# Genetic Investigation of the Patrilineal Kinship Structure of Early Medieval Ireland

Brian McEvoy,<sup>1</sup> Katharine Simms,<sup>2</sup> and Daniel G. Bradley<sup>1</sup>\*

<sup>1</sup>School of Genetics and Microbiology, Trinity College, Dublin 2, Ireland <sup>2</sup>School of Histories and Humanities, Trinity College, Dublin 2, Ireland

KEY WORDS Y-chromosome; surnames; DNA

ABSTRACT A previous study of Irish Y-chromosomes uncovered a likely patrilineal kinship basis to the most prominent early Irish tribal entity/kingdom, the Ui Néill, who dominated the North of the Island during the early medieval period (600–1,000 AD). However, it is unknown to what extent this was a general feature of the multitude of Irish kingdoms that existed over the same period. Irish surnames are patrilineally inherited in a similar manner to the Y-chromosome and their origin can often be traced to pre-existing tribal units. We genotyped 17 microsatellites in 247 Y-chromosomes from men with surnames that are purported to be derived from two dif-

Ireland at the dawn of history (ca. 500 AD) was divided into a patchwork of smaller political entities often described as kingdoms or tribes. The Irish language nomenclature of these often suggested shared kinship amongst the tribal grouping as they incorporated a putative founder's personal name along with a prefix or suffix suggestive of shared descent. These included the prefix Ui meaning "descendants of" and the suffix -acht meaning "people of" Examples include Uí Néill ("descendents of Niall") and Connachta ("Conn's people") (Mac Niocaill, 1972; Ó Cróinín, 1995). However, it is unclear whether these represented real or mythological founders. Even in the former case, it was not known whether the link to the founder was solely the preserve of a ruling family/elite or a wider feature of the tribal organization and society.

A recent high resolution investigation of Irish Y-chromosomes, using 17 short tandem repeat (STR) and several single nucleotide polymorphism (SNP) markers, revealed a predominant haplotype (and its descendents) shared by  $\sim 8\%$  of the population (Moore et al., 2006). This Y-chromosome termed the Irish modal haplotype (IMH) displayed a striking geographic specificity to the Northwest region of the island, an area that corresponded to the hegemony of the most prominent Irish dynasty, the Uí Néill. A network of Y-chromosomes from this area (see Fig. 1), showing the relationship of haplotypes to each other, clearly illustrates the predominance of the IMH. Approximately 20% of the population in the North-West region carried the IMH or closely related haplotypes (within one STR repeat unit, the so-called "IMH + 1") that are likely to have derived from the ancestral IMH by mutation over time. Using this mutational divergence, a most recent common ancestor was dated to  $\sim$ 1,010 years before present (YBP) (with a standard deviation of 390 years based on mutational rate uncertainty).

ferent tribes (*Eóganacht* and *Dál Cais*) from the Southern province of Munster, as well as a third cohort of random names from the same geographic area. Although there is some sharing of Y-chromosomes between surnames of the same putative origin, there was no clear distinction between either grouping and the control, suggesting that the level of Ui *Néill* patrilineal kinship was not a universal feature of Irish tribal units. In turn this argues that an extensive extended clan or biological legacy of an eponymous founding ancestor was not necessarily a crucial factor in their establishment. Am J Phys Anthropol 000:000–000, 2008. ©2008 Wiley-Liss, Inc.

Although the time-frame and geography were consistent with a link between the IMH and Uí Néill, additional analysis using surname information was employed to confirm the association. Like the Y-chromosome, Irish surnames are generally patrilineally inherited. They began appearing in the 10th and 11th centuries and virtually all include the prefixes Mac or O meaning "son of" or "grandson of" respectively followed by the name of a prominent ancestor (McLysaght, 1985). The system suggests that modern surnames are markers of shared patrilineal kinship and this was confirmed by examining the Y-chromosomes of Irish men with the same surname (McEvoy and Bradley, 2006). Ireland has a large body of surviving early genealogical records (in some cases based on 7th century AD sources) that trace the descent of leading Irish families over long periods of time (Ó Muraíle, 2003). These records often name a specific founding ancestor for a surname and also allow these ancestors in turn to be assigned to one of the pre-existing tribal groupings (see Fig. 2 as an example).

The occurrence of the IMH was therefore explored in a cohort of 59 men with surnames thought to derive from the Ui Néill and its putative founder, 5th century AD warlord, "Niall of the Nine Hostages." A comparison of

\*Correspondence to: Daniel Bradley, Smurfit Institute of Genetics, Trinity College, Dublin 2, Ireland. E-mail: dbradley@tcd.ie

Received 16 July 2007; accepted 18 January 2008

DOI 10.1002/ajpa.20823

Published online in Wiley InterScience

(www.interscience.wiley.com).

Grant sponsor: Health Research Board of Ireland; Grant number: RP/2004/155.

