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Species boundaries in the Herring and Lesser Black-backed Gull complex

J. Martin Collinson, David T. Parkin, Alan G. Knox, George Sangster and Lars Svensson



Caspian Gull *David Quinn*

ABSTRACT The BOURC Taxonomic Sub-committee (TSC) recently published recommendations for the taxonomy of the Herring Gull and Lesser Black-backed Gull complex (Sangster *et al.* 2007). Six species were recognised: Herring Gull *Larus argentatus*, Lesser Black-backed Gull *L. fuscus*, Caspian Gull *L. cachinnans*, Yellow-legged Gull *L. michahellis*, Armenian Gull *L. armenicus* and American Herring Gull *L. smithsonianus*. This paper reviews the evidence underlying these decisions and highlights some of the areas of uncertainty.

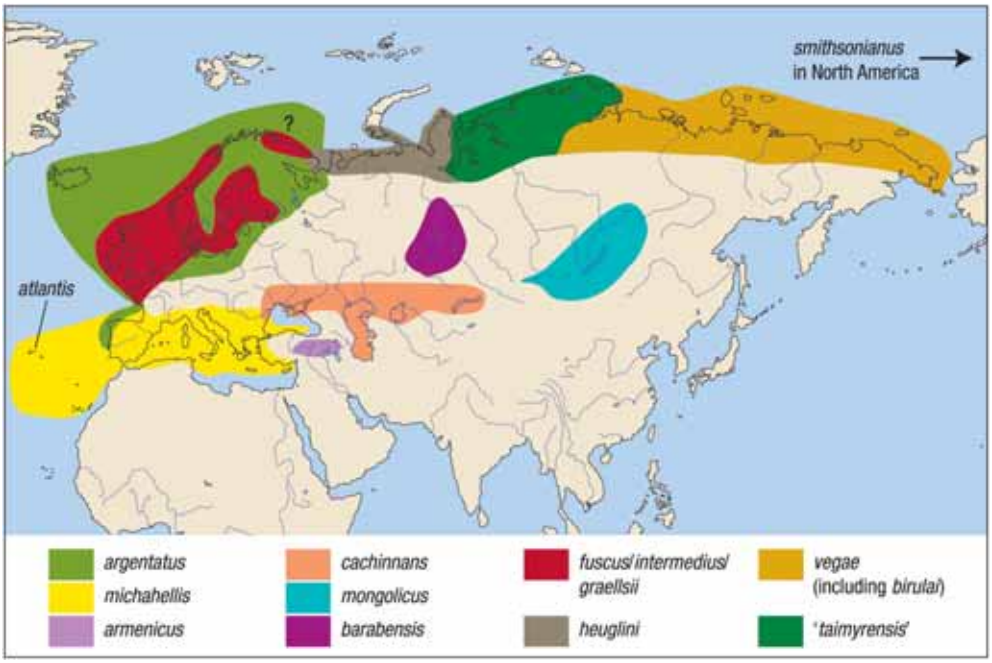
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We dedicate this paper to the memory of Andreas Helbig, our former colleague on the BOURC Taxonomic Sub-committee. He was a fine scientist who, in addition to leading the development of the BOU's taxonomic Guidelines, made significant contributions to our understanding of the evolutionary history of Palearctic birds, especially chiffchaffs and *Sylvia* warblers. He directed one of the major research programmes into the evolution of the Herring Gull complex. His tragic death, in 2005, leaves a gap in European ornithology that is hard to fill.

Introduction

Until recently, the Herring Gull *Larus argentatus* was treated by BOU as a polytypic species, with at least 12 subspecies: *argentatus*, *argenteus*, *heuglini*, *taimyrensis*, *vegae*, *smithsonianus*, *atlantis*, *michahellis*, *armenicus*, *cachinnans*, *barabensis* and *mongolicus* (Vaurie 1965; BOU 1971; Grant 1986; fig. 1). Other subspecies have been recognised, but are less widely accepted. The Lesser Black-backed Gull *L. fuscus* has also been treated as a polytypic species by BOU, with three subspecies: *fuscus*, *graellsii* and *intermedius*. Hereafter, we will refer to the various races of Lesser Black-backed and Herring Gull by their subspecific names, as outlined above, e.g. *graellsii* for *L. f. graellsii*. In the case of *atlantis*, we follow Dwight (1925) and Vaurie (1965) by including the Herring Gulls breeding along the coasts of northwest Africa, including the Azores, Madeira and Canary Islands, but not the coasts of Iberia. The problematic taxon *taimyrensis* is discussed in detail below, and the name is used in this paper to describe the birds breeding from the Ob River east to the Khatanga (Vaurie 1965). There has been no molecular work comparing the similar and intergrading taxa *argentatus* and *argenteus* directly and any reference to '*argentatus*' in this paper implies '*argentatus* and *argenteus*'.

The Herring Gull/Lesser Black-backed Gull complex has been cited as an example of a ring species (e.g. Mayr 1940, 1963). Herring and Lesser Black-backed Gull are treated as separate species (Brown 1967), but there is an apparent cline in mantle coloration from the darkest Lesser Black-backed, eastwards through Siberia (*heuglini*, *taimyrensis*, *vegae*), across North America (*smithsonianus*) to the palest birds (*argenteus*/*argentatus*), whose distribution overlaps with that of Lesser Black-backed Gulls in northern Europe. A 'southern ring' of potentially interconnected forms, from *atlantis*



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Fig. 1. Distribution of large white-headed gull taxa, based on Malling Olsen & Larsen (2003) and other data. The map does not show the range of the American Herring Gull *Larus smithsonianus*, or some of the other taxa within the complex that are uncontroversially accepted as being separate species, such as Great Black-backed Gull *L. marinus*, Glaucous Gull *L. hyperboreus*, Iceland Gull *L. glaucoides* and other North American and Siberian species.

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165. Adult European Herring Gull *Larus argentatus*, Fraserburgh, North-east Scotland, March 2005. Amid the confusing and complicated taxonomic issues, and identification problems that are increasingly associated with gulls at rubbish tips and in concrete environments, it is sometimes too easy to forget that we are dealing with some very attractive birds. The *argenteus* subspecies of Herring Gull is at the pale end of the circumpolar changes in mantle and wing colour, most famously formalised by Ernst Mayr, and 'Silver Gull' (Silbermöwe) is an appropriate vernacular name. In central Europe, *argentatus* hybridises with Caspian Gull *L. cachinnans*, which is expanding its range. This may eventually complicate both identification and taxonomic issues. Past episodes of hybridisation between these two taxa may explain why some Herring Gulls have the 'wrong' mtDNA and lie with the Aralo-Caspian clade.

through *michahellis*, *cachinnans*, *barabensis* and *mongolicus*, was also postulated (Mayr 1942; Barth 1968). The species boundary between Lesser Black-backed and Herring Gull is not universally agreed, and some authors (e.g. Cramp & Simmons 1983) have treated *heuglini* and *taimyrensis* as subspecies of the former, whereas others (Vaurie 1965; Grant 1986) treat them as races of the latter. Indeed, if one accepts that they form a ring species, it is not entirely clear why they are currently regarded as two species at all, and not one, as with another ring species, the Greenish Warbler *Phylloscopus trochiloides* (Irwin 2002; Collinson *et al.* 2003; Irwin *et al.* 2005).

Species Guidelines and gull taxonomy

The BOURC Taxonomic Sub-committee (TSC) has published its own guidelines for assigning species rank (Helbig *et al.* 2002; referred to throughout this paper as the 'Guidelines'). These were developed initially as an internal document, but they have now been adopted by several other taxonomic committees, including the Taxonomic Advisory Committee of the Association of European Records and Rarities Committees (AERC 2003). They attempt to set practical criteria that may be used to delineate species boundaries, broadly based upon a General Lineage species concept (de Queiroz 1998). The Guidelines are, in general, rather conservative. They demand that, for two taxa to be regarded as separate species, they should first be diagnosable at the taxon level: individuals must be clearly identifiable as belonging to one taxon or the other on the basis of genetically determined characters. Second, the Guidelines require that two taxa can be regarded as separate species only if they are likely to retain their separate genetic and phenotypic integrities in the future, i.e. the evidence suggests that they will not ultimately merge. The Guidelines also express a strong preference that taxonomic decisions be based on evidence published in peer-reviewed scientific literature. Gulls present particular problems for the delineation of species under these Guidelines: most of the taxa are very similar, yet all of them are rather

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variable, which makes diagnosis difficult; much of the identification literature has not been published in peer-reviewed journals; gulls frequently hybridise at low levels, and hybridising taxa are by definition never fully diagnosable with respect to each other; and finally, many gull taxa show unstable, rapidly changing ranges, which may bring distinctive taxa into secondary contact and create the opportunity for hybridisation.

Taxonomic decisions involving sympatric species (those for which the breeding ranges overlap significantly) are usually relatively easy to resolve. If two diagnosably distinct taxa, such as *argentatus* and *michahellis*, breed in sympatry without merging (because hybridisation is either very rare or absent), this is strong evidence of reproductive isolation and the taxa are best regarded as separate species (condition 1 of the Guidelines). Similar conclusions can be drawn for parapatric taxa (those whose ranges meet but do not overlap), and genuinely parapatric taxa that are diagnosably distinct and do not hybridise and merge are also best regarded as separate species (condition 2 of the Guidelines). This situation is rare among birds in temperate environments. Hybridising taxa are considered under condition 3 of the Guidelines: otherwise diagnosable taxa that hybridise are most appropriately treated as separate species if hybridisation is the product of recent contact due to range expansion and there is evidence that the taxa are sufficiently distinct that they are unlikely to merge (condition 3.1). They may also be treated as separate species under condition 3.2 of the Guidelines if hybridisation is limited to a narrow, stable hybrid zone, indicating restrictions to free gene flow, as with Hooded *Corvus cornix* and Carrion Crows *C. corone* (Parkin *et al.* 2003).

