

# Earliest northeastern Atlantic Ocean basin record of an auk (Charadriiformes, Pan-Alcidae): fossil remains from the Miocene of Germany

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**Abstract** Newly discovered fossil remains of an auk (Aves, Charadriiformes) extend the temporal range of Pan-Alcidae in the northeastern Atlantic Ocean basin and the geographic range of the clade during the Miocene. The new specimen consists of a partial ulna and a radius of a single individual. It represents the earliest fossil auk from the northeastern Atlantic Ocean basin and the first fossil remains of an auk reported from Germany. The specimen is from a moderately sized auk similar to the extant Razorbill *Alca torda*, which it also resembles in morphological features. A definitive taxonomic referral of the fossil is not possible, but the presence of *Alca* in the Miocene of the northeastern Atlantic Ocean basin would be congruent with the occurrence of this taxon in the northwestern Atlantic at the same time.

**Keywords** Alcinae · Alcini · Aves · Avian evolution · Fossil seabirds · Paleodiversity

## Zusammenfassung

**Frühester Nachweis eines Alkenvogels (Charadriiformes, Pan-Alcidae) im nordöstlichen Atlantik: Fossilreste aus dem Miozän Deutschlands**

Kürzlich entdeckte Fossilreste eines Alken (Aves, Charadriiformes) erweitern das bekannte zeitliche Vorkommen der Pan-Alcidae im nordöstlichen Atlantik und das geographische Verbreitungsgebiet der Gruppe während des Miozäns. Das neue Exemplar besteht aus einem Ulnafragment und einem Radius eines einzigen Individuums. Es stellt den ältesten fossilen Alken aus dem Nordostatlantik dar und den ersten Fossilrest eines Alken aus Deutschland. Das Exemplar ist von einem Alk mittlerer Größe, ähnlich dem heutigen Tordalk *Alca torda*, dem es auch in morphologischen Merkmalen ähnelt. Eine endgültige taxonomische Einordnung des Fossils ist nicht möglich, aber das Vorkommen von *Alca* im Miozän des Nordostatlantiks wäre in Übereinstimmung mit dem Nachweis des Taxons im nordwestlichen Atlantik zur selben Zeit.

## Introduction

Pan-Alcidae are pelagic charadriiforms that are characterized by wing-propelled diving and anatomical modifications associated with that highly derived method of prey pursuit. The 23 species of extant alcids are distributed across the northern hemisphere, and with regard to their general feeding habits and preferred habitats fill similar ecological niches as do penguins in the southern hemisphere (del Hoyo et al. 1996). The Alcidae are divided into two major clades, the Fraterculinae (i.e., auklets and puffins; includes the genera *Cerorhinca*, *Fratercula*, *Aethia*,

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and *Ptychoramphus*) and the Alcinae (i.e., auks, murrelets, murrelets, dovekies and guillemots; includes the genera *Alca*, †*Pinguinus*, *Uria*, *Alle*, †*Miocepphus*, *Cepphus*, †*Pseudocepphus*, *Synthliboramphus* and *Brachyramphus*; sensu Smith 2011a; extinct taxa are indicated by a dagger). The extinct flightless Mancallinae auks (includes the genera †*Miomancalla* and †*Mancalla*) from the Pacific Ocean basin represent the stem lineage of Alcidae (i.e., †Mancallinae + crown clade Alcidae = Pan-Alcidae).

Fossil remains of alcids are the most abundant within Charadriiformes, with approximately 17,000 specimens referred to the clade (reviewed by Smith 2011b). However, the abundance and relatively broad temporal range (Eocene–Pleistocene) of pan-alcid remains from the Pacific and northwestern Atlantic Ocean basins stand in stark contrast to the relatively small quantities of exclusively Pliocene or younger alcid fossils reported from the northeastern Atlantic Ocean basin (Fig. 1; Table 1; Smith 2011b). The first description of an auk from the northeastern Atlantic Ocean basin was that of Portis (1888, 1891) who designated a distal humerus from the Pliocene of southern Italy as the holotype specimen of †*Alca ausonia*. Additional isolated remains from the Pliocene of Belgium and Morocco were subsequently referred to *Alca* (Dyke and Walker 2005; Mourer-Chauviré and Geraads 2010; Table 1). A nearly complete, yet isolated *Alca* cranium was documented from the Pliocene of Spain (Sanchez-Marco 2003). However, species-level referral of that specimen remains uncertain because the holotypes of all six extinct species of *Alca* are humeri or lack comparable

