

### **The Phylogeny and Biogeographic History of the Tribe Alcini**

Nested in the order Charadriiformes is the family Alcidae. This group of birds is filled with marine wing-propelled diving birds like the puffins, auklets, and murrelets (Strauch, 1985; Smith, 2011). In addition, there are also auks and murres. These two birds form the tribe Alcini, a subset of the subfamily Alcinae. Including only species that have occurred in the Pleistocene epoch, the tribe consists of the thick-billed murre (*Uria lomvia*), the common murre (*Uria aalge*), the little auk (or dovekie) (*Alle alle*), the razorbill (*Alca torda*), and the (now extinct) great auk (*Pinguinus impennis*). All of these birds can be (or were) found in the Atlantic Ocean, but some are also distributed in the Pacific Ocean.

The murres are one such case of Alcini species living in both the Pacific and the Atlantic Oceans. The thick-billed murre can be found as north as the Arctic (Tuck, 1960; Gaston and Elliot, 2003; Dunn and Alderfer, 2011). In the Pacific Ocean, their southern range limit ends at the southern British Columbian coastline and the northern Japanese islands, while in the Atlantic Ocean the limit ends off the coasts of the Canadian Maritimes and Norway. During breeding periods, these murres choose to breed in colonies found just along the coasts of Alaska, East Asia, and Newfoundland and Labrador. Breeding colonies are also present in the Arctic, with many colonies located off the western coastline of Greenland and the entire coastline of Iceland. Most of the common murre's range overlaps with that of the thick-billed murre (Tuck, 1960; Gaston and Elliot, 2003; Dunn and Alderfer, 2011). However, its range is more southern, with its northern range limit ending at a lower latitude. In the Pacific Ocean, it can be found as south as the California coastline and the southern tip of India. In the Atlantic Ocean, its southern range limit ends in the southeast US (around Virginia) and off the coast of the Iberian Peninsula (i.e. Portugal and Spain). During breeding season, it shares many colonies with the thick-billed murres, provided they are not in the Arctic (Gaston and Elliot, 2003). The common murre also has its own colonies off the

western North American and western European coastlines. Other colonies of common murres can be found in the Sea of Japan, off the coast of the Kamchatka Peninsula in eastern Russia, the entire coastline of the UK, in the North Sea, in the Baltic Sea, and in the Norwegian Sea. The distribution of the two murres is shown in **Figure 1**.

The little auk is another case of an Alcini species being found in both sides of North America. Overlapping with the murres, they can be found as south as the Gulf of Maine on the west Atlantic Ocean (del Hoyo *et al.*, 1996). It is not seen off in the eastern Atlantic Ocean, skipping over the coastline of western European countries like Portugal and the UK. However, it occurs in the North Sea. In general, it is present in the North Atlantic and Arctic oceans (US Fish and Wildlife, 2006; Dunn and Alderfer, 2011). During breeding seasons, they establish colonies off the coasts of western Greenland, Iceland, and eastern Baffin Island, with most being found in the Greenland colonies, specifically in the Thule district (Salmonsén, 1974; US Fish and Wildlife, 2006; Dunn and Alderfer, 2011). Other colonies can be found on other Arctic islands and land masses such as Jan Mayen, Svalbard, Franz Josef Land, Novaya Zemlya, and Severnaya Zemlya (Strøm and Descamps, 2017). Colonies can also be found on the other side of North America in the Alaskan islands of Little Diomedé and St. Lawrence Island in the Bering Sea, but they are rare (Day *et al.*, 1988; Dunn and Alderfer, 2011). The distribution of the little auk is shown in **Figure 2a**.

The razorbill, unlike the other species, is only found in the Atlantic Ocean (del Hoyo *et al.*, 1996). Their southern range limit goes as far as North Carolina on the west Atlantic ocean and as south as the Moroccan coastline and the western half of the Mediterranean sea on the other side of the Atlantic (del Hoyo *et al.*, 1996; Dunn and Alderfer, 2011). During breeding periods, most razorbills gather in colonies in Iceland (Lloyd *et al.*, 1991; Chapdelaine *et al.*, 2001). Colonies can also be found off the coast of western Greenland, in the Baltic Sea, off the Norwegian coast, and around the British Isles (Nettleship and Evans,

1985; del Hoyo *et al.*, 1996; Gaston and Jones, 1998; Chapdelaine *et al.*, 2001; The Royal Society for the Protection of Birds, 2017). The distribution of the razorbill is shown in **Figure 2b**.