Some taxonomic decisions concern allopatric gulls (like *mongolicus*, whose breeding range does not overlap with that of any other large gull). Taxonomic decisions are often controversial in the case of allopatric populations, because it is more difficult to infer reproductive isolation between two or more taxa that never get the opportunity to interbreed. The best we can do is to look at the degree of difference between closely related allopatric taxa, and assess whether this is similar to the degree of difference between sympatric taxa that we know are separate species. Under the Guidelines, allopatric taxa should be treated as separate



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166. First-winter American Herring Gull *Larus smithsonianus*, St John's, Newfoundland, Canada, February 2007. Given the similarity between adult American and European Herring Gulls *L. argentatus*, it is counterintuitive to believe the mtDNA genetic data which splits the two taxa. However, the rather uniform dusky underparts of many first-year Americans, combined with the dark tail, was perhaps always a clue that *smithsonianus* had some 'Siberian' input.

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species if they are diagnosably distinct on the basis of one or more genetically determined characters (conditions 4.1 and 4.2), or on the basis of two or three characters in combination when any one of those characters by itself does not allow complete diagnosability (condition 4.3). However, in all 'condition 4' cases, the allopatric taxa must approach a level of distinctiveness seen in closely related sympatric taxa. It is not our intention that very small genetic differences between taxa should by themselves justify recognition of species status. When genetic differentiation is modest (e.g. Carrion and Hooded Crows, Parrot *Loxia pytyopsittacus* and Common Crossbills *L. curvirostra*), other evidence of reproductive isolation is essential. As will be seen later, there are cases where there is very little genetic differentiation among gull taxa that are widely accepted as 'good' species (e.g. Iceland *L. glaucoides*, Slaty-backed *L. schistisagus*, Glaucous-winged *L. glaucescens* and *smithsonianus* Herring Gulls). Conversely, morphologically well-differentiated taxa may show no evidence of reproductive isolation. In situations such as these, decisions are not made on genetic differentiation alone, but it has to be recognised that small genetic distance *and* poor phenotypic diagnosability may confuse the evolutionary picture in large gulls.

In the last 15 years, a large amount of new data relevant to gull taxonomy has become available. Not least are the enormous advances in identification, both in the field and in the hand, which have catalysed taxonomic review (for example, see Yésou 2002 for a summary of the whole white-headed gull group and Jonsson 1998a for the Lesser Black-backed complex). Other advances have taken place in the field of molecular phylogeny, in particular the genetic analysis of the relationships among gull taxa. Both lines of evidence have indicated a need for radical revisions of established gull taxonomy. Molecular phylogenies are generally published in peer-reviewed scientific journals, with a high standard of rigour and objectivity. The same cannot be said for advances in field identification, which, with few exceptions, are published in unrefereed magazines and books, on unmonitored websites, or are passed on by oral tradition; furthermore, they often involve the identification of (unverifiable) extralimital individuals. Some gull identification texts, such as Grant (1986) and Malling Olsen & Larsson (2004), are of a high standard, but many are not. We do not ignore informal non-peer-reviewed or anecdotal identification literature, but we recognise that some of it has to be treated with caution. Despite a growing confidence among birders in their ability to identify extralimital individuals, the evidence relating to such birds can be difficult to evaluate objectively. This in turn leads to the perception that taxonomic authorities are lagging behind experienced field observers.

To set the scene for a revision of gull taxonomy, we first review the genetic evidence that shapes our understanding of gull evolution. On the basis of this, the 'Herring/Lesser Black-backed Gull' complex is divided into independently evolving populations or lineages, among which taxonomic relationships are defined by morphological and behavioural characters. The result is a taxonomic arrangement that we believe better reflects our current understanding of the species limits within this complex group of birds.

Genetic analyses of gull evolution and species boundaries

Early attempts to unravel gull evolution using biochemical or molecular data (Tegelström *et al.* 1980; Ryttman *et al.* 1981; Johnson 1985; Snell 1991) found very little difference among the taxa, demonstrating that the currently recognised 'large white-headed gull' taxa have evolved so rapidly that it is not easy to determine their relationships (Wink *et al.* 1994; Heidrich *et al.* 1996). The taxa are closely related and (as with many northern hemisphere birds) much of their evolutionary history has probably been driven by the ebb and flow of glaciations. Recent studies using rapidly evolving genes have been more informative and have clarified our understanding of the relationships among these gulls. Many of these genes lie in small cellular structures called mitochondria, and evolve more rapidly than 'conventional' genes in the cell nucleus. The DNA sequence of the same gene is determined for each taxon under investigation, and phylogenies (or evolutionary trees) are generated, based upon genetic similarity (see Maclean *et al.* 2005). Since the genetic difference between two taxa depends upon how long they have been evolving independently, individuals with similar sequences are placed close together in a phylogeny. Two parts of the mitochondrial chromosome keep cropping up in gull genetics:

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these are the *cytochrome-b* gene (*cyt-b*) and the stretch of DNA called the 'control region'. The latter is not a real gene, but is involved with organising the way that the genes are read and replicated; it does, however, evolve rapidly and so is particularly useful for comparing closely related, or recently diverged, taxa.

Although phylogenies based on mitochondrial-DNA (mtDNA) sequences are widely used as a basis for taxonomic decisions, they are not without their limitations, and sometimes give an unrepresentative or misleading impression of the relationships between the taxa under review. It is well established that phylogenies based on a single gene may not represent the evolutionary history of a species accurately (this is well described for birders in Alström *et al.* 2003). The problems are exacerbated for taxa that have diverged only recently and may still hybridise or share genetic variations that were present in their common ancestor. Because mtDNA is transmitted through only the female line, even species that are effectively reproductively isolated by the infertility of hybrids may be able to share mtDNA lineages. Appendix 1 presents some examples that demonstrate the problems with mtDNA-based phylogenies.

Rather than seek potential problems with published phylogenies based on mtDNA, however, a more pragmatic approach is to take the most robust mtDNA phylogenies at face value, and then consider any complications that may arise when molecular and morphological data disagree. With this in mind, the most recent mtDNA studies make a lot of things clear, albeit raising many new questions as well. Broadly, the genetic results for many of the large white-headed gulls are consistent with rapid interglacial radiation from one of two glacial refuges (areas of suitable habitat that persisted during the ice ages). The following points summarise key issues which have emerged from the most recent genetic studies.

1. 'Herring Gull' should be split

Crochet *et al.* (2000, 2002) analysed the mitochondrial control region and *cyt-b* sequences of large white-headed gull taxa. They showed that these taxa form a monophyletic group (or clade) of closely related species, indicating that they have a recent common ancestor. Crochet and his colleagues identified a '*fuscus*' clade that included not only *fuscus*, *argentatus* and *michahellis*, but also Great Black-backed Gull *L. marinus* and a group of closely related Arctic (Siberian and American) taxa: Slaty-backed, Iceland and Californian Gulls *L. californicus*. In a similar study, Gay *et al.* (2005) confirmed this



Simon Stirrup

167. Third-winter Iceland Gull *Larus glaucoides*, Galway City, March 2007. Although plumage and structural features make this species easy to identify, genetically it forms part of the 'Siberian' clade, and it would be difficult, if not impossible, to try and identify one solely on the basis of a DNA sample.

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clade of closely related Arctic taxa, including Glaucous-winged, Glaucous *L. hyperboreus*, Iceland, Thayer's *L. glaucoides thayeri* and Slaty-backed Gulls. Interestingly, American Herring Gull (*smithsonianus*) also grouped within this Arctic/American/Siberian clade, rather than being particularly closely related to European Herring Gull (*argentatus*), suggesting that they may be different species. Together, the data suggest that at least one taxon (*smithsonianus*) currently included in the 'Herring Gull' complex should be treated as a separate species. The currently recognised 'Herring Gull' is not a homogeneous unit, but is paraphyletic in that taxa such as Great Black-backed Gull and Glaucous Gull, which are widely accepted to be distinct species, are embedded within it. By convention, paraphyletic species are not allowed (Maclean *et al.* 2005), and the 'Herring Gull', on the basis of genetic evidence, should be split into more species.

2. Gulls hybridise

It is well known that mtDNA sequences (haplotypes) that are characteristic of one taxon may also occur within individuals of another. This can be explained either by incomplete lineage sorting or by hybridisation. The former occurs where two taxa still possess one or more haplotypes that were present within the gene pool of their most recent common ancestor. This is commonly seen when two separate species have split from each other only recently, and analysis of the patterns of genetic variation within large gulls shows quite clearly that incomplete lineage sorting is partly responsible for the sharing of mtDNA sequences between recently evolved gull taxa (P. de Knijff pers. comm.). However, genetic sequences of one taxon can also be transferred to another taxon when individuals hybridise. Crochet *et al.* (2002) found genetic evidence for low levels of hybridisation between different gull taxa and concluded that the sharing of DNA haplotypes between taxa is partly due to hybridisation. There was no evidence of any restriction of gene flow in Lesser Black-backed Gulls between nominate *fuscus* and *graellsii*, supporting their treatment as conspecific. Indeed, there was evidence of gene flow between *fuscus* and *heuglini*, and even into East Siberian taxa such as *vegae*. Furthermore, perhaps due to their recent evolutionary origins and episodes of hybridisation, none of the American/Siberian taxa were genetically distinct, not even those that are morphologically quite divergent and universally accepted as different species, e.g. Slaty-backed and Glaucous Gulls.