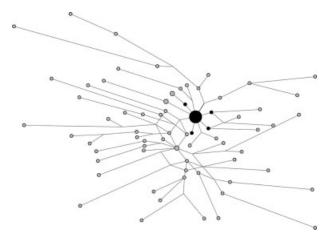
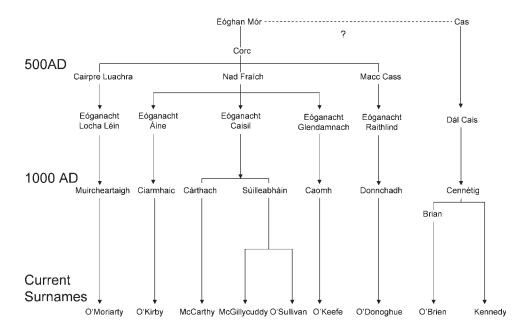


Fig. 1. Median Joining Network of Y-Chromosomes from North West Ireland. Networks are used to illustrate the interrelationship of different genetic loci, in this case Y-chromosomes. Each circle represents a different Y-chromosome haplotype, with circle area proportional to frequency, whereas the line between them is proportional to mutational divergence, or the number of STR repeat unit differences, between haplotypes. Data from 166 individuals within the R1b3 haplogroup are included and the most common Y-chromosome termed the IMH and its one-step mutational neighbors (IMH + 1) are marked in black. The IMH is significantly associated with surnames derived from the early medieval Ui Néill kingdom and this haplotype structure represents the signature or legacy of its founder ("Niall of the Nine hostages") and his clan. Network data taken from Moore et al. (2006).

Y-chromosomes from this group with those from the general Northwest Irish population as a whole, as well as a cohort of men from the same region with non-Ui Néill surnames, showed the IMH to be significantly enriched in the Ui Néill surname cohort. Taken together, the results suggested one prominent male progenitor for the Ui Néill tribal unit and, given the frequency of this Ychromosome, that the dynastic overlordship was accompanied by significant patrilineal kinship within the population/society. It is also a remarkable expression of the reproductive variance or social selection associated with power and hegemony. An earlier Y-chromosome study had identified an analogous effect on central Asian Ychromosomes attributed to the impact of Genghis Khan and his descendants (Zerjal et al., 2003).

The Uí Néill study was, however, unable to clarify whether the observed patrilineal kinship was a unique feature of this group or typical of early medieval population units and their foundation in other parts of Ireland. The Eóganacht meaning "Eoghan's people" were the political entity that ruled most of the Southern province of Munster from the 5th to 10th centuries AD and as such were considered the major contemporary rival of the Uí Néill in the North (Fig. 3A). Although their name derives from a pre-historic and quasi-mythological founder Eógan Mór, the group claimed descent from his apparently 5th century AD descendant "Corc" (see Fig. 2). The *Eóganacht* had several geographically distinct branches reputedly descended from Corc's sons. These were distinguished by additional suffixes, including the Eóganacht Caisil, Eóganacht Áine, and Eóganacht Locha



**Fig. 2.** Illustrative Genealogy of the *Eóganacht* Dynasty. The unique corpus of Irish genealogical records often allows the ancestors of modern surnames to be traced back to the founders of early medieval kingdoms/tribal units. In the case of the *Eóganacht* dynasty, the eponymous founder *Eóghan Mór* was reputed to have lived ca. 300–400 AD although the most recent common ancestor of the grouping is given as his great-great grandson Corc. His descendants are then reputed to have given rise to various branches of the *Eóganacht* confederation (*Eóganacht Caisil, Eóganacht Loch Léin*, etc.). The *Dál Cais* grouping, which came to dominate Munster from the *Eóganacht* in the 10th century AD, is widely believed to have forged a genealogical connection between its eponymous founder (*Cas*) and *Eóghan Mór* to legitimize the change in power. From the 11th century on, individual named founders emerged from these units giving rise to modern surnames (derived from the founder's personal name or nickname). By examining the Y-chromosomes of current bearers of these surnames it is possible to explore the extent to which these medieval tribal structures were real patrilineal kinship groups or simply bound together by foundation myth. Note: the time axis is intended as illustrative and is not to scale.

Dál Cais		Eógan	acht	General Munster		
Surname	Sample size	Surname	Sample size	Surname	Sample size 5	
Cahill	10	Cronin	8	Carroll		
Clancy	8	Doran	6	Coffey	9 6 12 11	
Heffernan	7	Kirby	8	Healy		
Hickey	6	McCarthy	7	Maher O'Connor		
Kennedy	7	McGillycuddy	7			
McGrath	6	Moriarty	8	O'Driscoll	8	
McMahon	5	O'Callaghan	10	O'Leary O'Loughlin O'Shea	6	
McNamara	4	O'Donoghue	7		5	
O'Brien	14	O'Donovan	2		6	
O'Dea	6	O'Flynn	6	Whelan	4	
O'Grady	7	O'Keefe	8	Total	72	
Total	80	O'Mahony	3			
		O'Sullivan	7			
		Quill	8			
		Total	95			

TABLE 1		Surnames	included	in	the study	
	•	Sumumes	inciauea	uu	ine siuuy	

Surnames were divided into three cohorts depending on putative surname origin: *Eóganacht, Dál Cais*, or a control group of unrelated surnames from the Munster region.

