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Postglacial colonization of Ireland by mustelids, with particular reference to the badger (*Meles meles* L.)

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Abstract. There exists some confusion as to the means by which Ireland developed its current mammalian fauna. In this paper, I use a multivariate analysis of cranial measurements to test the hypothesis that Irish mustelids should resemble their Scottish counterparts more so than those from England, thus providing morphological evidence for postglacial colonization via an Ireland/Scotland landbridge. An examination of badger (*Meles meles* L.), stoat (*Mustela erminea* L.) and otter (*Lutra lutra* L.) failed to provide support for this hypothesis. Based on these results and consideration of our knowledge of the ecology of these species, it is concluded that postglacial colonization via a landbridge was unlikely. Evidence for human-aided colonization is reviewed. It is concluded that, while further morphologic and genetic studies are very much required, the problem of postglacial colonization can only be solved through archaeozoological research.

Key words. Landbridge, multivariate morphometrics, carnivores, British Isles.

INTRODUCTION

The depauperate nature of the Irish vertebrate (and indeed invertebrate) fauna has been noted for some time (for review see papers in Sleeman, Devoy & Woodman, 1986). Ireland has twenty non-marine mammalian species, compared to forty-two in Britain and 134 on the European mainland (Corbet & Harris, 1991). Six species of carnivorous terrestrial mammal occur in Ireland. Five of these are members of the family Mustelidae: the stoat *Mustela erminea* L., the American mink *M. vison* Schreber, the pine marten *Martes martes* L., the otter *Lutra lutra* L. and the badger *Meles meles* L. The other carnivore present is the red fox (*Vulpes vulpes* L., a canid). Whilst the American mink is a known introduction (Smal, 1988), it has been assumed that the other species naturally colonized Ireland via a landbridge during the postglacial period (Fairley, 1984; Mitchell, 1986; Yalden, 1991). However, it is of note that there is no archeological evidence of many elements of the current fauna prior to the arrival of man. The earliest reported occurrence in Ireland of the five native carnivores are as follows: fox, Neolithic; pine marten, early Christian; stoat, 33,500 years BP—Castlepook cave fauna; badger, Neolithic; and otter, Bronze/Iron age (Stuart & van Wijngaarden-Bakker, 1985). Whilst one must acknowledge that archeological data from Ireland is very scant, it is somewhat unusual that remains of large species, such as the otter, badger and fox have not been found prior to the late Mesolithic/Neolithic.

There is currently some controversy as to the location (and indeed existence) of post-glacial landbridge(s) between Britain and Ireland (Yalden, 1981; Devoy, 1985; Mitchell, 1986; Sleeman *et al.*, 1986; Preece, Coxon & Robinson, 1986). Devoy (1985) conducted an exaustive review of the evidence for five proposed connections, and found the greatest amount of evidence for a 'low soggy, possibly shifting and partially discontinuous' linkage between N.E. Ireland and Scotland dated between 10,200 and 11,400 years BP. He found little evidence for a connection between Wales and Ireland (as proposed by Mitchell, 1986) or for a landbridge dated prior to 12,000 years BP (as proposed by Yalden, 1981). It is generally accepted that, if such a landbridge existed, it was relatively short-lived, discontinuous, and unlikely to have provided a suitable habitat for many of the current mammalian fauna (Corbet, 1962; Yalden, 1981; Stuart & van Wijngaarden-Bakker, 1985; Devoy, 1985). There appears to be little evidence for 'organized oakwoods advancing ... carrying those forest animals, the red deer and the wild boar, along with them' advocated by Mitchell (1986).

The existence of a species on the Irish mainland can be explained by four possible (non-exclusive) scenarios; (i) the species survived the glacial period in ice-free refugia, (ii) the species recolonized the country via a filter land-bridge, (iii) the species was accidentally introduced by humans, and (iv) the species was deliberately introduced by humans. These scenarios allow a number of hypotheses to be formulated and falsified (Lynch & Hayden, 1993),

1. It might be expected that, if the main migration route of a species was via Scotland, then one might expect recent Irish populations of that species to resemble, not their climatic and latitudinal equivalents in Wales

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and central England, but Scottish populations (Savage, 1966).

II. 'Relict' species should be morphologically (and genetically) more distinct from British populations than are populations of post-glacial immigrants.