cranial material. Furthermore, the limited number of other fossil skulls that are referable to *Alca* are also not referable to the species level and cranial comparisons are primarily limited to the only living species in the genus, *A. torda* (Smith and Clarke 2011). A large volant auk, †*Alca stewarti*, was described from Pliocene deposits in Belgium (Martin et al. 2001). Subsequently, additional isolated remains from the Pliocene of Belgium were attributed to †*A. stewarti*, †*A. ausonia*, and †*A. grandis* (formerly “†*A. antiqua*”; see Olson 2007 and discussion in Smith and Clarke 2011), as well as *Fratercula* (Dyke and Walker 2005). Although the figures presented by Dyke and Walker (2005) clearly show that those Belgian fossils are indeed referable to Alcidae, no diagnostic characters were provided to support the referral of specimens to distinct species (i.e., referrals were largely based on size rather than apomorphies), and further evaluation is needed to establish the taxonomic affinities of those specimens.

Here, we report a new alcid fossil that represents the earliest record of the clade from the northeastern Atlantic Ocean basin, as well as the first record of a fossil auk from Germany. The specimen consists of associated bones (radius and ulna) of a single individual, which were found in situ. It stems from middle/late Miocene deposits of the Wienerberger clay pit in Freetz near Sittensen (Schleswig–Holstein) and is the first avian record from this locality, which, in addition to fish and shark fossils (Klug and Klug 1999), also yielded remains of cetaceans (Hampe and Ritsche 2011).

## Methods

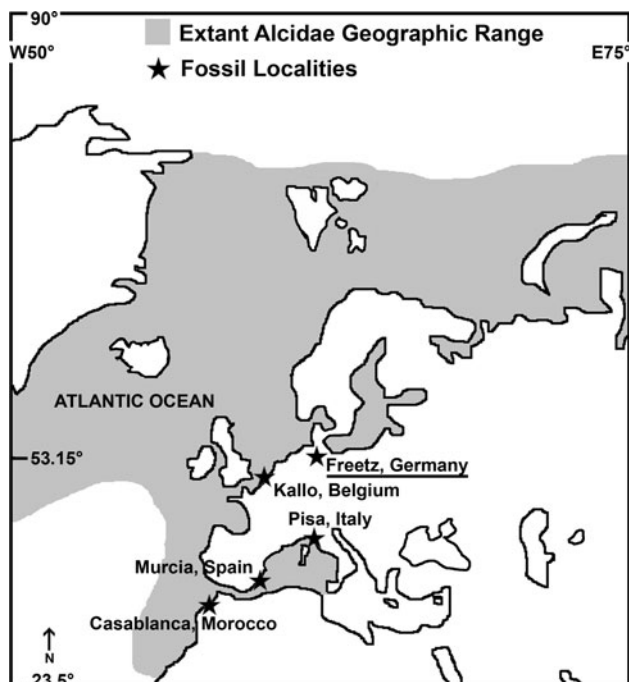
In the anatomical descriptions, the English equivalents of the Latin osteological nomenclature summarized by Baumel and Witmer (1993) are primarily used. The terminology of Howard (1929) is followed for features not treated by Baumel and Witmer (1993). Measurements follow those of von den Driesch (1976). All measurements were taken using digital calipers and rounded to the nearest tenth of a millimeter. Ages of geologic time intervals are based on the International Geologic Time Scale (International Commission on Stratigraphy 2012).