Léin, and were spread across the region in a strategic manner. Indeed because of this arrangement, some have observed that Munster may have been a confederation of dominant dynasties rather than a single kingdom with a paramount dynasty (Ó Corraín, 1972). This contrasts with the approach of other authors who refer to the *Eóganacht* as a single ruling dynasty, jointly dominating Munster (Mac Niocaill 1972; O Cróinín, 2005.) The Eóganacht were later displaced by another grouping called the Dál Cais, as the power of the former declined in the 10th century. This tribe were centered in the North of Munster (modern counties of Clare and Limerick). The name literally means "Cais' share" and their eponym, Cais, was reputed to be one of *Eógan Mór's* brothers but this is likely to be a later forging of genealogical records in an attempt to legitimize the change in regional power from Eóganacht to Dál Cais (Byrne, 2001).

We set out to investigate whether the Eóganacht and Dál Cais were each, like the Ui Neill in North, groupings based on shared patrilineal kinship stemming from foundation by a major ancestor and/or his clan. We assembled DNA samples from 247 men with surnames that are ultimately thought to derive from one of these tribes or from a control of random Munster surnames. Because Y-chromosomes and surnames are largely coinherited, we treat these cohorts are descendent populations of the tribal unit and compare high resolution Ychromosome haplotypes composed of 17 STRs between these and the control of random/unrelated Munster surnames. If the tribal population had contained as a substantial fraction the descendants of one founding male ancestor, then a higher level of concordance in patrilineal ancestry compared with control groupings is expected. By examining these patterns, it is possible to provide insights into the establishment of early medieval Irish kingdoms, which are difficult to obtain using incomplete historical knowledge.

# MATERIALS AND METHODS

## Sample collection and genotyping

A total of 247 individuals encompassing 35 surnames with origins in the province of Munster (Table 1 and Fig. 2) were examined. Two-hundred and twelve of these were collected for this study by postal request to relevant surname bearers. Participants were asked to submit a buccal check cell swab from which DNA was extracted using a standard phenol/chloroform protocol. The remaining 35 samples comprised seven randomly chosen individuals (the average surname sample size from the new data) from each of five surnames (O'Sullivan, O'Donoghue, McGillycuddy, McCarthy of putative *Eóganacht* origin and Kennedy, of putative *Dál Cais* ancestry) examined in a previous study (McEvoy and Bradley, 2006). All samples described were collected with informed consent.

Each sample was genotyped for 17 STR markers (DYS19-DYS388-DYS390-DYS391-DYS392-DYS393-DYS434- DYS435-DYS436-DYS437-DYS438-DYS439-DYS389II-DYS389II-DYS460-DYS461-DYS462) in three multiplex PCR reactions using primers and conditions previously described (Bosch et al., 2002; McEvoy and Bradley, 2006). The size of each STR fragment was determined by capillary electrophoresis using an Applied Biosystems 3700 DNA analyzer, carried out by the Genome Centre, Barts and the London Queen Mary's School of Medicine and Dentistry. A sample of previously determined genotype was included with each multiplex to ensure consistent and accurate results.

Although the question to be addressed here (evidence of patrilineal kinship within the Eóganacht and Dál *Cais*) is similar to that of the *Uí Néill* in the Northwest of Ireland (Moore et al., 2006), the study design is somewhat different. Specifically, multiple representatives of each surname were included, in an attempt to more accurately reflect the Y-chromosome diversity of each name, and allow the possibility of further investigation of putative sub-tribal branching patterns in the Eóganacht. Initially, the samples were divided by surname into three groups according to putative tribal origin: Eóganacht, Dál Cais or a random Munster Surname Control (Table 1). The latter category contains an assortment of names from the same geographic area as the Eóganacht and Dál Cais but which have little or no putative link to either grouping or each other. The designations were arrived at by reference to several historical and genealogical sources. These included the seventeenth-century genealogical compilations "Leabhar Muimhneach" (O Donnchadha, 1940), and "The Great Book of Irish Genealogies" compiled by Dubháltach

TABLE 2. Analysis of molecular variance (AMOVA)

	Eóganacht	/control	Dál Cais/control		Eóganacht/Dál Cais		Eóganacht + Dál Cais/control	
	Variance (%)	P-value	Variance (%)	P-value	Variance (%)	P-value	Variance (%)	P-value
Among populations (tribes) Among surnames within	-1.3	0.769	-2.5	0.952	1.4	0.055	-1	0.808
populations Within surnames	$28.5 \\ 72.8$	$\substack{< 0.00001 \\ < 0.00001 }$	$26.8 \\ 75.7$	$\substack{< 0.00001 \\ < 0.00001 }$	$\begin{array}{c} 12.2\\ 86.4\end{array}$	$<\!$	$\begin{array}{c} 20.9\\ 80.1 \end{array}$	${}^{< 0.00001}_{< 0.00001}$

The percentage of the variation in the sample population found at various levels in four comparisons involving tribal groupings.