The great auk is only modern species in the tribe Alcini that is extinct, with the last great auk and the last great auk egg being killed in Eldey Stack, Iceland, on the June of 1844 (Bengtson, 1984; Dunn and Alderfer, 2011). Past accounts state that its pre-extinction distribution was in the North Atlantic Ocean, with most individuals spending time on the western side and possibly going as south as Florida (Steenstrup, 1855). On the eastern side, there has been evidence of great auks having been distributed as south as the Mediterranean (Violani, 1974). During breeding seasons, there was a huge colony on Newfoundland's Funk Island that existed before an eventual mass slaughter led to an extirpation of great auks in 1800 (Grieve, 1855; Dunn and Alderfer, 2011). While they may have also bred off the coast of west Greenland, other colonies have existed off the Icelandic coastline; on Scotland's St. Kilda, Orkneys, and Shetland; and on Denmark's Faroe Islands (Bengtson, 1984).

Comparing all of the species of tribe Alcini, it would seem that they are all quite similar. All have overlapping ranges in the Atlantic Ocean throughout the year, and during breeding periods all species band into colonies on rocky islands where they nest on the rocky cliffs (Bengtson, 1984; Mowm and Árnason, 2001; US Fish and Wildlife, 2006; Regular *et al.*, 2009; Dunn and Alderfer, 2011). Even in these breeding grounds, the species of tribe Alcini can be allopatric with one another. In addition, all species feed mostly on fish, supplemented by crustaceans and other invertebrates (Bengtson, 1984; Birkhead and Nettleship, 1986; Cairns and Schneider, 1990; Ainley *et al.*, 1996; US Fish and Wildlife, 2006; Laver and Jones, 2007; Moody and Hobson, 2007; Karnovsky *et al.*, 2010), a lifestyle aided by their diving abilities. Members of the tribe Alcini also look quite similar to one another, with all species being dorsally black and ventrally white as well as having webbed

feet. However, with their morphological, dietary, and behavioural similarities, they are still genetically different from one another.

Phylogenetic analyses of these species using molecular data have resulted in a consensus that thick-billed murres and common murres both belong in the *Uria* genus and that the little auk can be alone in its *Alle* genus (Moum *et al.*, 2002; Baker *et al.*, 2007; Pereira and Baker, 2008; Smith, 2011). Based on morphological data, researchers also agreed that the great auk and the razorbill were more closely related to one another than to the other species and could both be considered as true auks (Dawson, 1920; Storer, 1945; Strauch, 1985). However, the point of contention in this phylogeny is how exactly the murres, the little auk, and the true auks relate to one another. According to the mitochondrial analyses of Moum *et al.* (2002) and Baker *et al.* (2007) the true auks are more closely related to the little auk than to the murres (**Figure 3**). Analysis of mitochondrial and nuclear data by Pereira and Baker (2008) suggest the opposite; the murres are actually more closely related to the little auk than to the true auks (**Figure 4**). Even more possible phylogenies exist if one does not discount those created in the 20th century as outdated (Strauch, 1985; Chandler, 1990; Chu, 1998). In 2011, Smith performed a phylogenetic analysis on the entire Charadriiformes order using both osteological and molecular data (**Figure 5**). In this analysis, he proposed a phylogeny of the Charadriiformes order that included a new taxonomic group -- the Pan-Alcidae -- that includes the families Alcidae and (the now extinct) Mancillinae. However, in his analysis, instead of providing his own phylogeny when examining the Alcini tribe, he gave up, describing the phylogenetic position of the little auk as possibly the most controversial topic in the Alcidae phylogeny and stating that the issue could only be solved with more comprehensive phylogenetic analyses of extant and extinct alcids. Later, he would update his phylogeny for the Charadriiformes, now basing his analysis on osteological and molecular data as well as observations on each species' skin, reproduction, diet, feathers, and

muscles (Smith and Clarke, 2015). Extinct species were also included in the analysis.

Although two different phylogenies were created for the Charadriiformes -- one was optimized for the diets of the species while the other was optimized for their geographic distribution -- both propose that the little auk and the true auks are in fact sister groups and agree with Moum *et al.* (2002) and Baker *et al.* (2007) (**Figure 6**).

With the phylogeny of the Alcids being controversial, it is not unreasonable to assume that the controversy also applies to estimations of divergence dates. Assuming Smith and Clarke's (2015) phylogeny is correct, the family Alcidae would have split into the subfamilies Alcinae and Fraterculinae in the Oligocene epoch, with the most recent common ancestor of all species in the subfamily Alcinae occurring around 24 million years ago. After three more divergences, the most recent common ancestor of all members of tribe Alcini would have occurred around 18 million years ago. On the other hand, Pereira and Baker (2008), using their molecular data-based phylogenetic analysis, believe that the family Alcidae actually started radiating around 55 million years ago, although they do note that not enough fossils and molecular data have been uncovered to properly support this theory. Their estimation for when the most recent common ancestor of the tribe Alcini species occurred is also shifted earlier. Instead of 18 million years ago (in the early Miocene epoch), they believe the most recent common ancestor occurred in the early Oligocene epoch.

