on Cotentin. MIV located French nearest neighbour in Cotentin or Brittany. The history of this elm in England is completely obscure and the present evidence is not sufficient to support any hypothesis of its origin

In the English analysis, the samples were widely scattered. The possible Continental analogues came under $\mathbf{B}^{h}_{F}$.lbdn and $\mathbf{B}^{h}_{F}$.lbdPan$_1$ in the French analysis.

(2) Pevensey. One sample represented the *Um* population of the Pevensey levels of Sussex. Only MII and MIII drew this sample into a large cluster, $\mathbf{B}^{b}_{J}$.bPan and $\mathbf{b}^{f}_{J}$.bP, respectively. French nearest neighbours located by MIV and MV were mainly in central Normandy or Cotentin but none was confirmed on visual inspection. Since $\mathbf{b}^{f}_{J}$.bP also includes four samples from the Kent population, one might suppose that the Sussex population shares a common origin with the latter. The differences between the Kent and Sussex populations, however, seem to discount the likelihood of either population being derived directly from the other.

In the English analysis, the Sussex sample was in $\mathbf{C}^{h}_{E}$.ban$_1$; the Continental analogues in the French analysis were mainly in $\mathbf{B}^{h}_{F}$.bPa.

(3) Cornwall. The extensive *Um* population of Cornwall and western Devon is represented by a single specimen which aggregated under $\mathbf{C}^{h}_{J}$.ban$_1$ (not in table) by MI and $\mathbf{b}^{f}_{J}$.bwan by MIII. The Continental distribution of the former group has its focus in western Brittany; the French members of $\mathbf{b}^{f}_{J}$.bwan are widespread in Normandy and sporadic in Brittany. No French nearest members were found by either MIV or MV, but the resemblances between the Cornish specimen and Breton samples from Cléden-Cap-Sizun (in $\mathbf{C}^{h}_{J}$.ban$_1$) and Primelin (in $\mathbf{b}^{f}_{J}$.bwan) were very close. An origin of the Cornish population from western Brittany seems very likely.

In the English analysis the Cornish sample aggregated under $\mathbf{C}^{h}_{E}$.ban$_1$; in the French analysis, the west Breton analogues were in $\mathbf{B}^{h}_{F}$.lban$_2$ and $\mathbf{B}^{h}_{F}$.lan.

(4) South Hampshire. This *Um* population, of special taxonomic interest as providing the type locality of *Ulmus minor folio angusto scabro* (Goodyer, 1636), the antecedent of *U. sativa* (Miller, 1768), occurs along the Hampshire coast south of the New Forest. The single sample aggregated under $\mathbf{D}^{h}_{J}$.lbdan$_1$, $\mathbf{B}^{b}_{J}$.lbdwPan and $\mathbf{a}^{f}_{J}$.lbdwPan (not in table) by MI, MII and MIII respectively. All three groups have their continental foci in Cotentin. No French nearest neighbour was identified by MIV; the French nearest neighbours, all confirmed by visual inspection, and all in Cotentin, were generated by MV. An origin of the South Hampshire population from Cotentin, on the opposite side of the English Channel, appears highly probable.

This sample aggregated under $\mathbf{C}^{h}_{E}$.ban in the English analysis; the continental analogues mainly occurred in $\mathbf{B}^{h}_{F}$.lbdPan$_2$ in the French analysis.

Other origins of the English populations

Taking for granted that no elm survived the last Glaciation, the following possibilities need to be considered to account for the English population for which a northern French origin appears unlikely:

(1) an origin in northern France from an extant population not encountered, (2) an origin in northern France from a population now extinct, (3) an origin from elsewhere in Europe, (4) evolution of the English population *in situ* from an Anglo-French population, (5) an origin by hybridization between other populations.

Possibilities (1) and (2) are not regarded as likely since the area covered by the French survey was large and the range of material collected extensive. Extinction of clones, given the strong vegetative reproduction of most of them, also appears improbable. Possibility (3) however is certainly relevant. It was possible to apply MV to unpublished material collected elsewhere in Europe and this produced two Continental nearest neighbours for *Up* from Spain and two for the East Anglia population, one in Lower Austria and the other in Poland. It has already been suggested that English *Ug* emigrated naturally from Central Europe. For two other populations, by process of elimination, a Continental oirign other than northern France is thought probable, mainly the Godmanchester and Carlton populations, though no nearest neighbours have yet been identified.

The English and Continental distribution of the gall mite *Eriophyes ulmicola* Nal. must now be considered. In England this is abundant on *Up* and also (probably a distinct race) on the three Anglo-French populations, Kent, Dengie and Clacton. It also occurs on the Colchester population to be considered below. It is noteworthy that it has not been found anywhere on the extensive East Anglia and Godmanchester populations nor on the smaller Carlton population. On the Continent, *E. ulmicola* is abundant throughout France. It is also frequent in parts of southern Europe (e.g. Yugoslavia, Sicily) and in eastern Germany.