MacFirbhisigh (Ó Muraíle, 2003). The 15th-century anthology in "Laud Misc. 610" (Meyer, 1911), which contains an early medieval collection of Munster genealogies, together with the genealogical anthologies in two 12th-century manuscripts, the Book of Leinster and Bodleian Library Rawlinson B 502 both edited by O'Brien (1962) as "Corpus Genealogiarum Hiberniae vol. i," were also consulted. These earlier texts were used to obtain as authentic a version as possible of the early medieval ancestral lines claimed for these families.

An additional 184 similarly genotyped Munster Y-chromosomes were taken from a previous survey of Ireland (Moore et al., 2006) and used solely to give a background Y-chromosome landscape of Munster (without respect to surname information which was not available for most of these samples). We refer to this as the geographic Munster sample to distinguish it from the Munster Surname control described above. All the genotype data described can be found at the authors' website http:// www.gen.tcd.ie/molpopgen/resources.php.

#### Statistical analysis

Analysis of molecular variance. To assess the differences in the patrilineal ancestry of the three groups (*Eóganacht, Dál Cais* and the Munster Surname Control), we employed an analysis of molecular variance (AMOVA) approach as implemented in the Arlequin package (Excoffier et al., 2005). AMOVA apportions the Y-chromosome diversity in the sample group to different levels: that between individuals of the same surname, between surnames of the same putative dynastic origin and between dynastic groups. For calculations, relationships were defined as the sum of the square differences over all loci and significance was gauged by randomly permuting individuals between groups over 10,000 replicate analyses.

**Phylogenetic reconstruction.** The relationship between Y-chromosomes was visualized using median joining networks, which simultaneously display a range of possible phylogenetic connections, in other words how Y-chromosomes relate to each other. These were constructed using the program Network 4.2 (Fluxus engineering available at www.fluxus-engineering.com) by initially applying the reduced median algorithm (Bandelt and Dress, 1992) followed by the Median-Joining method (Bandelt et al., 1995). This procedure was adopted for two reasons; firstly, to simplify networks of relatively large sample size which otherwise might be difficult to construct and secondly to ensure strict comparability to those produced in the earlier Ui Néill study (and reproduced here as Fig. 1) (Moore et al., 2006).

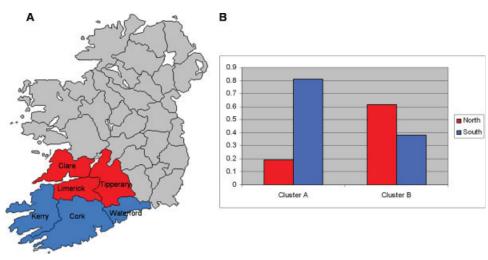
with a common origin) in these networks were initially defined as frequent and phylogenetically central (ancestral) Y-chromosomes with descendants taken as all one STR repeat unit neighbors and any further haplotypes that could be traced back to the ancestral Y-chromosome via a continuous (filled) pathway of increasing frequency. This criterion is identical to that used in a previous study of the Uí Néill dynasty in Northwest Ireland (Moore et al., 2006). The most recent common ancestor (TMRCA) of these lineages was calculated from the observed accumulated mutations from the ancestral Ychromosome (p statistic) (Morral et al., 1994). TMRCA estimates from the  $\rho$  statistic, along with associated standard deviations ( $\sigma$ ) (Saillard et al., 2000), were calculated in Network 4.2, using a mutation rate of 0.69 imes $10^{-3}$  per 25 years or 1 per 2,131 years for a 17 STR marker haplotype (Zhivotovsky et al., 2004).