Data from Crochet's team suggest both strong genetic differentiation within the large white-headed gulls (revealing boundaries between previously unrecognised species) and a lack of genetic differentiation (so far discovered) between taxa that are generally recognised as 'good' species. These data are broadly compatible with those of an independent team, led by Andreas Helbig, who used overlapping but more extensive mtDNA sequences (including part of the control region) to reveal a high-definition picture of gull phylogeny. The study by Liebers *et al.* (2004) built upon Liebers & Helbig (1999) and Liebers *et al.* (2001, 2002) to test directly the hypothesis that Herring Gulls are a classic ring species.

*3. Yellow-legged Gull (*michahellis*) and Armenian Gull (*armenicus*) are genetically distinct*

Liebers & Helbig (1999) studied the relationship between *michahellis* and *armenicus*. Analysis of control-region sequences showed that these are closely related but genetically distinct sister taxa, although hybridisation and morphologically intermediate birds were found at a mixed colony at Lake Beysehir, Turkey. In spite of this, and the implied potential for free genetic mixing, the mtDNA analysis revealed only limited evidence of *michahellis* sequences in the western *armenicus* populations, and none in the other direction. This was surprising, but suggested a degree of reproductive isolation between the two forms.

4. Southern 'yellow-legged' taxa are not a continuum of closely related forms

Helbig's analysis was then extended to include *atlantis*, *cachinnans*, *barabensis*, *mongolicus*, *graellsii*, *heuglini* and *taimyrensis* (Liebers *et al.* 2001). A related group was formed by *michahellis*, *atlantis* and *armenicus*, but whereas *michahellis* and *armenicus* were genetically distinct within this group, *michahellis* and *atlantis* were not. In fact, *michahellis* mtDNA haplotypes tended to be a subset of (or were recently derived from) *atlantis* DNA haplotypes, suggesting that *atlantis* was the ancestral form and that *michahellis* resulted from colonisation of the Mediterranean by birds from the current

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range of *atlantis*. Genetically, *armenicus* is relatively old (certainly older than *michahellis*), and it is likely that *atlantis*-like founders colonised the Mediterranean twice – the first time giving rise to *armenicus*, the second time (much later) giving rise to *michahellis*.

A second group was formed by *cachinnans*, *barabensis*, *mongolicus* and *graellsii/heuglini/taimyrensis*, these being genetically distinct from *michahellis*, *atlantis* and *armenicus*. Helbig's team found almost no evidence of gene flow between these two groups, in spite of their overlapping range (albeit at a low density and involving relatively few individuals) and occasional observations of hybridisation. In the Black Sea area, *michahellis* breeds in close proximity to *cachinnans*, while the range of *graellsii* overlaps with that of both *atlantis* and *michahellis*. The most genetically diverse taxon was *cachinnans* and it was placed basally in the phylogeny, suggesting that it was ancestral to the Siberian/Arctic taxa and Lesser Black-backed Gulls. Three taxa – *heuglini*, *taimyrensis* and *barabensis* – were very closely related; *barabensis* and *heuglini* were not distinguishable genetically, and genetic variation within *barabensis* was very small, suggesting that this taxon was a recently derived southern offshoot of *heuglini* and not, as had been previously assumed (Johansen 1960; Jonsson 1998b), a northern offshoot of *cachinnans*.

Reconstructing the evolution of these gulls suggests that *cachinnans* was long-established in a glacial refuge somewhere in the region of the Aral and Caspian Seas. Presumably during an interglacial, its range expanded northwards forming a population of gulls that subsequently evolved into *heuglini*/*taimyrensis*. More recently, birds from within the range of *heuglini* expanded south, giving rise to *barabensis*, which met *cachinnans* in secondary contact. There was evidence of gene flow between *barabensis* and *cachinnans* but, as with *armenicus* and *michahellis*, it was primary unidirectional (from *barabensis* into *cachinnans*, but not the other way). This suggests that free genetic mixing was not occurring, despite the lack of geographic barriers between the taxa. Hence Mayr's 'southern ring' of *atlantis*, *michahellis*, *cachinnans*, *barabensis* and *mongolicus* does not represent a valid taxonomic grouping, because several of the taxa are not particularly closely related to each other (de Knijff *et al.* 2005).

5. Lesser Black-backed Gulls are one or two species, not four or five

Liebers & Helbig (2002) used the mitochondrial control region to study the five northern taxa of 'Lesser Black-backed Gulls': *graellsii*, *intermedius*, *fuscus*, *heuglini* and birds that they assigned to *taimyrensis*. They analysed birds from the breeding grounds of each of these taxa and found that they were only very weakly differentiated, in general forming a single genetic



Chris Gibbins

168. Lesser Black-backed Gulls *Larus fuscus graellsii*, Tarragona, Spain, February 2006, with at least one *L. f. intermedius* (foreground). Identification of gulls is sometimes a process of iterative refinement. When a winter flock of *graellsii* presents an almost uniform appearance, it is tempting, and probably correct, to pick on the darkest bird and call it an *intermedius*. Such identifications are not usually independently verifiable, which does not mean that they are wrong, but as there is free gene flow and intergradation between *graellsii* and *intermedius* in northern Europe, assignment of an individual gull to subspecies depends more on where it breeds than what it looks like.

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group dominated by two mtDNA sequences that differed by only one DNA base pair. There was some evidence of hybridisation with *cachinnans*, and also with taxa from the Pacific, though on a very limited scale. None of these five taxa is genetically fully distinct from the others, consistent with a relatively recent divergence from a common ancestor and rapid range expansion. Nevertheless, certain patterns were evident: *heuglini* and *taimyrensis* were genetically more variable than the western taxa, of which *graellsii* was particularly uniform. This suggests that the eastern taxa are longer established, and that range expansion from ancestral populations of 'pre-*heuglini*' in northwest Siberia gave rise to *fuscus*, *intermedius* and *graellsii*. Whether this was by progressive expansion westwards, or by the separate evolution of *fuscus* and *graellsii* and their subsequent contact to produce *intermedius*, cannot presently be resolved. Gene flow across the range of the five subspecies is not completely unrestricted; there is isolation by distance. At over 4,000 km, the breeding range of the five taxa is much greater than the dispersal distances of individual gulls, so that birds at the extremes are geographically too far apart to meet and hybridise. Furthermore, the data indicated a significant (though incomplete) barrier to gene flow between *fuscus* and *heuglini*. Because there is no obvious environmental barrier to hybridisation between these taxa, Liebers & Helbig speculated that the boundary between *fuscus* and *heuglini* may approach the species level. There was, however, no genetic evidence for further splits within the 'Lesser Black-backed' grouping.

Yésou (2002) argued that the individuals of *taimyrensis* sampled by Liebers & Helbig (2002) were in fact taken from a location where many, perhaps all individuals, were of the form '*birulai*' (the characteristically yellow-legged western population of *vegae*). The implications of this will be discussed below.

6. The Herring Gull is not a ring species

The paradigm of the Herring Gull as a ring species had already been questioned (Allano & Clamens 2000; Yésou 2001a) by the time the emerging genetic picture was being evaluated and synthesised in Liebers *et al.* (2004). The last authors analysed not only the control region, but also the whole of the mitochondrial *cyt-b* gene, and greatly increased both the number of individuals and the number of taxa, to include *argentatus*, *smithsonianus* and other (mostly Pacific and Arctic) species. Their paper, boldly titled 'The Herring Gull is not a ring species', built on arguments put forward by Yésou (2001, 2002) and confirmed the finding of Crochet *et al.* (2002) that *smithsonianus* does not appear to be closely related to *argentatus* (which it would be if Herring Gull was really a ring species). Using Western Gull *L. occidentalis* as a more distantly related comparison (an outgroup), the deep genetic split between an Atlantic/Mediterranean clade of gulls ('Clade 1') and an Aralo-Caspian/Siberian clade ('Clade 2') was confirmed (fig. 2). Clade 1 comprised *atlantis*, *michahellis* and *armenicus* (as described in Liebers *et al.* 2001), also *argentatus*, Great Black-backed Gull and Palearctic individuals of Glaucous Gull. Clade 2 included *cachinnans*, *barabensis*, *heuglini*, *fuscus*, *intermedius* and *graellsii* as described above, and also Kelp Gull *L. dominicanus* and a mixed assemblage of genetically very similar taxa including *vegae*, *smithsonianus*, *mongolicus*, Slaty-backed, Iceland and Glaucous-winged Gulls, Nearctic individuals of Glaucous and some individuals of *argentatus*. Within Clades 1 and 2, *argentatus* and *cachinnans* were, respectively, the taxa with the oldest and most diverse mtDNA lineages, suggesting these to be the most direct descendants of the ancestral Clade 1 (Atlantic) and Clade 2 (Aralo-Caspian) gulls. No *smithsonianus* mtDNA sequences were found in *argentatus*, and *smithsonianus* was placed securely within a group of very closely related East Siberian/Pacific/Nearctic species. *Mongolicus* was shown to be closely related, not to *cachinnans*, but to the Pacific coast taxa (from whence its ancestors presumably colonised Mongolia only recently). Kelp Gull was shown to be a southern offshoot of the Lesser Black-backed taxa *fuscus*/*heuglini*/*taimyrensis*. Leaving aside for the moment the complication of two taxa (*argentatus* and *hyperboreus*) that have individuals in both clades, a putative evolutionary scenario for gulls was confirmed. As described earlier, two ancient glacial refuges are proposed – one in the North Atlantic where the ancestors of *argentatus* lived, and one in the Aralo-Caspian region that harboured the ancestors of *cachinnans*. North Atlantic 'pre-*argentatus*' gulls gave rise to two apparently reproductively isolated species: Great Black-backed (possibly originating in North America), and a yellow-legged 'pre-