The ancestors of the tribe Alcini have been hypothesized to have originated in the Pacific Ocean based on the higher diversity of extant pan-alcids in the Pacific (Storer, 1960; Olson, 1985; Pereira and Baker, 2008). However, Smith and Clarke (2015) argue that this is simply a reflection of advantageous advection of nutrient-rich water to the Pacific Ocean via ocean currents, an argument supported by Piatt and Springer (2003). Piatt and Springer (2003) provided evidence that an ocean current was able to advect nutrients and plankton (a food source for many alcids) from the Bering Sea to the Chukchi Sea (a 1200 km journey).

This, combined with coldwater upwelling, supported zooplankton populations in the Chukchi Sea. These plankton end up feeding a wide variety of species like murres and kittiwakes. This has been corroborated by Haney and McGillivray (1985), who observed how the distribution of seabirds in general tends to overlap with that of their food source (plankton), and Briggs *et al.* (1988), who found that the distributions of common murres and Cassin's auklets (*Ptychoramphus aleuticus*) in California overlap with those of plankton and other prey and that the distributions are related to coastal upwellings. In addition, the oldest known fossil of a pan-alcid (dated back to 34 million years ago) have been from the Atlantic Ocean (Chandler and Parmley, 2002; Wijinker and Olson, 2009). As a result, according to Smith and Clarke (2015), there does not appear to be a clear location of origin for the pan-alcids.

In any case, after their origination, pan-alcids, including ancestors of tribe Alcini, appear to have dispersed multiple times between the Pacific and North Atlantic Oceans, based on molecular (specifically mitochondrial and nuclear) data (Kidd and Friesen, 1998; Pereira and Baker, 2008). The route taken by them has been theorized to have either gone through Arctic coastal regions or through the Central American Seaway, with Pereira and Baker (2008) believing that the latter was used. Their reasoning is based on the fossil record, which suggests that the pan-alcids were already adapted to the ocean at this time. As a result, they could not have utilized the Arctic coasts as landmass was already present (Golonka *et al.*, 2003). In addition, the Arctic Ocean was believed to have been experiencing episodes of freshwater at the time, and the marine-adapted pan-alcids could not withstand that (Brinkhuis *et al.*, 2006). During their dispersal around the North American coastline, the travelling pan-alcids could have utilized the abundance of food along the coast, a product of upwelling bringing plankton to the surface (Konyukhov, 2002).

After their arrival in the Atlantic Ocean, it is believed that the most recent common ancestor of the tribe Alcini radiated into the *Alca*, *Alle*, *Pinguinus*, and *Uria* genera that are

(or have been) seen in recent history, explaining their presence in the Atlantic Ocean (Udvardy, 1963; Bédard, 1985). After the radiation, members of the *Uria* could have utilized the Arctic pathway during the periods of time when the Bering Strait was open and invaded the Pacific Ocean (Marincovich and Gladenkov, 1999; Pereira and Baker, 2008). Some little auks may also have used this pathway to establish a population in Alaska. However, that is only a guess; I was unable to find any literature detailing the history behind their localization in Alaska, possibly because there are extremely rare (Day *et al.*, 1988; US Fish and Wildlife, 2006). Regardless, the radiation seen in the Atlantic ocean (as well as the speciation seen in the Pacific Ocean) have been attributed to glaciation present in the Pleistocene (Moum *et al.*, 1991, O'Reilly *et al.*, 1993, Kidd and Friesen, 1998). The glaciation isolated the populations of the tribe Alcini into various glacial refugia, which restricted gene flow and aided the process of speciation.

In general, it would appear that much of the biogeographic history of the tribe Alcini has not yet been uncovered. The phylogeny of the tribe (and the Alcidae as a whole) seems to be constantly updated, while the history of the tribe's movement does not seem to be completely determined. One key weakness mentioned by Pereira and Baker (2008), Smith (2011), and Smith and Clarke (2015) is that the fossil record is quite lacking. Molecular data also does not appear to have been researched to the fullest extent. With more discoveries of Alcidae fossils and molecular data, perhaps a more concrete idea of the phylogenetic relations and biogeographic history of the tribe Alcini will be published soon.