## Institutional abbreviations

NCSM, North Carolina Museum of Natural Sciences, Raleigh, NC, USA;  
SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

## Comparative material examined

*Aethia psittacula* NCSM 18387, 18514;  
*Alca torda* NCSM 20058, 20502;



**Fig. 1** Pre-Pleistocene alcid fossil localities in the northeastern Atlantic Ocean basin

**Table 1** Previously published alcid fossils from the Pliocene of the northeastern Atlantic Ocean basin (for Pleistocene and Holocene remains of the Great Auk *Pinguinus impennis* see Hufthammer (1982); Burness and Montevecchi (1992); Fuller (1999); Stewart (2002a, b))

Taxon	Material	Provenance	Age	Geologic formation	References
† <i>Alca ausonia</i>	Distal humerus	Orciano Pisano, Italy	?Middle Pliocene	Unknown	Portis (1888, 1891)
† <i>Alca</i> sp.	Cranium	Murcia, Spain	?Late Pliocene	Puerto de Mazarron	Sanchez-Marco (2003)
† <i>Alca stewarti</i>	Isolated postcranial and cranial remains	Kallo, Belgium	Early Pliocene	Kallo Sands	Martin et al. (2001)
† <i>Alca</i> spp.	Isolated postcranial bones	Kallo, Belgium	Early Pliocene	Kallo Sands	Dyke and Walker (2005)
† <i>Fratercula</i> sp.	Ulna	Kallo, Belgium	Early Pliocene	Kallo Sands	Dyke and Walker (2005)
† <i>Alca ausonia</i>	Isolated postcranial bones	Casablanca, Morocco	Late Pliocene	Ahl al Oughlam Quarry	Mourer-Chauviré and Geraads (2010)

‘*Cephus storeri*’ Harrison, 1977 from the Pleistocene of England (Harrison 1977) is probably referable to *Alca torda*, but is too badly preserved for confident referral (Smith 2011a). Detailed evaluation of apomorphies supporting referral of listed species can be found in Smith (2011b)

*Alle alle* NCSM 18374;  
*Brachyramphus marmoratus* NCSM 18148, 18149;  
*Cephus columba* NCSM 18094, 18095;  
*Cerorhinca monocerata* NCSM 22316;  
*Fratercula arctica* NCSM 20461;  
*Stercorarius longicaudus* NCSM 10269, 17801;  
*Synthliboramphus antiquus* NCSM 17742, 18089;  
*Uria aalge* NCSM 17822, 18116.

## Systematic paleontology

Aves Linnaeus 1758  
Charadriiformes Huxley 1867  
Pan-Alcidae Smith 2011a  
Alcidae Leach 1820  
Alcinae sensu Smith 2011a  
Alcini Storer 1960  
Alcini indet. (cf. *Alca*)

### Referred specimen

SMF Av 594. Associated right radius and proximal and distal ends of the right ulna collected by Hartmut Schiek in 2010 (Fig. 2).