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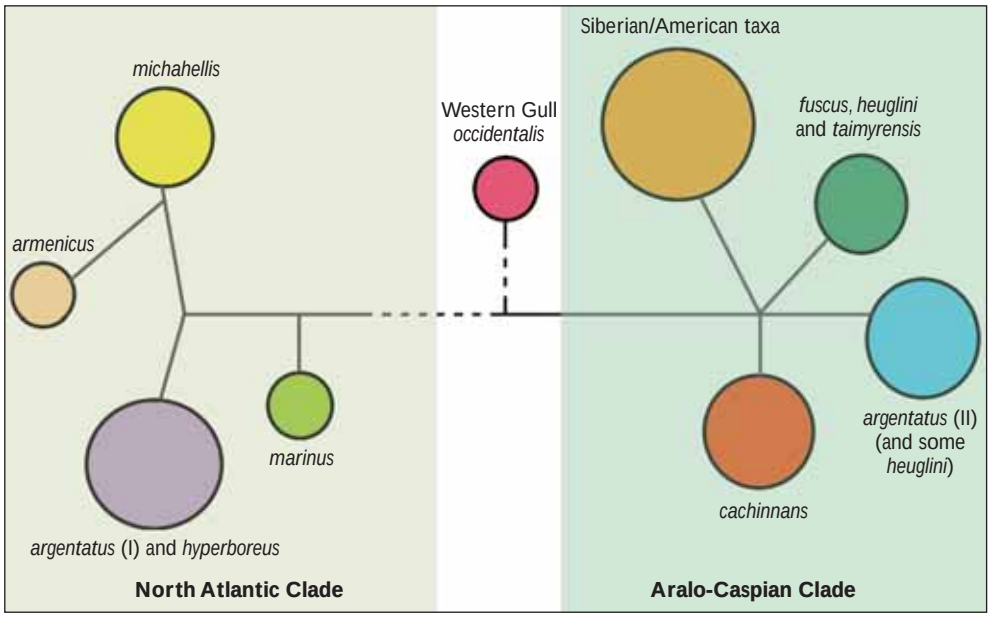


Fig. 2. Pictorial representation of the genetic relationships between large white-headed gulls. The lines represent genetic distance, the lengths of the lines being roughly proportional to the number of DNA mutations differentiating among the taxa. The filled circles represent a cluster of individual gulls with very similar or identical mtDNA sequences. The orange circle representing 'Siberian/American' taxa contains individuals of Iceland Gull *Larus glaucoides*, Glaucous-winged Gull *L. glaucescens*, American individuals of Glaucous Gull *L. hyperboreus*, Slaty-backed Gull *L. schistisagus*, as well as individuals of *smithsonianus*, *taimyrensis*, *mongolicus*, *vegae* and *heuglini*. The figure is based on Liebers *et al.* (2004), but very much simplified and with several anomalies removed. The occurrence of European and British Herring Gulls (*argentatus/argenteus*) with mtDNA sequences that fall within either clade may be due either to past hybridisation or to retention of ancient DNA sequences that were present in the ancestors of all the gulls.

atlantis' in the south. From here, *atlantis*-like birds colonised the eastern Mediterranean evolving into *armenicus*, which presumably became isolated during a subsequent glaciation. A second colonisation of the Mediterranean by *atlantis* gave rise to *michahellis*, which met *armenicus* in secondary contact in the eastern Mediterranean. From the Aralo-Caspian region, a process of contiguous population expansion driven by periodic climatic amelioration saw *cachinnans* birds moving northwards, evolving into *heuglini*, then west to become *fuscus*, and east to become the East Siberian and North American taxa *vegae*, *mongolicus* and *smithsonianus*. Thus, the Herring Gull is not a ring species.

The data suggest that 'large white-headed gull' divergence has been driven relatively recently by geographical separation, range expansion, and occasional long-distance colonisations over the last 300,000 years or even earlier (Crochet *et al.* 2002; de Knijff *et al.* 2005). Furthermore, for these gulls at least, there would appear to be no close relationship between genetic divergence and the evolution of reproductive isolation.

There is also the complication of *argentatus* and Glaucous Gull, which have individuals in both major genetic clades. There are two alternative explanations for this: (i) the retention of DNA variants that were present in a (presumably long-established and genetically diverse) common ancestor of Clade 1 and Clade 2 taxa, or (ii) more recent hybridisation between Clade 1 and Clade 2. For *argentatus*, it is possible that both have occurred. The Clade 1 mtDNA haplotypes found in *argentatus* are varied and basal to the phylogeny – suggesting that they are ancient. In contrast, the Clade 2 mtDNA haplotypes are more recent and less varied, and more suggestive of fairly recent hybridisation between *argentatus* and a Clade 2 taxon such as *cachinnans* or *fuscus*. Clade 1 DNA appears to be the 'original' for *argentatus*, hence the placing of this taxon within the North Atlantic assemblage. Glaucous Gull is different because all the Clade 1 mtDNA haplotypes came from the Palearctic, and all the Clade 2 from the Nearctic,

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suggesting a geographical basis to the genetic variation. Across its range, Glaucous Gull is observed to hybridise frequently only with *argentatus* in Iceland, and with *smithsonianus* in Alaska. This hybridisation may have led to Glaucous Gull acquiring the mtDNA of another taxon at some point during its evolution. Hence its molecular phylogeny is obscured because, in some parts of the range, its own evolving mtDNA sequences have been replaced by those from another taxon.

7. Nuclear- and mitochondrial-DNA comparisons

The occurrence of both Clade 1 and Clade 2 haplotypes in *argentatus* and *hyperboreus* has important implications for the way gull phylogenies are interpreted. Over the course of time, mtDNA lineages will be lost from the population, more or less randomly, as females with those mitochondrial sequences die without leaving any offspring. If new sequences were not created by mutation, all individuals within a taxon would eventually share the same mtDNA (see Maclean *et al.* 2005). Consequently, if we came back in 50,000 years time, it is possible that all Clade 1 haplotypes would have been lost from *argentatus*, and we would resolve it, entirely falsely, as a Clade 2 taxon. How do we know that other gull taxa within the current phylogeny have not been displaced by similar random events? Furthermore, if gull taxa can adopt, by hybridisation, the mtDNA sequences of another taxon, how can we be certain about the placement of any taxon? For example, is it possible that *smithsonianus* is really a close relative of *argentatus*, but that it hybridised with a North American taxon and adopted the mtDNA of that taxon? Both of the North American *marinus* specimens examined by Crochet *et al.* (2003) yielded 'Siberian' (possibly *smithsonianus*) mtDNA haplotypes (see also de Knijff *et al.* 2005), presumably a result of past or currently observed hybridisation. These complications do not just make gull phylogenies difficult: they may cause entirely false conclusions to be drawn about species boundaries. The problems are not insoluble, and they can be partly resolved by the simultaneous analysis of nuclear DNA and morphology. While mtDNA sequences are driving our understanding of gull evolution and are enormously informative, it must be recognised that splits or lumps based *solely* on mtDNA cannot be regarded as robust.

Nuclear genes evolve and diverge more slowly than does mtDNA. Studies of the nuclear DNA of gulls have been more limited in scope, and the results are less informative because the very recent radiation of this group has not allowed much time for the genetic divergence of nuclear genes. Two studies (Panov & Monzikov 1999 and de Knijff *et al.* 2001) did not directly sequence nuclear genes, but drew up partial phylogenies using a crude variant of genetic fingerprinting. Panov & Monzikov limited their analysis to the relationship between *argentatus* and *cachinnans* as part of a broader behavioural and morphological study, and revealed clear evidence for regular hybridisation along a long, but narrow, contact zone accounting for a small part of the Russian populations of both taxa. In particular, they found evidence in the Volga basin for the introgression of *argentatus* genetic fingerprints into *cachinnans*. De Knijff *et al.* (2001) studied nuclear genes in *cachinnans*, *atlantis*, *michahellis*, *argentatus*, *fuscus*, *graellsii*, *intermedius*, *heuglini* and *taimyrensis*. Their analysis did not really resolve any of the taxa as being genetically distinct from the others because the method is relatively insensitive, although it has now been improved (P. de Knijff pers. comm.). However, in common with other studies, their results suggest rapid evolution of gulls, and continued gene flow between taxa. Their tentative phylogenetic tree put *cachinnans* as a basal group, supporting the existence of the ancestral Aralo-Caspian gull clade, and based upon an entirely distinct set of genetic data. The five 'Lesser Black-backed' taxa which they examined also grouped together, as did *atlantis*/*michahellis* with *argentatus*. So although the analysis did not radically alter our existing understanding of gull phylogenetics, it was broadly consistent with the mtDNA data for the same taxa.