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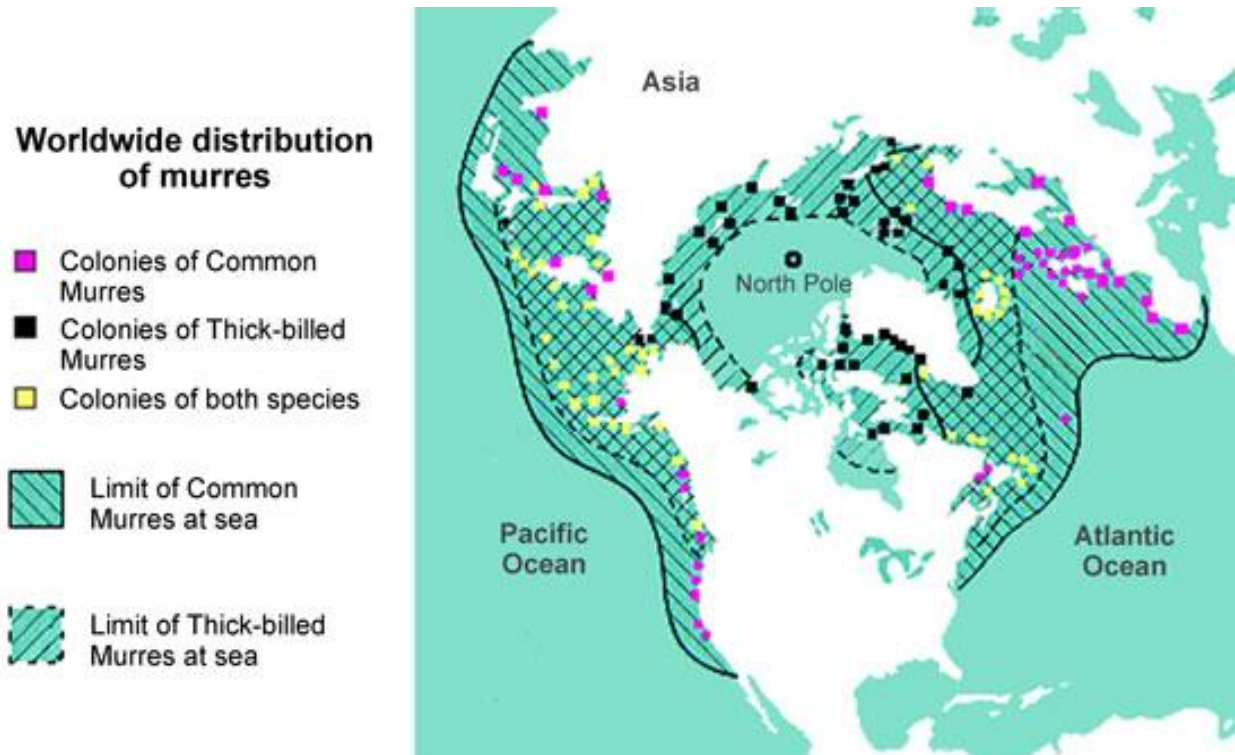