### Locality and age

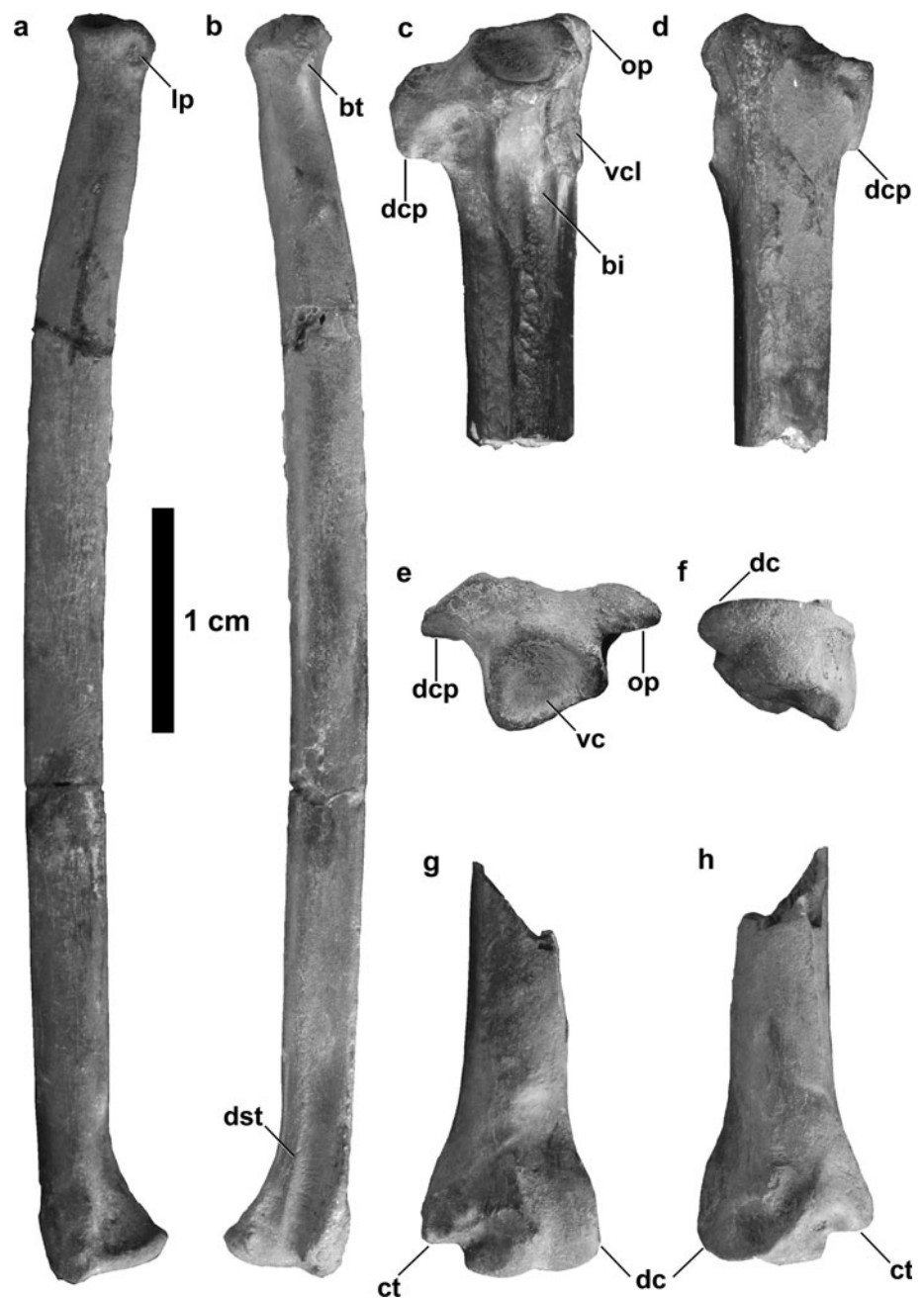
Freetz near Sittensen, Schleswig–Holstein, Germany, clay pit of Wienerberger brickworks (53°18′19.14″N, 9°32′08.61″E); middle/late Miocene (Tortonian, 11.6–7.2 Mya), Gramian or Langenfeldian regional stage (see Gürs and Schnetler 2004; Hampe and Ritsche 2011, for further information on the locality).

### Description and comparison

In comparison with other Charadriiformes, all Pan-Alcidae are characterized by some degree of dorsoventral compression