A hypothesis that appears to cover both the biometric data and the distribution of the gall mite is that the putative introductions from France *(Um)* and Spain *(Up)* each carried with them their own race of *E. ulmicola,* while material introduced from Central Europe happened to be mite-free and is unaffected by the mite races on introductions from France and Spain.

Possibility (4), evolution *in situ,* might account for the Braughing population. A separate introduction of this small population into the interior of England seems unlikely and it may have arisen by clonal mutation from the Hundon population.

Hybridization is a possibility (5) for the origin of the Colchester population. It seems feasible to account for the biometrical feature of the group by assuming that hybridization occurred between the Clacton or Dengie populations on the one hand, and the East Anglia population on the other, possibly, too, with some introgression from native *Ug.*

Taxonomy

The first taxon requiring consideration is *Up*. Nearest neighbours of English *Up* were only found in Spain, but material intermediate between it and *Um sensu lato*, either in respect of foliar or habit characters, was encountered both in southern and northern France. Grounds for maintaining it as a distinct species are not supported by the present investigation.

The leaves of the unilateral elm (*U. plotii* Druce (1911), first described as *U. sativa* Mill. var. *lockii* Druce (1907)) resemble those of some samples from Cotentin and Brittany very closely. It is concluded that it is deserving of no more than varietal status under *Um*.

The Cornish and South Hampshire populations were associated together by Melville (1938) as the English representatives of a species *U. stricta* Lindl. distinct from other English *Um*, the South Hampshire population as var. *goodyeri* Melville. Later, Melville (1960) amended the names respectively to *U. angustifolia* (Weston) Weston var. *cornubiensis* (Weston) Melville and *U. angustifolia* var. *angustifolia*, retaining the association of the two taxa within a single species, but with the South Hampshire elm now as the type.

The data presented here provide no basis for separating the species *U. angustifolia* from *Um* sensu lato nor for associating the Cornish and South Hampshire populations closely with each other, the former having apparently originated from western Brittany and the latter from a different stock in Cotentin.

History and Prehistory

The historical evidence relating to the main elm populations of eastern England has already been published by Richens (1958, 1959, 1961 a, b, 1965, 1967). The general conclusion then, and now to be modified, was that most of these and *Up* were introduced in the late pre-Roman Iron Age. Some supplementary evidence on populations not covered earlier are given below.

Up.

This is the only widespread population in western England and a southern or western centre of origin is thought likely. Early place names based on Old English *elm* that probably refer to this population include Elmley Castle (Wo), recorded from the eighth century (Mawer and Stenton, 1927), and, earlier still, if the usual derivations from Celtic *lem* (elm) are correct, the River Leam and Leamington (Wa) (Gover *et al.* 1936) and Limpsfield (Sr) (Gover *et al.*, 1934).

It is also likely that the elms referred to in the tenth century Anglosaxon charter relating to Western super Mare (Ss) analysed by Grundy (1933) were *Up*.

If the elm pile excavated from beneath the Roman wall at Gloucester (Knowles and Fullbrook-Leggatt, 1934) is *Up*, as seems most likely, one must presume that trees of mature size of this population existed in Roman times.

East Anglia

There are two early place names baded on *elm*, Elmsett (Sf), recorded from the tenth century (Ekwall, 1960), and Elmham. There are places called Elmham in both Norfolk and Suffolk. It is difficult to be certain which of these is referred to in early documents but the name occurs in the ninth century as a Bishop's see in East Anglia. Since the see is mentioned by Bede though not its exact location, the name is likely to go back at least to the seventh century.

The place name Elmsted, recorded from the ninth century (Ekwall, 1960) is in an area where this population is abundant. The place name Lympne, recorded as *portus Lemanis* in the first century, is derived by Ekwall (1960) from *lem* and is also in a region where the present population is frequent. Elm charcoal, most likely from this population too, has been excavated at Canterbury from Roman levels (Jenkins, 1950).

Dutch elm

The circumstances of the introduction of this elm into England are well attested. All accounts (Plukenet, 1696; Miller, 1759) are in accord with the story that it was imported from the Netherlands in the reign of William III. It was being distributed from the Brompton Nursery under the name Dutch elm in 1699 (Green, 1956).

Cornwall

It was argued in the previous paper that this population was not established at the time of the emigration into Brittany since elm is the one common tree whose Breton name is not derived from the corresponding Cornish term (later *elou*). A *terminus ad quem* for its introduction can be inferred from its present distribution, Cornwall and western Devon, largely coterminous with the Celtic kingdom of Cornwall before its absorption into the west of England in the ninth century. One would suppose that the cultural contacts of the Celtic kingdom were with Brittany rather than the rest of England and that the elm was introduced before the English annexation. Place names based on *elou* such as Trevella and Treloan are known from the later Middle Ages (Doble, 1938, 1941).