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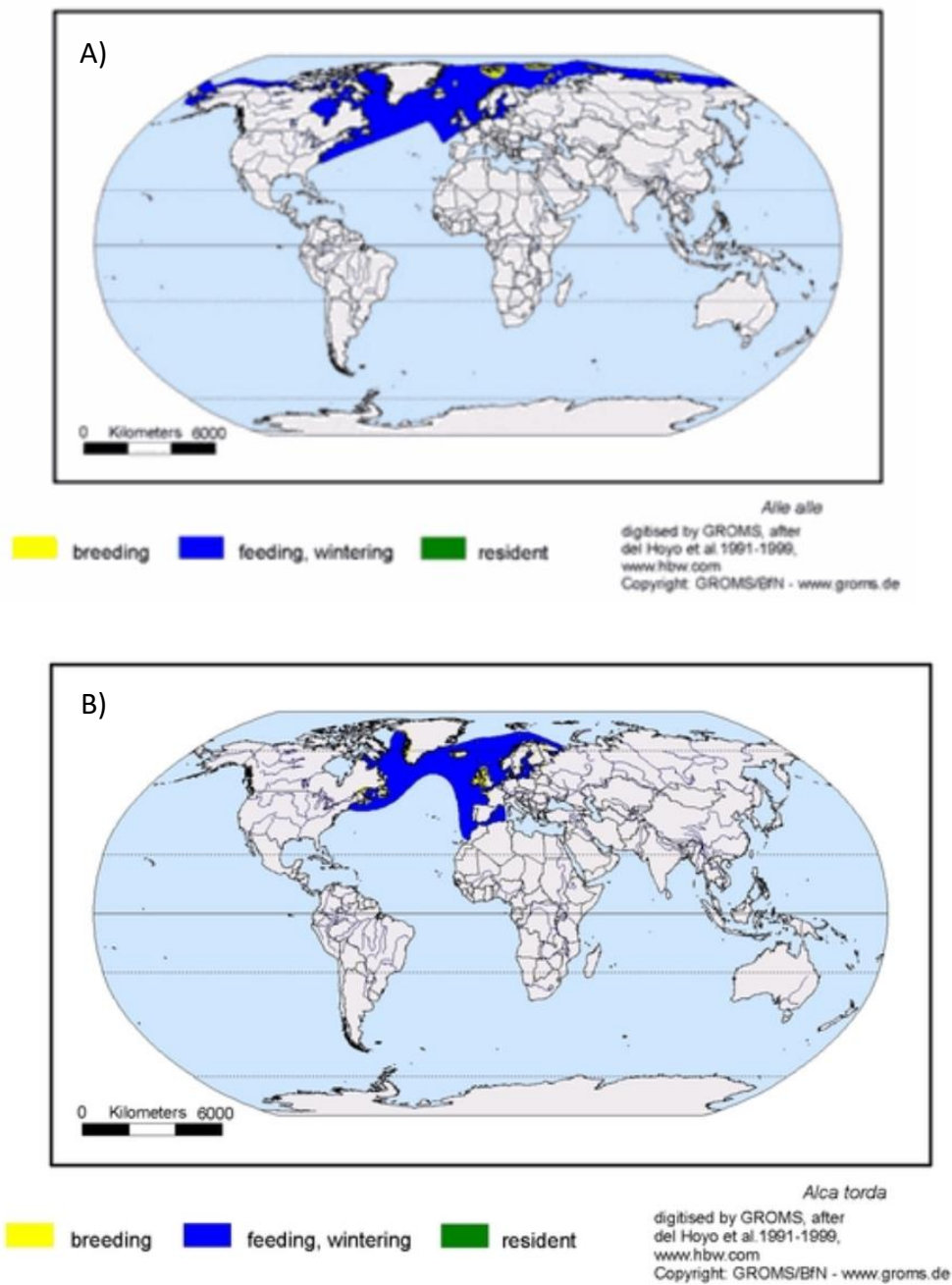
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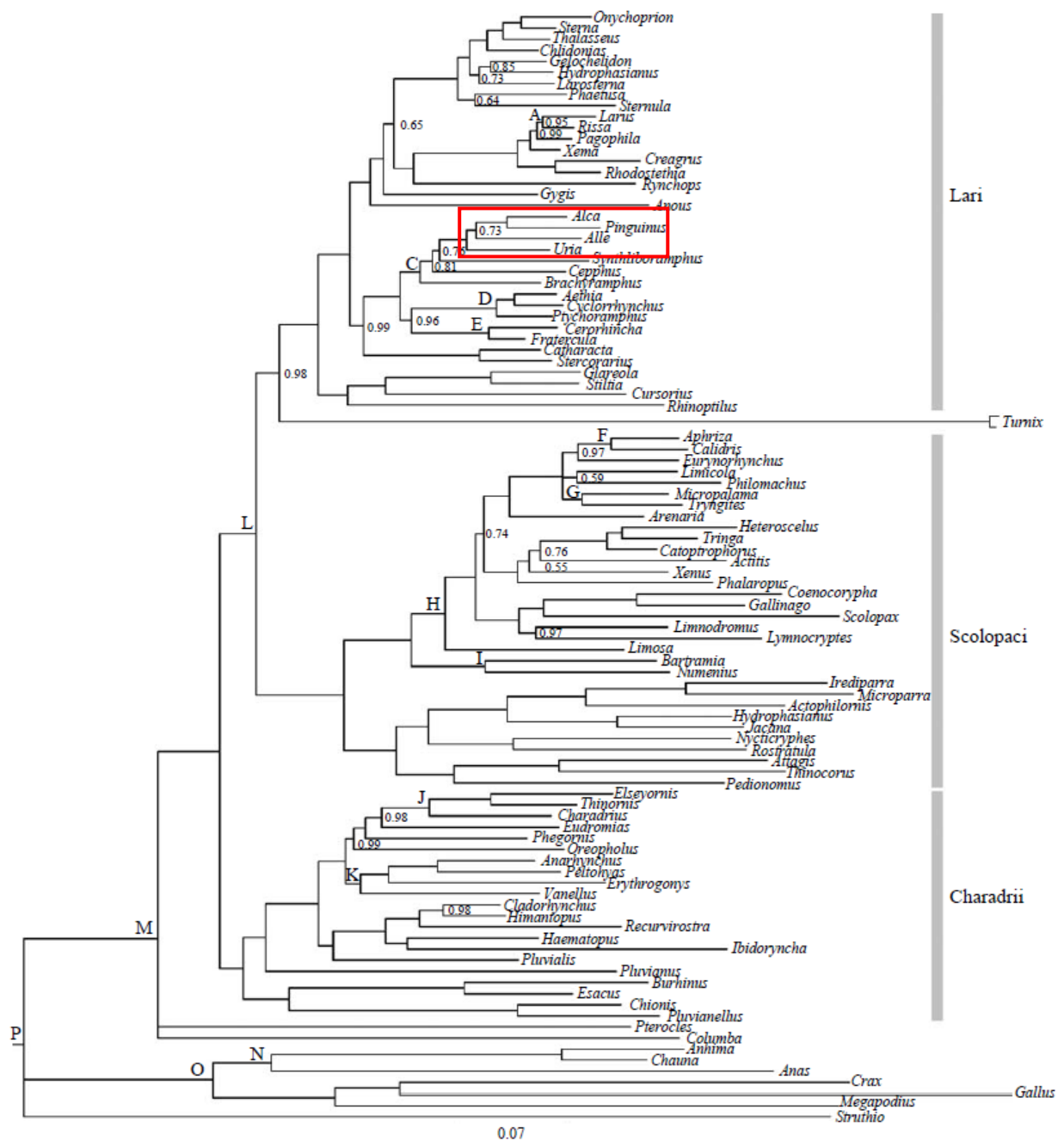
## Figures