Discrete individual lineages (those Y-chromosomes

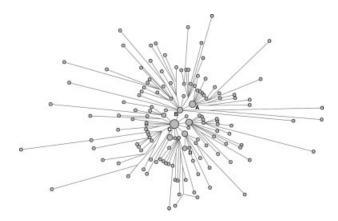
### **RESULTS AND DISCUSSION**

We used the co-inheritance of surname and Y-chromosome to examine the extent of shared patrilineal kinship in two early medieval Irish tribal units/kingdoms. 247 Ychromosomes from 35 modern surnames were divided into three cohorts based on the origin of their surname: Eóganacht, Dál Cais or a random Munster Surname control (Table 1). We formally assessed the significance of patrilineal ancestry differences between the various groups using a hierarchal AMOVA approach (Table 2). Neither the *Eóganacht* nor the *Dál Cais* surname groupings (nor both together) showed significant differences at the tribal level when compared with the Munster Surname control sample (P = 0.769, 0.952 and 0.808,respectively), indicating that neither designation is under-laid by extensive shared ancestry as a whole. The Eóganacht versus Dál Cais division is estimated to account for 1.4% of the variation, just escaping formal significance (P = 0.055). In contrast, in all comparisons, a highly significant proportion of the total variance (between 12.2 and 28.5%) is explained by surname divisions confirming these more recent markers (<1,000 years) of patrilineal ancestry to be significant.

A summary statistic like AMOVA may miss more subtle linkages between the surnames. We therefore further investigated the data by visualizing the relationship of Y-chromosomes to each other using median-joining networks. We first examined the background geographic Munster Y-chromosome sample for the signature or genetic legacy of a prominent founding male (see Fig. 4) analogous to that associated with the Ui Néill in Northwest Ireland (Moore et al., 2006). Theoretically, and as practically observed in the Northwest, this is manifest as a frequent Y-chromosome (the IMH in the case of the

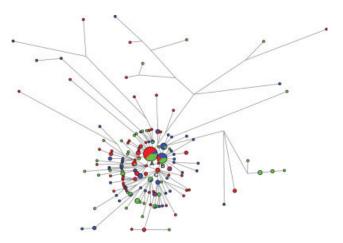


**Fig. 3.** (A) Map of Ireland showing the southern province of Munster and its six historical counties (colored). For some analyses, samples were divided by paternal origin into a Northern (red) and Southern (blue) geographic cohort. (B) Proportion of individuals from Cluster A and B in Figure 5 that originate from the Northern and Southern region of Munster.



**Fig. 4.** Median Joining Network of a Munster Geographic Y-Chromosome sample. As with Figure 1, only samples within the major Irish haplogroup R1b3 are shown (n = 157). Each Y-chromosome is represented by a circle with its frequency proportional to area. The lines between circles indicate the mutational divergence. Haplotypes A and B are synonymous with those identified in Figure 5. Haplotype C appears to be the 17 STR marker extension of the previously identified AMH whereas haplotype D is the IMH.

Uí Néill) orbited by closely related but less common haplotypes that derived from the ancestral type by mutation over time (see Fig. 1). Although such a structure is somewhat evident in the center of the Munster geographic Y-chromosome network, there are several reasons to suggest it is not an equivalent to the Uí Néill and IMH. The Munster central/ancestral Y-chromosome (marked C in Fig. 4) is considerably less frequent than the IMH in the Northwest (3.8% vs. 12.5%) but is surrounded by more extensive and frequent diversity. These observations together suggest a considerably older foundation event (TMRCA dated at 2,600 YBP vs. the 1,010 YBP estimate for the IMH lineage). Secondly, the lineage does not show the striking geographic specificity observed with the IMH to the Northwest region. For instance the same cluster is also apparent in a sample from the Eastern Irish province of Leinster and also



**Fig. 5.** Median Joining Network of the Munster Surname Sample (n = 247). Each Y-chromosome is represented by a circle with its frequency proportional to area. Colored "slices" indicate the frequency of the different surname types in each haplotype: Red for *Eóganacht*; Blue for *Dál Cais*, and Green for the Munster Surname control. The lines between circles indicate the mutational divergence. Haplotypes A and B are the most frequent Y-chromosomes and form the ancestral type for two clusters defined as one-step mutational neighbors of the A and B haplotypes. Haplotype C is the most common haplotype in a general Munster geographic sample (see also Fig. 4).

occurs in a similarly genotyped population of Y-chromosomes from Iberia (Bosch et al., 2002). A truncated six marker haplotype of this Munster ancestral Y-chromosome corresponds to the previously identified Atlantic modal haplotype (AMH). The AMH is postulated to have an ancient origin in an Iberian refugial population from where parts of Western Europe were re-colonized after the last ice age (Wilson et al., 2001). Based on these observations, we propose that this haplotype may be the 17 STR marker extension of the AMH lineage and exclude it as a specific signature associated with a recent tribal founder, comparable to the IMH. The extended 17 marker (DYS19-DYS388-DYS390-DYS391-DYS392-DY-S393-DYS434-DYS435-DYS436-DYS437-DYS438-DYS439DYS389I-DYS389II-DYS460-DYS461-DYS462) AMH profile (14-12-24-11-13-13-11-11-12-15-12-12-13-29-11-12-11) diverges two repeat units from the IMH (14-12-25-11-14-13-11-11-12-15-12-13-29-11-12-11) at DYS390 and DYS392. However, it is possible that greater migration to Munster relative to the Northwest over the past 1,000 years (associated with Norman and English conquest) may dilute such a signature in the Munster geographic sample.