Lynch & Hayden (1993) provided a preliminary examination of variation between Irish and British mustelids using a multivariate statistical examination of cranial measurements. In this paper, I further quantify variation between British and Irish populations of the badger, stoat, and otter. I show how morphological data are inconsistent with colonization via a Scottish/Irish landbridge, and discuss further objections to such a colonization route based on our current knowledge of the ecology of these species.

MATERIAL AND METHODS

Data were available from the crania of adult stoat, otter and badger originating from either Ireland, England or Scotland. Material was examined in the collections of the Royal Museum of Scotland (Edinburgh), the Natural History Museum (London), the Ulster Museum (Belfast), the National Museum of Ireland (Dublin), University College Dublin, Bristol University, Edinburgh University, Aberdeen University and the University of Sussex. Specimens were subjectively aged on the basis of sutute closure and appearance of the skull (see Lynch, 1993 for further details).

Eleven standard cranial measurements were taken from all specimens. These are defined in Lynch & O'Sullivan (1993) and were; condylobasal length, basilar length, length of the maxillary tooth row, palatal length, zygomatic breadth, mastoid breadth, inter-orbital breadth, post-orbital breadth, width of the post-orbital constriction, breadth across the maxillary canines, and breadth across the maxillary molars.

Data were pooled by species, country and sex (Table 1). For each of the five sex by species combinations (insufficient female otters were available from England), the magnitude of differences in cranial form between specimens from the three countries was examined using the following multivariate statistical procedure—data were log-transformed prior to subjection to a principal component analysis of the pooled within-group covariance matrix (a 'multiple group principal component analysis' *sensu* Thorpe, 1988). This generated eleven principal components, the first of which summarized cranial size variation. The remaining ten components were entered into a canonical variate analysis (CVA) which assessed the degree of difference between the samples from the three countries. The Mahalanobis distance (D^2) between groups was taken as an index of morphological similarity, and these values were corrected for sample size using the formula in Marcus (1993). The analysis of the ten principal components after the first has, in effect, size-corrected the data in a manner akin to that of Burnaby (1966).

All analyses were carried out using SAS™ version 6.06. SAS/IML code for the multiple group principal component analysis is available upon request from the author.

TABLE 1. Samples utilized in the examination of relationships between Irish, English and Scottish mustelids.

Species	Sex	Ireland	England	Scotland
Badger	Male	43	66	18
	Female	61	36	16
Otter	Male	25	5	23
Stoat	Male	26	67	76
	Female	15	14	60

TABLE 2. Summary statistics for variation between British and Irish mustelids. 'IE' is the Mahalanobis distance between Irish and English samples, 'IS' and 'ES' that for Ireland & Scotland, and England & Scotland, respectively. All distances are significant at a minimum of $P<0.005$, except those marked 'ns', which are nonsignificant.

Species	Sex	Size	Wilks' Λ	IE	IS	ES
Badger	Male	In	0.581	2.71	1.65	0.72
		Out	0.504	2.78	2.00	0.90
	Female	In	0.611	1.74	2.64	0.62
		Out	0.519	2.65	3.72	0.80
Otter	Male	In	0.371	2.90	5.90	0.69(ns)
		Out	0.339	4.04	6.34	0.88(ns)
Stoat	Male	In	0.231	14.34	15.03	2.38
		Out	0.332	8.38	12.70	1.54
	Female	In	0.172	33.32	19.58	4.21
		Out	0.474	4.74	4.57	1.64

RESULTS

Table 2 gives the summary statistics for the examination of variation between the three sites. All Mahalanobis distances

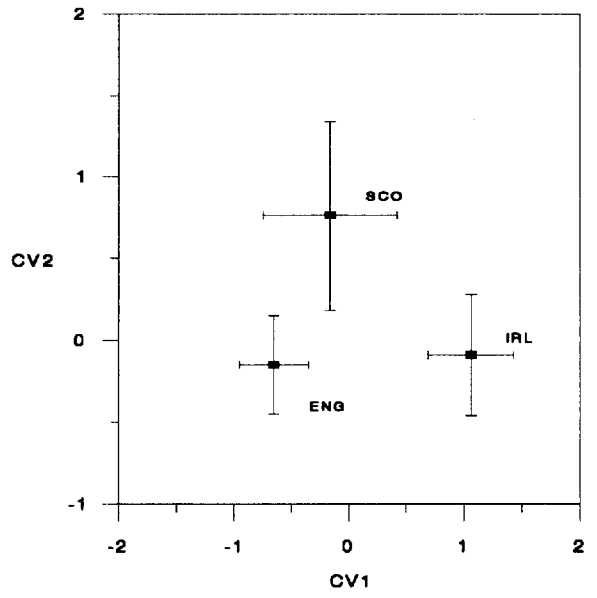

FIG. 1. Separation of Irish (IRL), English (ENG) and Scottish (SCO) male badgers on the basis of two canonical variates derived from a 'size-out' analysis. Circles represent 95% confidence intervals for the group mean.