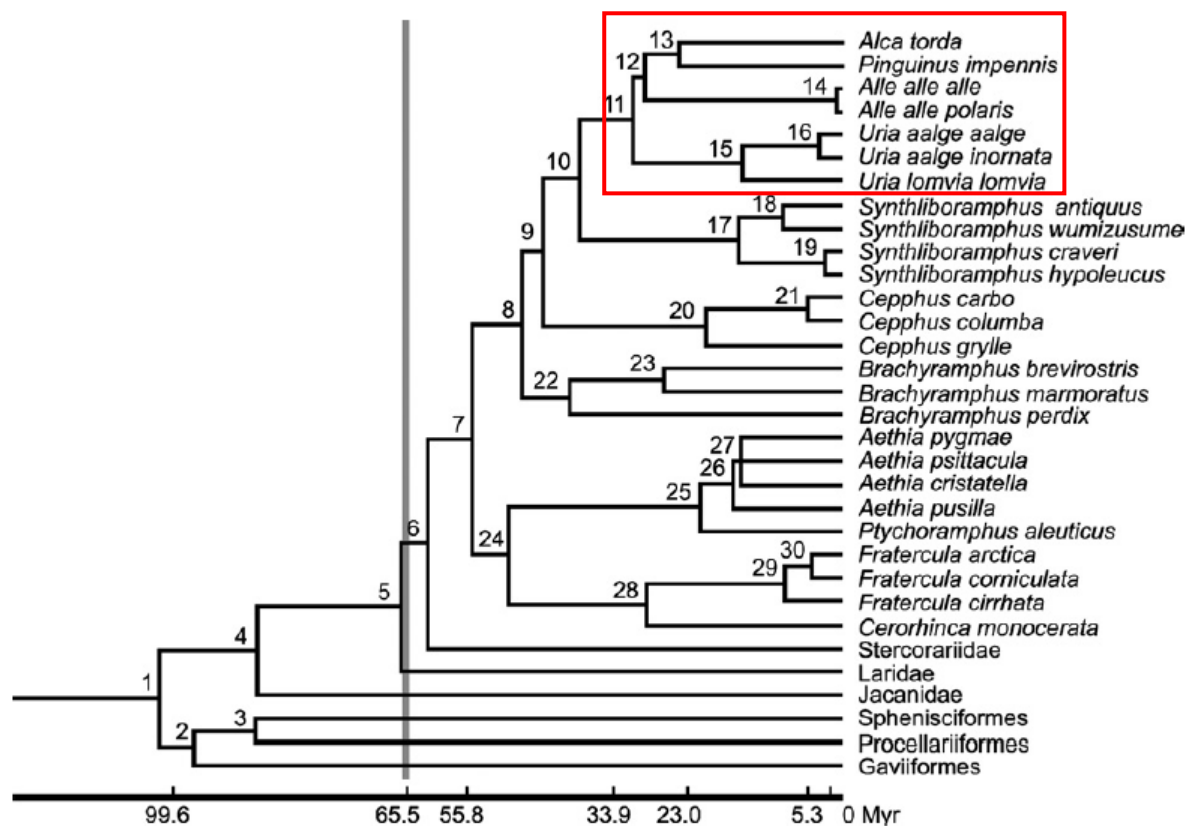
**Figure 1.** The distribution of common and thick-billed murres (*Uria aalge* and *Uria lomvia* respectively), with colonies containing common murres, thick-billed murres, or both murres highlighted. Taken from Gaston and Elliot (2003).