We next investigated the novel Munster surname data for evidence of important additional founding lineages (see Fig. 5). Two potential founding male signatures (frequent Y-chromosomes surrounded by subsidiary diversity) are apparent, centered or ancestral on haplotypes A and B in Figure 5, and there appears to be some prima facia enrichment of Eóganacht and Dál Cais surnames within these two types and their extended clusters (defined as one step STR mutational neighbors). Although relatively small sample sizes prevent definitive investigation of individual surnames histories, many of the genetic linkages between them are consistent with historical sources. This is particularly true of putative connections within the last 1,000 years. For example, the O'Sullivan and McGillycuddy surnames share the same modal haplotype A (modal types are likely to represent the major surname founder's Y-chromosome) a result confirmed by larger sample sizes from a previous study (Fig. 6A) (McEvoy and Bradley, 2006). Historical sources indicate the McGillycuddy surname originated from an O'Sullivan in the 16th century (McLysaght, 1982; Mc-Lysaght, 1985). A second and earlier example concerns Kennedy and O'Brien both of which were putatively founded by single 10th century ancestors who were paternal uncle and nephew respectively (McLysaght, 1985). Our findings are consistent with this since the mode of the Kennedy surname identified in a previous surname study (McEvoy and Bradley, 2006) is cognate with that of O'Brien identified here (Fig. 6B).

However, linkages (as judged by Y-chromosome relatedness) older than 1,000 years are less consistent with genealogical expectations. Although clusters A and B in Figure 5 include the modes of several *Eóganacht* and Dál Cais surnames respectively, they also contain surnames from the control group while missing others of the same tribal designation. For instance, although group A encompasses the putative Eóganacht O'Keefe, O'Sullivan, O'Donoghue and Kirby names, it also includes several other non-Eóganacht names including O'Connor, O'Leary and O'Shea. Furthermore, there is little consistency with the putative branching order of the different Eóganacht sub-groups (see also Fig. 2). For example McCarthy and O'Sullivan are reputedly members of the Eóganacht Caisil branch but do not share closely related modal founder Y-chromosomes, this despite O'Sullivan's links to the apparently more remote Eóganacht Glendamnach [via O'Keeffe] and Eóganacht Aine [Kirby] branches. Similarly, group B contains not only the modes of the Dál Cais names O'Brien, Kennedy, McNamara and possibly O'Dea but also the Eóganacht name O'Callaghan and the control surname O'Loughlin.

Neither cluster A nor B has a significant enrichment of *Eóganacht* or *Dál Cais* individuals respectively compared with the Munster surname control ( $\chi^2$  test P =0.23 and P = 0.10, respectively). Thus, although the haplotypes A and B may well point to some connections, neither they, nor the results in general, strongly support a widespread paternal kinship amongst the members of

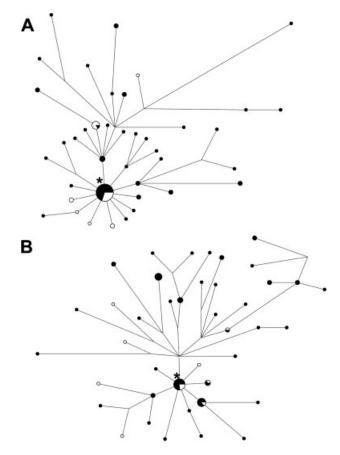


Fig. 6. Median Joining Network of surname inter-relationships. (A) O'Sullivan (black, n = 61) and McGillycuddy (white, n = 21), both of putative *Eóganacht* origin (B) Kennedy (black, n = 63) and O'Brien (white, n = 11), both of *Dál Cais* origin. Only haplogroup R1b3 Y-chromosomes are shown for ease of illustration (this excludes a total of 10 singletons from other haplogroups). The haplotypes corresponding to the presumed O'Sullivan and Kennedy ancestral founders are marked \*(and these are Haplotypes A and B, respectively from Figure 5). The modal types of the McGillycuddy and O'Brien surnames are cognate with each of these respectively, and several additional samples are within one mutational step of this node. Data for all surnames except O'Brien are taken for McEvoy and Bradley (2006).

the *Eóganacht* or *Dál Cais* populations as a whole. A caveat is that the two nodes fall in a dense part of the Irish Y-chromosome phylogeny, which may reduce power to detect differences.