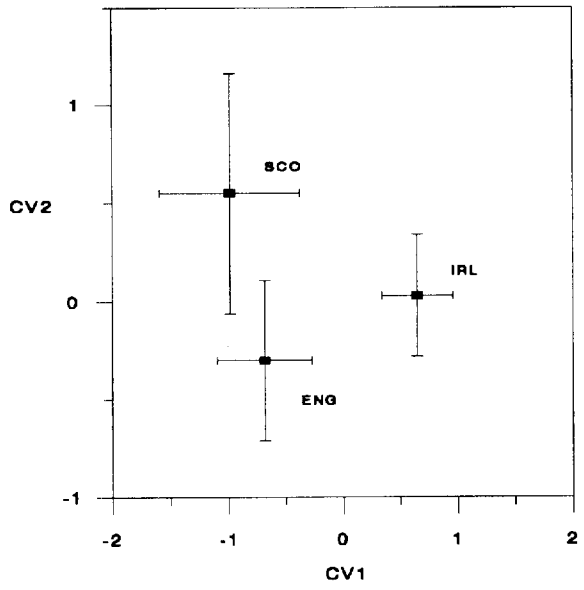

FIG. 2. Separation of Irish (IRL), English (ENG) and Scottish (SCO) female badgers on the basis of two canonical variates derived from a 'size-out' analysis. Bars represent 95% confidence intervals for the group mean.

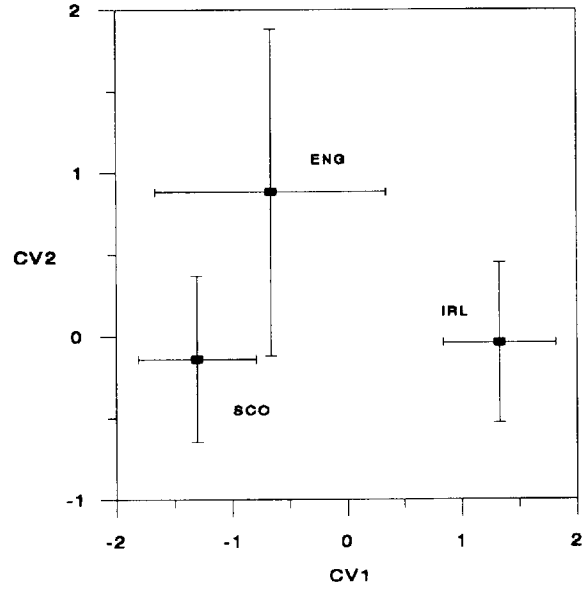

FIG. 3. Separation of Irish (IRL), English (ENG) and Scottish (SCO) male otters on the basis of two canonical variates derived from a 'size-out' analysis. Bars represent 95% confidence intervals for the group mean.

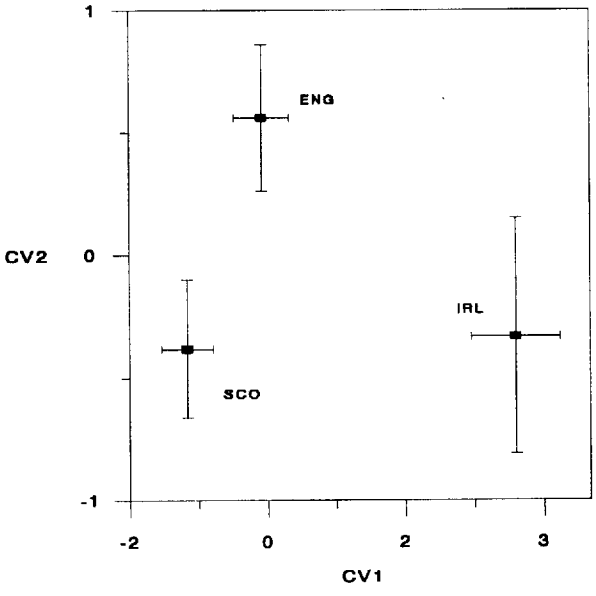

FIG. 4. Separation of Irish (IRL), English (ENG) and Scottish (SCO) male stoats on the basis of two canonical variates derived from a 'size-out' analysis. Bars represent 95% confidence intervals for the group mean.