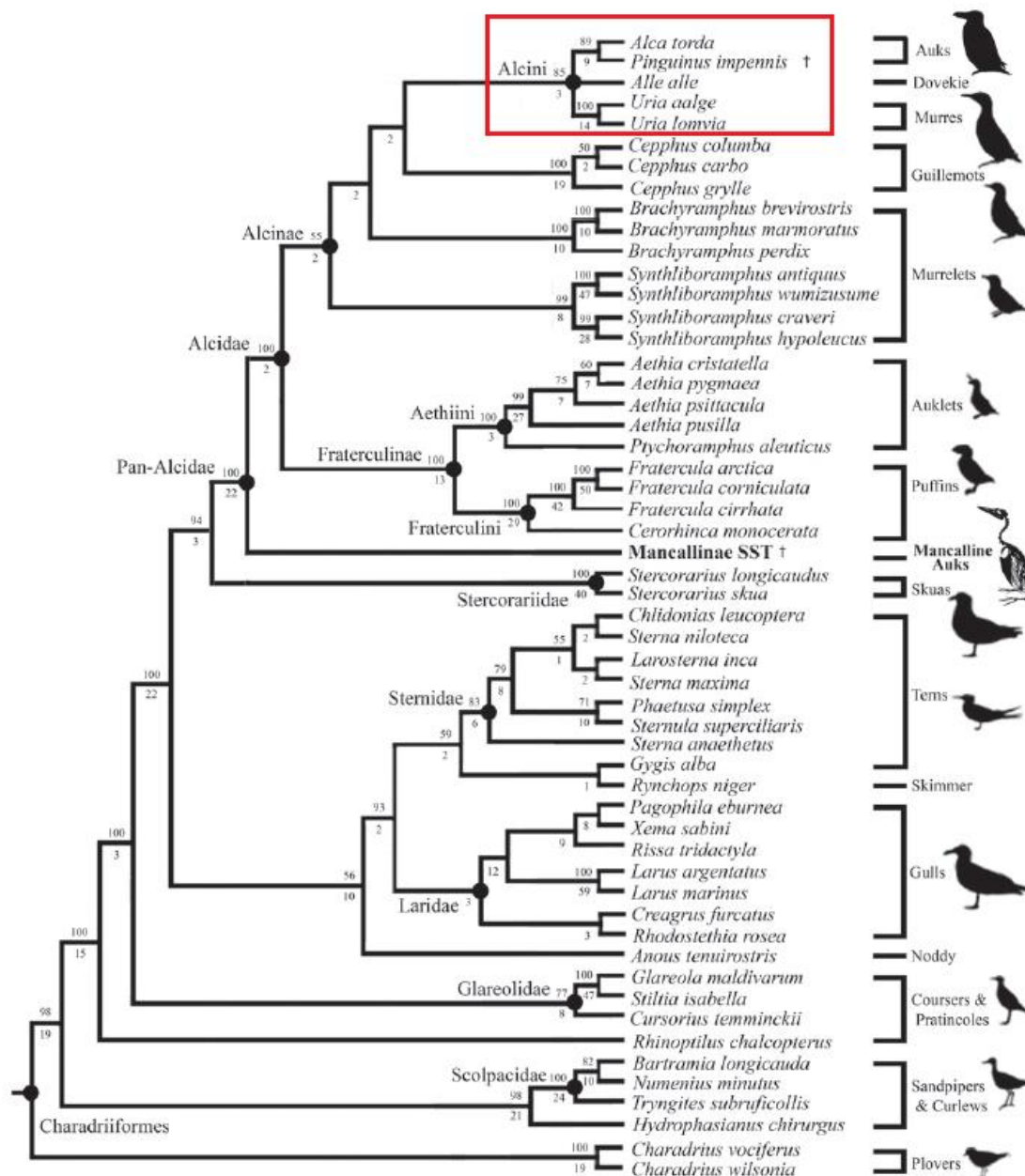
**Figure 2.** The distributions of the little auk (*Alle alle*) (A) and the razorbill (*Alca torda*) (B) during periods of breeding, feeding, and wintering. Digitized by the Global Register of Migratory Species based on distributions described by del Hoyo *et al.* (1996).



**Figure 3.** A cladogram representing the results of a phylogenetic analysis based on mitochondrial data and performed by Baker *et al.* (2007) on the order Charadriiformes. Time progresses from left to right in the phylogeny. The taxon of interest (tribe Alcini) is highlighted in red. Adapted from Baker *et al.* (2007).