It is none-the-less curious that haplotypes A and B, the joint second and third most common Y-chromosomes in the geographic Munster sample (at 2.2% and 1.6%, respectively), are enriched in the surname sample (*Dal Cais, Eoganacht* and Munster surnames) at 12.9% and 6.5%, respectively. This may simply reflect exaggerated stochastic sampling effect because Y-chromosomes of the same surname are known not to be, on average, independent of each other (King et al., 2006; McEvoy and Bradley, 2006). Alternatively, in view of the apparent inability of putative genealogical connections to explain the observation, they may reflect the presence of geographic sub-structure in Munster. In this regard, it is interesting to note that clusters A and B are significantly different in terms of the geographic origin of individuals when divided into Northern and Southern Munster geographic cohorts (see Fig. 3B). A further hint in this direction comes from AMOVA comparisons. Although neither  $D\acute{al}$  Cais nor Eóganacht samples are different from the general Munster sample, there is a much higher (although not formally significant) differentiation between the two groups that have substantial differences in geographic origin. It is also incidentally evidence against later claims that the  $D\acute{al}$  Cais and Eóganacht had a shared founding ancestor; a claim widely dismissed as politically motivated 10th century revisionism designed to legitimize the rise in regional power of the  $D\acute{al}$  Cais over the Eóganacht (Byrne, 2001).

Although our analysis cannot exclude the possibility that some level of patrilineal kinship underlaid the Munster Eóganacht and Dál Cais entities, it does seem that if any existed it was not comparable in extent to the widespread kinship in the contemporaneous Uí Néill grouping from the North of the Island, presumably the descendants of the ancestral eponym "Niall of the Nine Hostages" and his clan. The results suggest that the establishment and population structure of different kingdoms did not conform to one simple model, despite nomenclature which could indicate that members shared descent from a founding male. However, they do not necessarily preclude the establishment of the Southern entities by an individual or elite family but suggest that conditions were such that this was not accompanied by, or indeed dependent on, an extraordinary growth of that ruling family. Although records are limited, some historical observations seem to support a genuine contrast in the foundation and subsequent leadership structure of the different units consistent with these Y-chromosome data. The over-lordship of the *Eóganacht* showed a lack of dynastic cohesion compared with the Uí Néill and was passed between different branches of the Eóganacht confederacy and beyond; furthermore *Eóganacht* regnal records are disorganized and pedigrees of individual kings are difficult to coherently trace (Byrne, 2001). Indeed some have proposed that the co-incidence of geography, politics and genealogy in the Eóganacht origin legend is so neat that it suggests a political alliance created the genealogy and shared foundation myth (Charles-Edwards, 2000) rather than representing the establishment of a kingdom driven by a single successful clan, as appears to be the case with the Uí Néill in Northwest Ireland.

More generally, it has been argued that variations in tribal nomenclature themselves signify different origins and therefore cannot (always) be considered equivalent. Population names ending in -acht may be earlier and less reliably tied to an identifiable ancestor than those using the more definite Ui ("descendants of") prefix (MacNeill, 1911) and our results, although not conclusive, are consistent with such a suggestion. It is also relevant to note that contemporary records and accounts begin earlier in Northern parts of the country compared with the South giving a greater degree of historicity and credibility to the Uí Néill founding account. Which differences-social, environmental or other-between the two areas were the causes of the divergent origins/patrilineal structures cannot be directly answered with these data or from the limited historical knowledge of society at the time.

There are several potential confounding factors that could also contribute, in part at least, to lack of correspondence between Y-chromosomes and the Munster kingdoms. Incorrect categorization of surnames into dynastic groupings would obviously reduce power to detect increased patrilineal kinship within these. Over the course of Irish genealogical history there is a well recognized tendency for the contemporary forging of these records to accord with shifting political circumstances or, at later times, to retrospectively aggrandize certain families (Simms, 1987; Ó Corráin, 1998). Stochastic changes in the frequency of surnames ("drift") may also be a potential complication. Since the 10th century, some Eóganacht and Dál Cais surnames may have become extinct and as a result the sub-set surviving and included in this study may not be representative. An analogous "drift" may also feature on the Y-chromosome side, altering the frequencies of later Y-chromosome introductions relative to the founding type. Non-paternity and adoption events are also expected to dissociate an initial link between a surname and the Y-chromosome of its founder. Although it is difficult to control or account for all of these, they are arguably just as likely to confound the prior Uí Néill finding suggesting the contrast is real.

#### CONCLUSION

Although many additional early medieval Irish population units remain to be investigated, it seems clear that there was no standard patrilineal kinship structure to these entities. Thus, although the Ui Néill and Eóganacht are often thought of as major contemporary rivals from the North and South of the island respectively, genetic evidence combined with surname information suggest they were founded, established and perhaps lead by different means and this may reflect wider differences in organization of Irish tribal societies.

#### ACKNOWLEDGMENTS

The authors are grateful to all volunteers who contributed DNA samples. They also thank N. Ó Muraíle for his advice on surname origins.