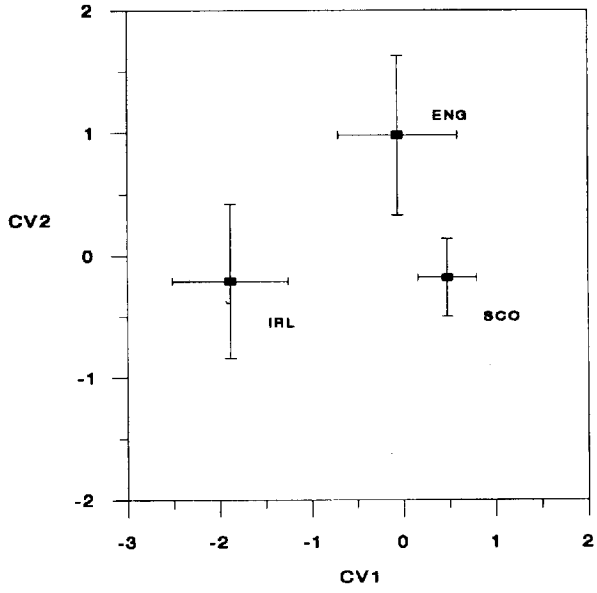

FIG. 5. Separation of Irish (IRL), English (ENG) and Scottish (SCO) female stoats on the basis of two canonical variates derived from a 'size-out' analysis. Bars represent 95% confidence intervals for the group mean.

were statistically significant (at $P<0.005$), except for that between English and Scottish otters (D^2 of 0.62, non-significant), and in all cases English and Scottish specimens were more like each other than either was to Irish specimens. Male Irish badgers were more similar to those from Scotland than those from England (D^2 of 2.00 versus 2.78; Fig. 1), whereas the opposite was true for the female badgers (Table 2; Fig. 2). Irish otters were more like English otters than their Scottish counterparts (D^2 of 4.04 versus 6.34; Fig. 3).

Both male and female Irish stoats were more like English stoats than those from Scotland (Table 2; Figs 4 and 5). Thus, in four out of five comparisons, Irish specimens were more like English specimens than Scottish, thus providing no craniological evidence for colonization via an Ireland-Scotland landbridge (Hypothesis I above). The distances between British and Irish stoat populations was greater than those between British and Irish populations of other

species, perhaps being evidence for relict status (Hypothesis II above).

DISCUSSION

Significant morphological differences have been demonstrated between English, Scottish and Irish badger, otter and stoat populations, in accordance with results from other studies (Lynch & Hayden, 1993; Lynch *et al.*, 1996). Four (out of five) comparisons established Irish populations as being more like their English counterparts than Scottish, thus providing little craniometric evidence for colonization by a landbridge linking Ireland and Scotland. The case of the stoat is of interest as the Irish stoats were a sample from County Antrim in the north of the country. This sample showed little affinities with counterparts in Scotland. The relatively large degree of differentiation between Irish and British stoat populations may be indicative of relict status (see below). Given the above results, one cannot disprove the theory of a recent origin for the otter and badger populations.