Crochet *et al.* (2003) used a different technology to examine nuclear DNA from *marinus*, *michahellis*, *fuscus*, *argentatus*, *hyperboreus* and *smithsonianus*. Again, they found only very low levels of divergence among the taxa, which contrasted with the strongly structured phylogeny based on mtDNA, and which did not provide a solution to the *smithsonianus* problem. And again, the low level of divergence is consistent with the relatively recent radiation of the taxa (they estimate speciation events occurring 100,000 to 500,000 years ago), combined with ongoing hybridisation. In fact, they concluded

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that intraspecific genetic diversity is accounted for almost entirely by hybridisation. This is not to imply that hybridisation is out of control, and that distinct gull taxa are currently merging. A reasonable mathematical estimate for gene flow between *argentatus* and *fuscus*, based on nuclear-DNA data, is that one hybrid per year successfully breeds with each parental species (Crochet *et al.* 2003). In the long term, small amounts of hybridisation can homogenise nuclear-DNA sequences across taxa and there are other examples of distinct species, such as crossbills and Galapagos ground finches *Geospiza*, that maintain species boundaries with little genetic differentiation, in spite of real or apparent hybridisation (Sato *et al.* 1999; Piertney *et al.* 2001). Furthermore, the data in Crochet *et al.* (2003) strongly suggested that the distinctiveness of the gull taxa was being maintained through selection against hybrids. In short, gull taxa are maintaining distinct morphologies by natural selection, in spite of the genetic 'scars' left by hybridisation, an argument for the continued importance of 'morphology-based' taxonomy.

8. General conclusions about genetic data

The implications of these genetic analyses for individual gull taxa will be discussed below. But what are the general lessons? First, molecular data reveal unsuspected examples of partial or complete reproductive isolation between gull taxa, and thereby provide strong evidence that valid species boundaries have previously been overlooked. Second, although molecular divergence between taxa may imply reproductive isolation, reproductive isolation does not necessarily produce significant genetic divergence, certainly not within the relatively short timescale of the evolution of these birds (i.e. good gull species may not have had time to become totally genetically distinct). Third, hybridisation between gulls is ongoing, and may obscure phylogeny; hybridisation may also make it difficult to define diagnostic characters for some taxa, and this has to be borne in mind when assessing potential species boundaries.

Taxonomic conclusions for the Herring Gull/Lesser Black-backed Gull assemblage

Lesser Black-backed and Herring Gulls are specifically distinct. They breed extensively in sympatry without merging, demonstrating effective reproductive isolation. On the occasions where hybridisation has been observed, the hybrids are fertile, though not necessarily as fit as pure-bred birds. Reproductive isolation is maintained largely by behavioural and morphological factors influencing female mate choice. There is an extensive range of species-specific displays, and females choose a mate of their own species on the basis of long-call vocalisations and posture, and the colour of bare parts, eye-ring and mantle (Tinbergen 1953; Brown 1967). Similar isolating factors may operate between other gull taxa, and must be considered when defining species boundaries. The ability of two closely related taxa to interbreed is in some respects a retained ancestral character, and may not always be taxonomically informative. For gulls, it is important to remember that failure or inability of two taxa to interbreed does not correlate well with the genetic difference between them (Liebers *et al.* 2004).

The Atlantic taxa – Herring Gull and Mediterranean, Atlantic and Armenian Yellow-legged Gulls

Mediterranean *michahellis* and Atlantic Yellow-legged Gulls *atlantis* are fairly similar in structure and plumage, and appear to be closely allied, a conclusion that was confirmed by genetic analyses described above. Although some *atlantis* may be identifiable in the field, especially individuals from the distinctive Azores population, the two taxa intergrade and are not diagnosably distinct; at present there is no evidence to support a species-level split between them (de Knijff *et al.* 2001; Liebers *et al.* 2001), although the continued recognition of at least two subspecies is desirable. There is a need for further research into the affinities of birds breeding in coastal Morocco and on the Atlantic coast of Portugal. Birds breeding along the north coast of Spain, which can be distinguished on the basis of plumage, vocalisations and structure (Teyssèdre 1983; Carrera *et al.* 1987), may also merit subspecific recognition, but are genetically very similar to *michahellis* (Pons *et al.* 2005).

Northwards range expansion of *michahellis* has brought it into limited contact with *argenteus* in northwest Europe (Nicolau-Guillaumet 1977; Marion 1985), and occasional hybridisation with both *argenteus* and *graellsii* has been recorded (e.g. Yésou 1991). Hybridisation is not unusual for individuals at the edge of their

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range, where potential mates are scarce, and has little taxonomic significance. However, on the west coast of France, *michahellis* and *argenteus* have bred in mixed colonies for nearly 30 years and mating is strongly assortative, i.e. mixed pairs are much rarer than would be expected if mating were random (Yésou 1991). The two taxa effectively ignore each other, and there is little if any evidence of merging (Yésou 2002; Pons *et al.* 2004). Criteria for separating *michahellis* and *atlantis* from other gulls, in immature and adult plumages, through bare-part coloration and vocalisations, have been well described (Glutz & Bauer 1982; Teyssèdre 1983, 1984; Dubois & Yésou 1984; Filchagov 1993, 1999; Garner & Quinn 1997; Klein & Buchheim 1997; Klein & Gruber 1997; Liebers & Helbig 1999; Dubois 2001).

As defined by Helbig *et al.* (2002), *michahellis/atlantis* fulfils diagnosability and other criteria for specific rank, separate from Herring Gull. Together with the clear genetic differentiation between *michahellis*/*atlantis* and all other taxa, these data indicate a prolonged period of independent evolution that has led to a level of reproductive isolation consistent with species boundaries between *michahellis/atlantis* and both *argentatus* and *fuscus/graellsii/intermedius*.

Liebers & Helbig (1999) carefully analysed the extent of morphological diagnosability in Armenian Gull *armenicus*, finding small but significant differences from *michahellis* in the long-call vocalisations, and also in wing-tip pattern. Other characters, such as wing and head length, differ statistically, but there is considerable overlap. Their molecular data showed evidence of reproductive isolation, although this is not complete because of limited maternal gene flow from *michahellis* into *armenicus* populations (although not in the opposite direction). So, although the breeding colonies of *armenicus* are well within the dispersal distance of *michahellis* in the eastern Mediterranean (and hybridisation is known to occur), *michahellis* and *armenicus* are genetically distinct and there is no evidence of introgression on a scale to suggest that the two taxa will merge. Thus, *michahellis* and *armenicus* are diagnosable by a combination of bill markings, wing-tip pattern, biometrics and mtDNA; by treating them as



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169. Adult Yellow-legged Gull *Larus michahellis* Tarragona, Spain, February 2006. It is difficult to believe now that this distinctive species was ever lumped with Herring Gull *L. argentatus*. The bright yellow legs, red-orange eye-ring and stout bill are distinctive, and many individuals can be identified on voice alone. When *michahellis* and *argentatus* breed in some of the same colonies in northwest Europe, they most often virtually ignore each other. Both *michahellis* and the closely related Armenian Gull *L. armenicus* appear to have evolved from founder populations that colonised the Mediterranean region from ancestral ranges on the Atlantic coasts.

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largely allopatric taxa with occasional hybridisation, they fulfil species criteria 3 or 4.2 defined by Helbig *et al.* (2002).

Previously, *michahellis* and *atlantis* have been split by some authorities from Herring Gull but lumped with *cachinnans*; this was the position previously adopted by *British Birds* (*Brit. Birds* 86: 1–2) and is the current treatment in Dickinson (2003). However, *michahellis* and *cachinnans* are essentially parapatric, separated by breeding habitat, although they breed in near sympatry in Poland and Romania, where hybridisation has been suspected, but not proven (Klein & Buchheim 1997; Faber *et al.* 2001). Both morphological and behavioural evidence suggest a high degree of reproductive isolation (this is covered in more detail under the section on *cachinnans* below), and the genetic evidence confirms that *michahellis* and *cachinnans* should not be treated as conspecific.

The TSC has recommended that Yellow-legged Gull and Armenian Gull be treated as separate species (Sangster *et al.* 2005) – a recommendation which, of course, parallels decisions made by other European taxonomic committees.

- Yellow-legged Gull *L. michahellis* (polytypic, incl. subspecies *michahellis*, *atlantis* and possibly other populations that may deserve subspecific recognition)
- Armenian Gull *L. armenicus* (monotypic)

Caspian (Pontic) Gull – cachinnans

Perhaps no taxon better demonstrates the contribution that birders have made to gull identification than *cachinnans* (Yésou 2002). As recently as 1995, few people were identifying extralimital Caspian Gulls, yet a combination of ringing data and careful field observation has shown that this (sometimes) distinctive taxon is not an uncommon visitor to northwest Europe (Klein 1994; Gruber 1995; Garner & Quinn 1997).

Both nuclear and mitochondrial DNA strongly suggest that *cachinnans* is conspecific with neither *argentatus* nor *michahellis/atlantis*. However, *cachinnans* is morphologically variable, and the problem for the assessment of diagnos-



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170. Adult or near-adult Caspian Gull *Larus cachinnans*, Histria, Romania, August 2006. In the space of ten years this species has gone from 'first' to 'mega' to 'non-rarity' status in Britain, thanks to a combination of ringing studies that showed that the species was on the move into northwestern Europe and some very sharp birding. It was previously considered to be closely related to the Yellow-legged Gull *L. michahellis*, but the genetic data suggest that this species is more closely related, and possibly ancestral, to Lesser Black-backed Gull *L. fuscus*. Extensive white tongues to the inner webs of the outer primaries are characteristic of this species, and although the iris colour is variable, many adult Caspian Gulls have striking dark eyes. The open-winged posture during long-call display is characteristic of Caspian Gull, and the scientific name refers to its unusual dry 'laughing' call.