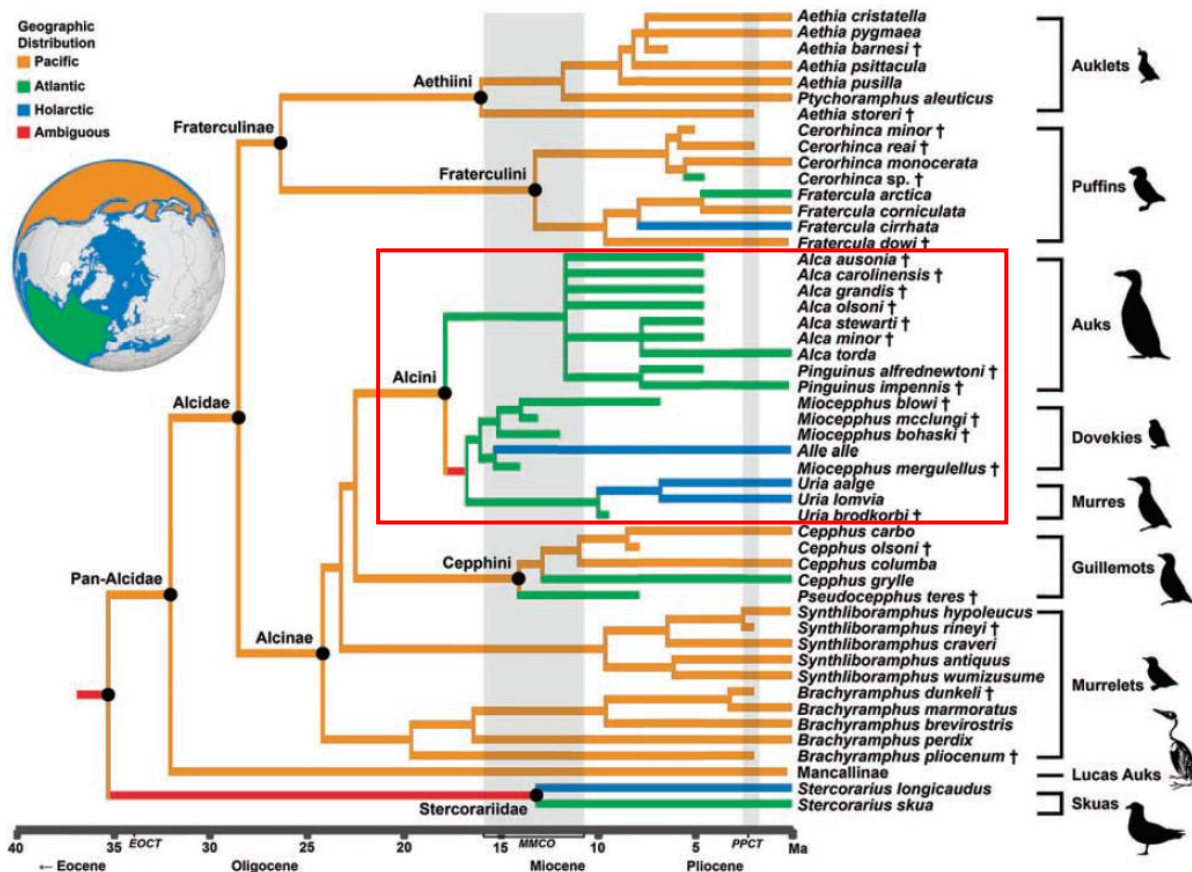


**Figure 4.** A cladogram representing the results of a phylogenetic analysis based on mitochondrial and nuclear data that was performed by Pereira and Baker (2008) on the family Alcidae. The bottom axis represents the times of divergence in units of millions of years ago. The thick vertical line represents the boundary between the Mesozoic and Cenozoic Eras. The taxon of interest (tribe Alcini) is highlighted in red. Adapted from Pereira and Baker (2008).



**Figure 5.** A cladogram representing the results of a phylogenetic analysis based on molecular and osteological data. The analysis was performed by Smith (2011) on the order Charadriiformes. Time progresses from left to right in the phylogeny. Crosses represent extinct species. The taxon of interest (tribe Alcini) is highlighted in red. Adapted from Smith (2011).





**Figure 6.** A cladogram representing the results of a phylogenetic analysis based on morphological, molecular, and ecological data. The cladogram is optimized based on the distribution of the species. The phylogenetic analysis was performed by Smith and Clarke (2015) on the entire order Charadriiformes. The bottom axis represents times of divergence in terms of millions of years ago. EOCT, MMCO, and PPCT stand for the Eocene-Oligocene climatic transition, Middle Miocene climatic optimum, and Pliocene-Pleistocene climatic transition respectively. Crosses represent extinct species. The taxon of interest (tribe Alcini) is highlighted in red. Adapted from Smith and Clarke (2015).