#### LITERATURE CITED

- Bandelt H-J, Dress AWM. 1992. Split decomposition: a new and useful approach to phylogenetic analysis of distance data. Mol Phylogenet Evol 1:242–252.
- Bandelt H-J, Forster P, Sykes BC, Richards MB. 1995. Mitochondrial portraits of human populations. Genetics 141:743– 753.
- Bosch E, Lee AC, Calafell F, Arroyo E, Henneman P, de Knijff P, Jobling MA. 2002. High resolution Y chromosome typing: 19 STRs amplified in three multiplex reactions. Forensic Sci Int 125:42–51.
- Byrne FJ. 2001. Irish kings and high-kings. Dublin: Four Courts.
- Charles-Edwards TM. 2000. Early Christian Ireland. Cambridge: Cambridge University Press.
- Excoffier L, Laval G, Schneider S. 2005. Arlequin ver. 3.0: an integrated software package for population genetics data analysis. Evol Bioinformatics Online 1:47–50.
- King TE, Ballereau SJ, Schurer KE, Jobling MA. 2006. Genetic signatures of coancestry within surnames. Curr Biol 16:384–388.
- Mac Niocaill G. 1972. Ireland before the Vikings. Dublin: Gill and Macmillan.
- MacNeill E. 1911. Early Irish population-groups: their nomenclature, classification and chronology. Proc R Irish Acad 29 (Section C):59–144.

- McEvoy B, Bradley DG. 2006. Y-chromosomes and the extent of patrilineal ancestry in Irish surnames. Hum Genet 119:212–219.
- McLysaght E. 1982. More Irish families. Dublin: Irish Academic Press.
- McLysaght E. 1985. Irish families: their names, arms and origins. Dublin: Irish Academic Press.
- Meyer K. 1911. The laud genealogies and tribal histories. Zeitschrift für Celtische Philologie 8:291–338.
- Moore LT, McEvoy B, Cape E, Simms K, Bradley DG. 2006. A Y-chromosome signature of hegemony in Gaelic Ireland. Am J Hum Genet 78:334–338.
- Morral N, Bertranpetit J, Estivill X, Nunes V, Casals T, Giménez J, Reis A, Varon-Mateeva R, Macek Jr. M, Kalaydjieva L, Angelicheva D, Dancheva R, Romeo G, Russo MP, Garnerone S, Restagno G, Ferrari M, Magnani C, Claustres M, Desgeorges M, Schwartz M, Schwarz M, Dallapiccola B, Novelli G, Ferec C, de Arce M, Nemeti M, Kere J, Anvret M, Dahl N, Kadasi L. 1994. The origin of the major cystic fibrosis mutation ( $\delta$  F508) in European populations. Nat Genet 7:169–175.
- Ó Corraín D. 1972. Ireland before the Normans. Dublin: Gill , and Macmillan.
- O Corráin D. 1998. Creating the past: the early Irish genealogical tradition. Peritia 12:177–208.
- Ó Cróinín D. 1995. Early medieval Ireland 400–1200. Essex: Longman.
- Ó Cróinín. 2005. A new history of Ireland, Vol. 1. Oxford: Oxford University Press.

- Ó Donnchadha T, editor. 1940. An Leabhar Muimhneach. Dublin: Oifig Díolta Foillseacháin Rialtais, Dublin.
- Ó Muraíle N, editor. 2003. The great book of Irish genealogies. Dublin: De Búrca.
- O'Brien MA. 1962. Corpus Genealogiarum Hiberniae, Vol. 1. Dublin: Dublin Institute for Advanced Studies.
- Saillard J, Forster P, Lynnerup N, Bandelt HJ, Norby S. 2000. mtDNA variation among Greenland Eskimos: the edge of the Beringian expansion. Am J Hum Genet 67:718–726.
- Simms K. 1987. From kings to warlords: the changing political structure of Gaelic Ireland in the later Middle Ages. Suffolk: Woodbridge.
- Wilson JF, Weiss DA, Richards M, Thomas MG, Bradman N, Goldstein DB. 2001. Genetic evidence for different male and female roles during cultural transitions in the British Isles. Proc Natl Acad Sci USA 98:5078–5083.
- Zerjal T, Xue Y, Bertorelle G, Wells RS, Bao W, Zhu S, Qamar R, Ayub Q, Mohyuddin A, Fu S, Li P, Yuldasheva N, Ruzibakiev R, Xu J, Shu Q, Du R, Yang H, Hurles ME, Robinson E, Gerelsaikhan T, Dashnyam B, Mehdi SQ, Tyler-Smith C. 2003. The genetic legacy of the Mongols. Am J Hum Genet 72:717-721.
- Zhivotovsky LA, Underhill PA, Cinnioğlu C, Kayser M, Morar B, Kivisild T, Scozzari R, Cruciani F, Destro-Bisol G, Spedini G, Chambers GK, Herrera RJ, Yong KK, Gresham D, Tournev I, Feldman MW, Kalaydjieva L. 2004. The effective mutation rate at Y chromosome short tandem repeats, with application to human population-divergence time. Am J Hum Genet 74:50-61.