Lynch & Hayden (1993) proposed the following scenario to explain the occurrence of the carnivora in Ireland. The fauna of the Castlepook Interstadial (35,500 years BP) includes a number of species which occur either at present or in the recent past (wolf *Canis lupus* L., mountain hare *Lepus timidus* L. and stoat; Stuart & van Wijngaarden-Bakker, 1985). With the subsequent climatic deterioration (during which time two-thirds of the island's landmass was covered with glaciers), a number of the species present would have faced adverse conditions and would have become extinct. Species adapted to tundra conditions (wolf, hare, brown bear *Ursus arctos* L., arctic fox *Aloplex lagopus* L., lemmings *Dicrostonyx torquatus* Pallas & *Lemmus lemmus* L., reindeer *Rangifer tarandus* L., giant Irish deer *Megaceros giganteus* Blumenbach, and stoat) would have survived to recolonize the island during the Woodgrange Interstadial, as previously suggested by Fairley (1984) in an Irish context, and Yalden (1991) for Britain. This range contraction, and subsequent expansion, may explain the sub-specific status of the Irish hare and stoat, perhaps due to long-term isolation from the British stock from which it must have originated. During the interstadial, a landbridge between Britain and Ireland may have allowed some natural recolonization, but colonists would have faced a genetic bottleneck as well as the further deterioration of climate that was to characterize the Nahanagan Stadial. The timing of the putative landbridge just prior to, or during, the Nahanagan Stadial would have meant that colonists had to contend with an average annual air temperature in the region of -5°C (Mitchell, 1986) while populations were becoming established. It is unlikely that woodland species, such as the badger or pine marten, would have survived such an adverse climate, with its unsuitable vegetation (Yalden, 1992). This would have resulted in only the subarctic faunal element surviving into the start of the Littletonian, and the extinction of the giant Irish deer and reindeer. Subsequent climatic amelioration may have resulted in the further loss of species such as the two lemmings (Stuart & van Wijngaarden-Bakker, 1985; Yalden, 1992). The colonization of the island by humans (approx 9000 years BP) would have allowed accidental or deliberate introduction of species. Thus, the stoat, brown bear and wolf may have survived the Devensian Cold Stage in refugia, whilst the fox, pine marten, badger, and perhaps the extinct wildcat (*Felis silvestris* Schreber), were post-glacial immigrants (either natural or aided by man). The aquatic otter could have naturally colonized Ireland at any stage, as the Irish sea (especially at N.E. Ireland) probably did not prove a barrier to colonization.

The general ecology of the badger offers a number of objections to the use of a landbridge by the species. Firstly, the dispersal and colonization ability of the species would not appear to be great (Cresswell, Harris & Jeffries, 1990). Kruuk & Macdonald (1985) have described badgers as contractionists by nature, and said that they do not rapidly colonize vacant habitats. There is direct evidence for this in studies on two populations in Great Britain, one in Avon (Cresswell *et al.*, 1990), and one in Gloucestershire (Cheeseman *et al.*, 1993), where recolonization from high density areas into previously occupied (and thus highly suitable) habitat took over a decade to complete. On the other hand, Sleeman (1992) and Sleeman & Mulcahy (1993) offer evidence for higher than previously reported levels of movement in a badger population in Cork (Ireland), although admittedly the sample sizes reported were rather small, and no badgers were seen to take up residence in areas outside their clans territory. More interestingly, Bevanger (1985) notes rapid colonization of central Norway after World War II, although it must be admitted that colonizing an area like central Norway from the south of the country, may be easier than colonizing Ireland via a landbridge.

Secondly, badgers avoid bogland and low-lying marshy areas and are thus not found in lowlands liable to flooding (Neal & Cheeseman, 1991; O'Corry-Crowe, 1992), surely a characteristic of any putative landbridge. Furthermore, as Griffiths (1994) notes, although modern badger distributions cannot be used to assess species distributions in the past, there is only one known late-glacial or post-glacial record of the badger in Scotland, thus perhaps indicating that the badger never reached the putative landbridge before it's closure, as happened for the many species which did not invade Britain until any landbridge between Britain and Ireland had disappeared (e.g. bank vole *Clethrionomys glareolus* Schreber, microtine rodents *Microtus* spp., and polecat *Mustela putorius* L.).

Interestingly, neither the badger, weasel *Mustela nivalis* L., pine marten nor the fox occur on any of the islands that would have formed part of an Irish–Scottish landbridge. As mentioned above, otters could have naturally colonized Ireland. Could man have introduced the badger (and perhaps the pine marten) to Ireland? A number of lines of evidence support this idea. Mustelids are, in general, valuable commodity species, and have in the past been transported by humans from site to site and utilized for food and clothing (Griffiths, 1991, 1993; Mithen, 1994; Whittle, 1994; Rafferty, 1994). Large-scale changes in the fauna of an island due to the arrival of humans are not unknown; for example, the current mammalian fauna of