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ability is that the full range of variation has probably not been formally published (Liebers & Dierschke 1997; Gibbins 2003). There is also hybridisation with *argentatus* along a narrow zone where the taxa meet in eastern and central Europe, which makes it difficult to distinguish the range of variation within pure *cachinnans* from the variation that results from hybrids (Panov & Monzikov 1999; Neubauer *et al.* 2006). Nevertheless, a substantial body of identification literature suggests multiple characters by which many individuals can be recognised. These will not be repeated in detail here (see, for example, Panov *et al.* 1991a,b, Garner & Quinn 1997, Klein & Gruber 1997, Liebers & Dierschke 1997, Jonsson 1998b) but include: distinctive structural features of the bill and legs; wing and neck length and posture; an apparently diagnostic pattern of white tongues on the inner webs of the outer primaries of adults; specific body-feather patterns on young birds (especially first-winters); and characteristic underwing and greater-covert patterns. The voice is distinctive, as is the long-call posture (though this may be cultural rather than genetic; Tinbergen 1953). Clearly, *cachinnans* and *argentatus* fulfil diagnosability requirements for species status.

Sometimes, *cachinnans* breeds in close geographical proximity to *michahellis* with no significant hybridisation, perhaps in part due to differences in their preferred habitat. The taxa are phenotypically distinct and there is no evidence of gene flow, suggesting that they are reproductively isolated. The range of *cachinnans* also approaches that of *barabensis*, with which it has previously been regarded as conspecific (Johansen 1960). There is some evidence of hybridisation between the two, but it is very limited and unidirectional: *barabensis*-type mtDNA has been found in individuals that are phenotypically *cachinnans*, but not vice versa (the implication being that *barabensis* females are mating with *cachinnans* males and their progeny are being incorporated into the *cachinnans* population, perhaps by the female offspring becoming imprinted upon their fathers). This is a similar situation to that which exists between *armenicus* and *michahellis*. A degree of reproductive isolation is implied, though this is possibly incomplete – individual gulls in Kazakhstan (or wintering in Arabia) are sometimes of intermediate character between *barabensis* and *cachinnans*, and may be impossible to assign to either form (Johansen 1960). Introgression of *cachinnans* into *barabensis* populations has been inferred from morphological studies (Panov & Monzikov 2000), although these authors showed only that some *barabensis* individuals were close to *cachinnans* in some characters, which does not necessarily imply intergradation. On all morphological, behavioural and vocal criteria, *barabensis* is much closer to *heuglini* than to *cachinnans*. Thus, there is no compelling evidence to suggest that *barabensis* and *cachinnans* should be treated as conspecific, whereas there is convincing evidence that, as the best description of the relationship between the taxa, they should be split.

The problem of cachinnans–argentatus *hybridisation*

A broad zone of introgression was described by Panov & Monzikov (1999) as a cline from the Volga (pure *cachinnans*) to eastern Scandinavia (pure *argentatus*). In fact, what was described was a broad zone in which individual gulls often showed mixed characters of either taxon, but there was limited genetic evidence of introgression of *argentatus* genes into the Volga basin. Hybridisation has been inferred in expanding *cachinnans* colonies in eastern Europe (Faber *et al.* 2000; Neubauer *et al.* 2006; Yakovets 2006), and has probably been occurring intermittently for some considerable time where these two taxa meet. It was even suggested that eastern '*omissus*' *argentatus* may result from previous episodes of hybridisation between *argentatus* and *cachinnans*. Although the fitness of hybrids has never been formally tested, true reproductive isolation between *cachinnans* and *argentatus* probably does not exist, and we have to consider whether the taxa are merging. Neubauer *et al.* (2006) analysed the situation in most detail in Poland, where both *argentatus* and *cachinnans* have recently expanded their numbers and range (*argentatus* from the north, *cachinnans* from the south). In central Poland, the two taxa have come into contact and are breeding. Neubauer *et al.* regarded *argentatus* and *cachinnans* as diagnosably distinct, and confirmed the ecological (habitat) differences between the two taxa. Birds in central Poland that could not be identified because they fell outside the range of variation of their reference populations of *argentatus* and *cachinnans* from Poland and elsewhere, or

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that showed mixed characters, were treated as hybrids. Whether these really are hybrids or are just unidentifiable is difficult to determine, but two observations strongly support the hybrid suggestion: 1) they occur predominantly in central Poland where the two taxa coexist; and 2) pairings occur between the two taxa. There are approximately 200 pairs of gulls each year with some sort of hybrid *argentatus/cachinnans* pairing/contribution, in a 300-km zone across the middle of Poland. This is out of a population of about 1,500 pairs of *argentatus* (a recent colonist but its population is steady or declining) and 500 of *cachinnans* (rapidly expanding in numbers and range from the south). The data are consistent with recent (20 years) secondary introgression driven by range expansion, especially that of *cachinnans* from the south. We cannot predict whether this hybridisation might eventually lead to the merging of the two taxa. There is a possibility that as *cachinnans* continues to exploit refuse tips across Europe, it will continue to spread northwest, hybridising freely with *argentatus* to form a hybrid swarm (a mixed population of individuals with variably intermediate appearances due to multi-generation interbreeding) or a cline, and so would no longer fulfil the Guidelines criteria for separate species (Helbig *et al.* 2002). It is also possible that a stable hybrid zone will develop (satisfying Guidelines criterion 3.2), or that they will become sympatric and reproductively isolated like *argentatus* and *michahellis* in western Europe (satisfying criterion 1.2). The TSC cannot make confident predictions about this, but to assert that in future the taxa will merge and should therefore remain lumped requires several assumptions that cannot currently be supported by evidence, especially while we know nothing about the long-term fitness of the hybrids. The mtDNA evidence is unequivocal – *argentatus* and *cachinnans* are quite different evolutionary lineages, and cannot be lumped – and the evidence for hybridisation cannot be shown to be taxonomically any more significant than hybridisation between White-headed *Oxyura leucocephala* and Ruddy Ducks *O. jamaicensis*, i.e. the result of range expansion bringing divergent but reproductively compatible taxa into contact. However, we recognise that this is a situation that should be kept under review, and we cannot discount the possibility that *cachinnans* will begin to merge with *argentatus* through hybridisation.

In the light of these data, we recognise that *cachinnans* fulfils diagnosability criteria and has maintained its identity over evolutionary time despite close contact and proven hybridisation with other gull taxa. It should therefore be treated as a separate species:

- Caspian Gull *L. cachinnans* (monotypic)

There is variation within *cachinnans*, and western birds ('*ponticus*' from the Black Sea) have been described as showing more white in the primaries than eastern birds. It is not, however, certain that this geographic variation would withstand a critical examination, so for now we treat Caspian Gull as monotypic, with considerable individual variation. There is need for a rigorous assessment of morphological variation within and between populations of *cachinnans*, to establish whether there is sufficient differentiation to merit the recognition of any subspecies.

Lesser Black-backed Gulls – L. fuscus

It has previously been proposed that the Baltic Gull *L. f. fuscus* should be split from the other subspecies of Lesser Black-backed Gull, on the basis of plumage and structural characters, moult cycle, foraging and migration strategies (Sangster *et al.* 1999). However, mantle colour varies clinally from *graellsii* through *intermedius* to *fuscus*, and field identification of *fuscus* is probably impossible, except on the basis of geographical location (Barth 1966, 1968; Jonsson 1998a; Gibbins 2004a; Muusse *et al.* 2005). 'Soft' characters such as foraging strategy and migration routes are likely to be environmentally constrained, and not taxonomically informative. Using a long sequence of mtDNA, Liebers & Helbig (2002) found a continuous gradation from *graellsii*, through *intermedius* to nominate *fuscus*, confirming genetic arguments presented by Crochet (1998), suggesting little if any reproductive isolation. This genetic cline more or less parallels the changes in mantle colour across the range. Under the Guidelines, we therefore intend to continue to treat nominate *fuscus*, *intermedius* and *graellsii* as subspecies within a single species.

The systematics of the three west Siberian taxa *heuglini*, *taimyrensis* and *barabensis* are unclear. They have been poorly described in the literature until quite recently, when more information has become available (Filchagov *et al.* 1992b; Eskelin & Pursiainen 1998; Rauste 1999;

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Panov & Monzikov 2000; Buzun 2002). Generally, *taimyrensis*, the name usually given to the taxon breeding from the Ob to the Khatanga (Vaurie 1965), has been regarded as the pale end of a cline in mantle coloration running from dark-mantled *heuglini* in the west to paler-mantled *taimyrensis* in the east. Yésou (2002) reported that birds now breeding within the accepted range of *taimyrensis* are in fact phenotypically identical to the generally yellow-legged '*birulai*' form of the East Siberian 'Herring' Gull *vegae*. There is a sharp divide in average mantle colour between birds breeding west of the Ob (*heuglini*) and those breeding east of the Ob (*birulai* = *vegae*) (Yésou 2001b). A minority of intermediates occurring from the Ob eastwards to southwestern Taimyr (not farther east) are in some respects phenotypically intermediate and might be labelled '*taimyrensis*', but Yésou suggested that if *taimyrensis* ever existed as a valid taxon, it was the result of hybridisation between western *vegae* ('*birulai*') and eastern *heuglini* in some sort of unstable hybrid zone. There is nevertheless a cline in *heuglini* mantle colour, getting paler from west to east (Buzun 2002). It may be sensible to recognise this differentiation taxonomically, although the degree of difference is very slight.