South Hampshire

It seems almost an exaggeration of coincidence that the area occupied by this small population includes one place name, Lymington, believed by Ekwall (1960) to be based on the Celtic *lem*. As already stated, the population was clearly characterized as *Ulmus minor folio angusto scabro* in the early 17th century.

The place-name evidence, taken in aggregate, suggests that most of the major elm populations were *in situ* at the end of the Roman occupation. Two considerations suggest that the Romans were not, however, responsible for their introduction: (1) the pattern of distribution appears to bear no relation to Roman centres of population or trading routes, and (2) one place name based on Celtic *lem*, Lympne (K), is on record from before the Roman occupation. So, we are left with the hazardous task of devising a reasonable hypothesis to account for the introduction of the various elm populations in the pre-Roman era. To do this, a tentative model based on the following assumptions has been constructed: (1) in general, the earlier that an elm population had been introduced, the greater its present area of distribution (Age and Area postulate); (2) elms will not have been introduced if any elm other than *Ug* was nearby; (3) elms would have been introduced from the nearest conveniently available source; (4) the putative date of introduction of any population should not be earlier than archeological evidence of settlement; and (5) putative source and site of introduction in England should be linked by archeological evidence of immigration route or trading contact.

We start then with the most extensive population, *Up*, for which an introduction from northern Spain has been suggested. Direct trading contacts between SW England and the Iberian Peninsula are evidenced for the Late Bronze Age, as shown by the distribution of double-looped palstaves (Hawkes, 1952). An early date such as this could explain why this elm was obtained from Spain rather than France if the supplementary assumption is made that *Um* had not yet been introduced from southern to northern France.

The next most extensive populations are the East Anglia and Godmanchester populations, for which an origin in Central Europe is suspected. If it is assumed that these populations were introduced about the same time via the Wash, the only available English elm other than *Ug* would have been *Up*, far away to the south-west, if in fact it was introduced first.

A concurrent introduction is just as feasible. It is suggested that these populations were obtained via the Elbe, the upper basin of which is the major location of *Um* in north Central Europe. The Elbe is a well authenticated trade route, notably for amber (de Navarro, 1925), and trading contacts between central Germany and eastern England are evidenced by the distribution of cast-flanged axes (Fox, 1952) in the Early Bronze Age, and Taunton-Hademarschen socketed axes (Butler, 1963) in the Late Bronze Age.

Finally, the smaller, mainly coastal populations of Kent and Essex can be supposed to have been the last of the prehistoric introductions to arrive and to have been imported from northern France, which, it is assumed, had received its elms meanwhile from further south. If it is accepted that this last phase of introduction was of Iron Age date, then posible supporting distributions are those of prehistoric salt pans (Nenquin, 1961) *(Fig. 1j)* and of the coins of the Coriosolites (Allen, 1958) *(Fig. 1k)* who inhabited what is now northern Brittany.

Motives for introduction may have varied. The use of elm as cattle fodder was well established by Roman times and is frequently invoked as an explanation of the Atlantic elm decline. This use probably persisted throughout the period that we have been considering. Elm is also a preferred timber for constructing bows, second to yew. Elm bows are known from Mesolithic times and their use, at least for hunting, can be regarded as likely throughout the pre-Roman period. Elm is the preferred timber for the naves of spoked wheels on account of its cross grain. Planting elm for this purpose is feasible in Iron Age times but probably not earlier. The last possibility, that elm was a cult tree, must also be considered, especially for *Up*. The earliest literary reference to elm, by Homer, describes its planting around graves, presumably reflecting Mycenean practice. The elm at the entrance to Hades, described by Virgil, may be another example of the same conception. It is interesting to note (Clay, 1929) that at least two Bronze Age barrows on Salisbury Plain had the burial either on an elm plank or in an elm trunk, though unfortunately one cannot be sure of the species. Two Celtic tribes in Gaul were named after trees, the Lemovices, after elm, and the Eburovices, after yew. It may be or may be not a coincidence that these are the two bowyers' trees. Also, these two trees have survived as cult trees in churchyards in many parts of Europe till the present day. *Up* is frequent in most villages on Salisbury Plain in contrast to its absence from many chalk uplands elsewhere. It is perhaps not wildly improbable that the communities that arranged the long-distance transport of the blue stones from the Prescelly Hills of Pembrokeshire to Stonehenge for cultic purposes in the 2nd millenium BC should have also arranged the long-distance transport of elm from Spain, possibly also for cultic purposes, and to the same destination.

Fig. 1l summarizes these hypotheses in diagrammatic form.

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