Corsica is almost entirely of human origin, with most of the native species being exterminated shortly after the arrival of man (Vigne, 1988, 1992). Badgers are present on a number of the Mediterranean Isles, and it has been contended that the Cretan badgers are post-glacial introductions (Groves, 1989). During the eighteenth and nineteenth centuries, badgers, stoats, brown hares (*Lepus europaeus* Pallas), mountain hares, hedgehogs (*Erinaceus europaeus* L,), and moles (*Talpa europaea* L.) were introduced to various Scottish islands (Brown, 1882; Yalden, 1991) and badgers were transported from the continent to Britain (Weightman, 1988). Lastly, van Wijngaarden-Bakker (1990) notes, on the basis of the absence of red deer (*Cervus elaphus* L.) remains in Irish Mesolithic sites, that the species must have been a late immigrant into the country, i.e. after colonization by man, and thus after any possible landbridge, and therefore must have been an introduced species (see also Woodman, 1978), as it was on the Mediterranean Islands, along with all other extant wild ungulates (Schüle, 1993).

It is obvious that the results presented here, pose more questions than they answer. They do, however, offer a framework for future work on the origin of the mammalian fauna of Ireland, work which should proceed along three routes; morphology, genetics, and archaeozoology. Further morphological studies are obviously required. In particular, a study of the introduced American mink would be of interest, though patterns of variation are likely to be greatly affected by anthropogenic influences. The examination of mink reported in Lynch & Hayden (1993) is somewhat invalidated as it appears that the Scottish mink utilized were ranch animals, not feral, and thus probably not indicative of feral stocks, given the differences between ranch and feral animals (Lynch & Hayden, 1995). There is no feral Scottish material available in any of the museum collections visited during the course of this study. Therefore, a study of the bank vole may prove more fruitful, given the species recent introduction to Ireland and the fact that it has not been interfered with by humans. Unfortunately, insufficient material exists in museum collections to examine variation in the pine marten in the British Isles. A study of the remaining extant carnivore, the fox, is currently underway. However, as Endler (1977) notes, there always remains a problem with separating the effects of localized adaptation and past history on morphological variation.

There has been little study of genetic variation between British and Irish populations of mammals. While there is a relatively good knowledge of genetic variation within countries for certain species (e.g. *Mus musculus domesticus* Schwartz & Schwartz; Berry *et al.*, 1991; Ryan, Duke & Fairley, 1993) there have been no published studies of variation between countries for these species, and we know virtually nothing about genetic variation among carnivores in the British Isles. Indeed, the only published study comparing British and Irish mustelids is that of Lynch *et al.* (1993) on the badger, which found significant isozymal differences between English and Irish badgers.

An examination of genetic variation within the British Isles may allow an estimation of the time of divergence between Irish and British populations and tracing of the origin of the Irish populations. For example, a recent (in the region of 10,000 years) divergence between Irish and British stoat populations may be indicative of postglacial colonization, whereas a divergence time in the region of 40,000 years would be consistent with the refuge hypothesis presented above. Such work has the advantage that large numbers of specimens would not be required. In addition, with the advent of polymerase chain reaction (PCR) techniques, it is now possible to obtain short DNA segments from fossil and sub-fossil material for analysis using the highly sensitive technique of DNA fingerprinting (Pääbo, 1989). Such genetic work is not, however, without problems. It is unlikely that the analysis of mitochondrial DNA would be able to separate time periods of this magnitude (10,000 versus 40,000 years), and there remains some difficulty with the formulation of applicable genetic distance statistics (A.W. Ryan, pers. comm.). PCR analysis of bone DNA is similarly of limited use as one is restricted to using random short chains of DNA which are unlikely to be homologous across samples, thus requiring the complete DNA sequence of the study animal prior to analysis, data which is currently unavailable for all mustelids. It is thus likely that archaeological studies will offer the best means by which the question of post-glacial colonization can be answered. Our knowledge of the past history of Irish mammals is remarkably scant, and it may be that future excavations will unearth specimens which invalidate the above conclusions.

Naturally, to state that humans *could* have introduced a species to Ireland, does not imply that they *did* in fact introduce that species. However, given man's propensity for the introduction of species, the possibility must be addressed. What is clear from the above is that there is little craniological evidence for post-glacial colonization of Ireland via a landbridge connecting Ireland and Scotland. While there may be evidence for an England–Ireland landbridge, there is no geological evidence for same. Indeed there are objections to colonization via any landbridge based on ecological characteristics of many of the species in question. It is concluded that while genetic and morphological studies are greatly desirable, they are not without serious problems, and that archeological research is the only means by which the question of the post-glacial colonization of Ireland will be answered.

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