Liebers & Helbig (2002) showed genetically that breeding birds from the ranges of *heuglini*, *taimyrensis* and *barabensis* are very closely related, and that *barabensis* is clearly related to 'Heuglin's' rather than Caspian Gull. Generally, *barabensis* is morphologically distinct from Caspian Gull, but the limited introgression detected by Liebers & Helbig (2002) is perhaps reflected in the field. Studies of breeding *barabensis* have demonstrated small population-level differences from *heuglini* in plumage pattern and biometrics (Panov & Monzikov 2000). It remains possible that, as more data become available, *barabensis* will be recognised as a separate monotypic species, but the current uncertainty about the extent of intergradation with *heuglini* leads us to retain it as part of the *heuglini* group.

Any taxonomic decision on the relationship of *heuglini* and *barabensis* with *fuscus*, *intermedius* and *graellsii* will be borderline. The latter



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171. Adult Lesser Black-backed Gull *Larus fuscus*, Tampera, Finland, August 2007. This is a 'Baltic Gull' *L. f. fuscus*. Without its rings this would not normally be diagnosably distinguishable from *L. f. intermedius* as an extralimital vagrant. However, the long-winged and slightly built appearance may be a clue to its identity, and moult-cycle differences with respect to other Lesser Black-backed taxa may help to identify some individuals. There is no substantial evidence to suggest that it should be split from *L. f. intermedius* or *L. f. graellsii*, but its relationship with *L. f. heuglini* is much more borderline, there being only restricted gene flow and very little if any observed mixed pairing in spite of close contact between the taxa.

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group arose through rapid range expansion of *heuglini*-like ancestors into northern Europe. Although most *heuglini* are distinguishable from nearly all *fuscus*/*intermedius*/*graellsii* on the basis of mtDNA, the genetic differences are minimal and there is considerable overlap, suggesting that some introgression may still occur. This was the conclusion reached by Liebers & Helbig (2002), who suggested that their data were consistent with a significant, though incomplete, barrier to gene flow between *fuscus* and *heuglini*. Behavioural data, on the other hand, indicated no hybridisation between these taxa (Filchagov *et al.* 1992a), in spite of their close geographical contact around the Kola Peninsula and the White Sea. The taxa are separated on the basis of habitat preferences, *heuglini* nesting primarily on inland tundra, and *fuscus* generally restricted to the coast. Diagnosability is a problem. The identification criteria for *heuglini* with respect to the near-identical *graellsii* remain uncertain; the proven occurrence of *graellsii* in Finnish refuse tips, where many of the putative identification criteria for (extralimital) *heuglini* have been defined, makes the data very difficult to interpret (Gibbins 2004a).

There is much work still to be done on 'Heuglin's Gull'. Genetic sampling of *taimyrensis* is incomplete and the taxon itself may not be valid. Diagnosability of *heuglini* has not been confirmed with respect to *fuscus*/*intermedius*/*graellsii*. Although many gull workers recognise Heuglin's Gull *L. heuglini* as a distinct species, until further genetic sampling has been undertaken it is more defensible to recognise the five (or six) subspecies – *fuscus*, *intermedius*, *graellsii*, *heuglini*, (*taimyrensis*) and *barabensis* – as members of a single clinal, polytypic species, with a slight step between *heuglini* and *fuscus*.

It is probable that *vegae* is not a 'Lesser Black-backed Gull'. Although field impressions of *vegae* suggest that it resembles a pale *heuglini* (Yésou 2001, 2002), *vegae* genetically belongs to the Siberian/Arctic group discussed below, and Yésou argued convincingly that hybridisation is limited and/or sporadic. The problem is the genetic status of *taimyrensis*. Birds within the historical range of this taxon are genetically part of the *heuglini* group (Liebers & Helbig 2002; Liebers *et al.* 2004) but phenotypically of the



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172. Adult Lesser Black-backed Gull – presumed to be 'Heuglin's Gull' *Larus f. heuglini*, Khor Kalba, United Arab Emirates, March 2006. Identification of adults of this taxon with respect to the virtually identical *L. f. graellsii* is still not fully resolved, although there may be population-level differences in average structure and primary pattern. Tampere rubbish dump in southwest Finland has become the place to see this taxon in Europe, but the occurrence of *graellsii* in Finland has confused the identification literature, and further work is ongoing. Taxonomy of the 'Siberian' gull taxa *heuglini*, *taimyrensis*, *barabensis*, *vegae* and *mongolicus* remains controversial, and several different arrangements would be defensible on current evidence, under slightly differing species concepts and interpretations of the data.

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vegae group (Yésou 2002). It appears that there is a sharp genetic divide between 'West Siberian Gulls' and 'East Siberian Gulls', and a sharp (if slight) morphological (phenotypic) divide, but it is not clear that the phenotypic and genetic divides coincide. This is explicable if it is assumed that hybridisation is taking (or has taken) place, as stated by Yésou (2002).

The recommendation is therefore to recognise:

- Lesser Black-backed Gull *L. fuscus* (polytypic, with subspp. *fuscus*, *intermedius*, *graellsii*, *heuglini*, *taimyrensis*, *barabensis*)

Although *taimyrensis* is included here, we acknowledge that it may be best synonymised with *heuglini* or be regarded as a transient *heuglini* x *vegae* hybrid population.

The 'Siberian' grouping – vegae, mongolicus *and* smithsonianus

Genetically, these three taxa lie within a Siberian assemblage that also contains a number of relatively uncontroversial and (although hybridisation is not uncommon) broadly reproductively isolated species such as Slaty-backed and Glaucous-winged Gulls. These are more closely related to Lesser Black-backed than to *argentatus*, and, despite the fact that the whole Siberian grouping is under-represented in the genetic studies, it is unlikely that they are members of *L. argentatus*.

The identification of American Herring Gull, *smithsonianus*, has been discussed thoroughly in Lonergan & Mullarney (2004) and Adriaens & Mactavish (2004). Both of these papers were written primarily as guides to the identification of vagrant *smithsonianus* in western Europe, and concluded that many individuals may be separable from European Herring Gulls on plumage characteristics. American *smithsonianus* are more distinct from European birds in first-winter plumage than as adults, although there is much overlap; many individuals of each age group are essentially unidentifiable and the taxon has not been shown to be diagnosably distinct on the basis of plumage. However, to retain *smithsonianus* as a subspecies of *L. argentatus* would make that species paraphyletic ('Herring Gull' would then include the distantly related *smithsonianus* but not the more closely related taxa such as Great Black-backed Gull, etc.), a situation we prefer to avoid. It has also been reported that *argentatus* does not respond to vocalisations of *smithsonianus*, and that this underlies taxon recognition – the implication being that a degree of reproductive isolation may exist (Frings *et al.* 1958). On current evidence, therefore, *smithsonianus* should be recognised as distinct from *L. argentatus*. Geographic variation within *smithsonianus* exists, but has not been fully documented, and there may be a case for the recognition of subspecies of *L. smithsonianus* in the Nearctic (Jonsson & Mactavish 2001; de Knijff *et al.* 2005).

What of the relationship between *smithsonianus* and *vegae*? Although the genetic differences are minimal, about 90% of the *smithsonianus* so far sampled carry mtDNA haplotypes that are not found in *vegae* (Liebers & Helbig 2004; de Knijff *et al.* 2005). There are also structural differences (Chu 1998). On the other hand, they are not 100% genetically distinguishable, and *vegae* and *smithsonianus* show some plumage similarities – there is, for example, considerable overlap in the dark-bodied, pale-headed appearance of first-winters of both taxa (shown by representative photographs in Moores 2003). Although there is overlap, adult *vegae* tend to be darker on the mantle than *smithsonianus* and generally to have more black pigmentation (as far as P3) on the primaries (Gibbins 2004b). The black subterminal primary markings of *vegae* generally lack the 'W' shape described for *smithsonianus*, and features such as eye-ring colour, head streaking, iris and leg pigmentation differ on average too. However, the taxa are not 100% diagnosably distinct on genetic or morphological criteria and, at present, the evidence for more than subspecific differentiation is not overwhelming. There is at least as much morphological difference between *vegae* and *smithsonianus* as there is between *smithsonianus* and *argentatus*, and many ornithologists regard *vegae* and *smithsonianus* as specifically distinct. They may well be right. However, under the Guidelines they do not fulfil the criterion of diagnosability and, in recognition of the uncertain relationships between these taxa, we recommend that *vegae* and *smithsonianus* continue to be treated as conspecific.

The relationship between *mongolicus* and *vegae* is borderline, and its evaluation is made difficult by geographical variation, which may not yet be fully described within both taxa. Genetically, it is impossible to say whether *mongolicus* is derived from *vegae* or from Slaty-backed Gull (Liebers *et al.* 2004; de Knijff *et al.* 2005). Genetically, it is not a Caspian Gull, and

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173. Adult American Herring Gull *Larus smithsonianus*, St John's, Newfoundland, Canada, February 2007. The asymmetric 'W' of the black subterminal bands to the primaries, looking quite spikey on the outer webs, is characteristic of this species. The AOU Committee on Classification and Nomenclature has considered and, at the time of writing, rejected the split of *smithsonianus* from European *argentatus* (see http://www.aou.org/committees/nacc/proposals/2007_B_votes_web.php3). That committee regards the genetic data as insufficient to support a split, which shows how delicately balanced some of these taxonomic decisions are. Differences in accepted species definitions and the perceived value of stability can lead to significant differences in opinion between authorities. Indeed, one member of the American Committee confessed to having given up with large white-headed gulls, which is an understandable but, in a Palearctic context, unsatisfactory standpoint.

there are marked plumage differences from this species (Yésou 2001), with which it has previously been regarded as conspecific. Population-level differences between *mongolicus* and *vegae* include the greater extent of black pigmentation in the primaries of adult *mongolicus* and that taxon's restricted head-streaking in winter plumage (Yésou 2001; Moores 2003; Gibbins 2004b). Gulls wintering in Korea are thought to be *mongolicus* on plumage characteristics and habitat preferences (Moores 2003), but this cannot be confirmed objectively. It cannot be shown that diagnosability conditions can be fulfilled and, although recognising that this is a close call, the most defensible option is to follow Yésou (2002) and recognise *mongolicus* as conspecific with *vegae*. Further study may, of course, change this position.

In summary, the recommendation is to recognise:

- American Herring Gull *L. smithsonianus* (polytypic, with subspp. *smithsonianus*, *vegae*, *mongolicus*)

We accept that others may prefer to recognise two or three species, although this would not affect the British List.

Conclusions

There is still much to be learnt about what we used to call simply Herring Gulls and Lesser Black-backed Gulls before we can be confident that we understand the relationships of the component taxa. The biological relationships of these gulls, their behaviour and even their morphology may change more rapidly than taxonomists can keep pace with. It is clear that the former ring-species arrangement that put three taxa in *L. fuscus*, and at least 12 in *L. argentatus*, while giving full species status to *L. marinus* and several Siberian/Arctic gull species, does not reflect the evolutionary or the biological relationships of the birds themselves. Under the Guidelines, we recommend the following taxonomy (Sangster *et al.* 2007):

- Caspian Gull *L. cachinnans* (monotypic)
- Lesser Black-backed Gull *L. fuscus* (polytypic, with subspp. *fuscus*, *intermedius*, *graellsii*, *heuglini*, *taimyrensis*, *barabensis*)
- American Herring Gull *L. smithsonianus* (polytypic, with subspp. *smithsonianus*, *vegae*, *mongolicus*)
- Herring Gull *L. argentatus* (polytypic, with subspp. *argentatus* and *argenteus*)

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- Yellow-legged Gull *L. michahellis* (polytypic, including subspecies *michahellis*, *atlantis* and possibly other populations that may deserve subspecific recognition)
- Armenian Gull *L. armenicus* (monotypic)

The taxonomy recommended above recognises 20 years of new research into the evolution and identification of Herring/Lesser Black-backed Gulls. It accepts the genetic evidence that the 'Herring Gull' is not a ring species, and that *argentatus*, *michahellis*, *armenicus* and *marinus* form a group of reproductively isolated species that are not closely related to the rest of the complex. The taxonomy also recognises that 'Lesser Black-backed Gulls' evolved by a process of contiguous range expansion from a refugial population of 'pre-*cachinnans*' birds in the Aralo-Caspian region. These populations expanded north to west Siberia, then both west into northern Europe (*fuscus*, *intermedius*, *graellsii*) and east into northern Siberia (*heuglini*). Defining species boundaries within this group is always going to be difficult because the taxa with contiguous ranges are in general very closely related. Species boundaries here are controversial, and a conservative arrangement is recommended that is consistent with the Guidelines (Helbig *et al.* 2002) but recognises that there are other potential species boundaries that must be kept under review.

In general, we are adopting a taxonomy that assumes that the genetic groupings described by Liebers *et al.* (2004) and summarised in simplified form in Maclean *et al.* (2005) (fig. 2) are likely to delineate the species boundaries that, on the basis of current evidence, are best supported. In some cases, this assumption is backed by strong morphological, plumage and behavioural evidence for biological reproductive isolation. For example, the recognition of Great Black-backed, Lesser Black-backed, Yellow-legged and Armenian Gulls as specifically distinct from Herring Gull is generally uncontroversial and could be supported on morphological and behavioural grounds without any genetic evidence. We have then extrapolated the argument to use genetic differentiation as a guide to other potential species barriers, such as the separation of American Herring Gull from Herring Gull, and of Caspian Gull from all other taxa. We have recognised, or continued to recognise, separate species that fall within a single genetic grouping if there is good evidence of strong reproductive isolation and morphological divergence (such as for Glaucous-winged, Iceland and Slaty-backed Gulls). This approach has produced a taxonomy that is similar to that proposed by Yésou (2002) and others, but with some differences, most noticeably the retention of *smithsonianus* and *vegae* as conspecific. If *vegae* and *smithsonianus* were formally shown to be diagnosable, either on the basis of morphology or genetics, this decision would no longer be supportable under the Guidelines, and we would welcome further data to clarify this situation.

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Dr J. Martin Collinson, Biomedical Sciences, Institute of Medical Sciences, University of Aberdeen, Aberdeen AB25 2ZD
Prof. David T. Parkin, Institute of Genetics, University of Nottingham, Queen's Medical Centre, Nottingham NG7 2UH
Dr Alan G. Knox, Historic Collections, King's College, University of Aberdeen, Aberdeen AB24 3SW
George Sangster, Stevenshof 17, 2312 GM Leiden, The Netherlands
Dr Lars Svensson, S:ta Toras väg 28, S-260 93 Torekov, Sweden

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Appendix 1. Discrepancies between nuclear and mitochondrial DNA.

Western Gull *L. occidentalis* and Glaucous-winged Gull *L. glaucescens* hybridise commonly along the west coast of the USA and Canada and there is evidence of nuclear gene flow between the two species across the hybrid zone (Bell 1996). In contrast, there appears to be no introgression of mitochondrial DNA, and the genetic distance between the two species suggests that they last shared a common ancestor over one million years ago (this compares with an estimate of 300,000 years for the evolution of the whole Herring/Lesser Black-backed Gull complex of which *glaucescens* is a part) (Liebers *et al.* 2004; de Knijff *et al.* 2005). Assuming that *glaucescens* has been adequately sampled, the most likely explanation is perhaps that only the male hybrids are fertile (in line with Haldane's Rule), so hybrid females (that alone are ensuring that mtDNA is passed to the next generation) never get the chance to introduce the mtDNA of one species into the other. The example also shows how very distantly related gulls with very effective partial reproductive isolation may nevertheless hybridise extensively (de Knijff *et al.* 2005).

Recent studies of wagtails *Motacilla* based on mtDNA suggested a deep genetic divide in both Yellow Wagtails *M. flava* and Citrine Wagtails *M. citreola*, with nominate Citrine Wagtails within an 'eastern' yellow wagtail clade and *calcarata* Citrine Wagtails within a 'western' yellow wagtail clade (Voelker 2002; Ödeen & Björklund 2003). If this represents the true phylogeny of Citrine Wagtails, it would be very strong evidence that Citrine Wagtail should be split. However, Ödeen & Björklund (2003) also reported a separate phylogeny, based on a nuclear DNA. It placed nominate and *calcarata* Citrine Wagtails together, as members of a single clade, in effect 'repairing' the phylogeny produced by mtDNA, while maintaining the separate (species-level) distinction of eastern and western *flava* wagtails. This is not the place for a detailed discussion of the problems associated with these types of analyses, but it is sufficient to state that caution is required when building or interpreting phylogenies based on mtDNA, especially when these conflict with 'conventional' morphology-based phylogenies. This caution impacts on the conclusions we can make on the basis of published gull phylogenies.

Nor is it always the case that nuclear DNA tells a conservative story that tempers the excesses of mtDNA. Bensch *et al.* (2006) showed that although Willow Warblers *P. trochilus* show very little variation in their mtDNA across the species (much less than the variation seen in chiffchaffs (*sensu lato*) *P. collybita/ibericus*), they also harbour a rich and relatively ancient pool of alleles at several nuclear loci. It is suggested that the mtDNA diversity seen in Willow Warblers is artificially low as the result of strong selection in the past, whereas the nuclear DNA accurately reflects a complicated evolutionary history. There may even have been introgression of nuclear alleles from a (now extinct) diverged *Phylloscopus* taxon. The paper highlights the fact that phylogenetic trees based only on mtDNA may be seriously biased, and not reflect the true evolution of the species because its patterns of inheritance do not fully reflect that of the species involved (Hudson & Coyne 2002; Ballard & Whitlock 2004).

Looking back

One hundred years ago:

'COMMON TERNS ON THE HOLYHEAD SKERRIES. It is generally supposed that these birds do not breed on the Skerries, and that the rocks are occupied during the breeding season exclusively by Arctic Terns and a few Roseate Terns (*cf.* H. E. Forrest, *Vert. Fauna N. Wales*, p. 375). That this is not the case has recently been proved by her Grace the Duchess of Bedford, who has been good enough to forward me a Common Tern (*Sterna fluviatilis*), which killed itself against the telephone wire whilst she was visiting the colony. Her Grace added, "several were seen". HEATLEY NOBLE.' (*Brit. Birds* 2: 64, July 1908)

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