of the humerus, radius and ulna. The new specimen (SMF Av 594; Fig. 2) has a similar degree of ulna shaft compression to that of most pan-alcids (e.g., *Alca* and *Uria*), and is unlike that of *Cephus* spp., †*Divisulcus demerei* and †*Pseudocepphus teres* (more rounded) or the flightless taxa †*Pinguinus* and †Mancallinae (extremely compressed; Smith 2011a, b; see Smith 2013a, fig. 3). As in all Pan-Alcidae, the dorsal cotylar process of the ulna of SMF Av 594 is cranially projected in comparison with the more restricted condition of other charadriiforms. The cranial margin of the dorsal cotylar process of the new specimen is rounded as in most Alcinae (straight in †*Alca olsoni*, †*A. stewarti*, and Fraterculinae; Smith 2011b). In size and overall morphology, the ulna most closely resembles that of *A. torda*. The olecranon of the ulna is shorter (i.e., less medially projected) than that of *Alca torda*, †*A. stewarti*, †*A. olsoni*, †*A. carolinensis* and species of *Uria*, but similar to that in †*A. grandis* and †*Miocepphus bohaski* (Wijnker and Olson 2009; Smith and Clarke 2011). As in *Cephus* and some species of *Alca* (e.g., *A. torda*, †*A. carolinensis*), the ventral margin of the ventral cotyla is less deeply notched than in other Alcidae (e.g., *Uria lomvia*). The ventral margin of the ventral cotyla is more rounded in †*Miocepphus blowi* and †*M. bohaski*, the stem lineage representatives of Alcidae (i.e., †Mancallinae) and in Stercorariidae, the sister taxon of Pan-Alcidae. There are no crests that join the ventral collateral ligament tubercle and the ventral cotyla of the ulna as are present in †*Miocepphus* and *Uria*. The tubercle for attachment of the ventral collateral ligament is oval in shape as in *Cephus*, †*Miocepphus*, and *Uria*. That tubercle is more triangular in outline in *Alca*, *Alle*, and †*Pinguinus*. On the distal end of the ulna, the caudal margin of the dorsal condyle is rounded as in †*M. bohaski* and †*A. olsoni*, rather than angled as in †*A. carolinensis* and species of *Uria*. The carpal tubercle forms a nearly 90° angle with the ventral condyle in ventral view and is not projected distally (i.e., ‘hooked’) as in *Cephus*.

**Fig. 2** Newly referred pan-alcid fossil from the middle/late Miocene of Freetz, Germany (SMF Av 594). Radius in ventral (a) and dorsal (b) views. Proximal end of right ulna in ventral (c), craniodorsal (d), and proximal (e) views. f–h distal end of right ulna in distal (f), ventral (g) and dorsal (h) views. *bi* brachial impression, *bt* bicipital tubercle, *ct* carpal tubercle, *dc* dorsal condyle, *dcp* dorsal cotylar process, *dst* division of sulcus tendinosus, *lp* ligamental papilla (sensu Howard 1929), *op* olecranon process, *vc* ventral cotyla, *vcl* ventral collateral ligament tubercle



The radius also closely resembles that of extant *A. torda* in size and morphology, but differs in the wide shaft and the less strongly defined sulcus tendinosus. A distinct bicipital tubercle is present on the proximal end of the radius. The bicipital tubercle is less distinct in the murrelets (*Brachyramphus* and *Synthliboramphus*), and there are no records of those taxa from the Atlantic Ocean basin (Smith 2011b). The ligamental papilla (sensu Howard 1929) is rounded and positioned ventrally adjacent to the humeral cotyla. The tendinal sulcus located on the dorsal surface of the distal radius is divided by a crest. That crest is absent in the auklets (*Aethia* and *Ptychoramphus*), the puffins (*Fratercula* and *Cerorhinca*), and the dovebies (*Alle* and †*Miocepphus*). The

absence of the crest dividing the distal tendinal sulcus of the radius is likely not related to overall body size, as the crest is present in both small and large Alcinae such as *Synthliboramphus antiquus* (229 g) and *Uria lomvia* (964 g; Dunning 2008; Smith 2011b). Among extant and extinct Atlantic taxa for which measurement data are available, SMF Av 594 is most similar in size to †*M. bohaski* (Table 2). However, with respect to its morphology, SMF Av 594 agrees most with *Alca* and may represent one of the smaller species in that clade (e.g., †*A. minor* or *A. torda*). Ratios of radius to humerus length in Alcinae suggest that SMF Av 594 would have had a humeral length of approximately 75 mm (Table 2), a value that is within the range of values reported for extinct and

**Table 2** Measurements of extant and extinct Atlantic alcid species (mm)

Taxa	gIR	pwR	dwR	glU	dwpU	cpU	cdU	gIH	rR:H
German auk (SMF Av 594)	56.9	5.1	5.5	–	7.2	9.0	8.1	~75 <sup>a</sup>	–
† <i>Miocepphus bohaski</i> (USNM 237270)	53.6	4.8	5.0	55.5	8.3	10.4	7.5	~70 <sup>a</sup>	–
† <i>Miocepphus blowi</i> (USNM 237207)	–	–	–	–	7.6	10.9	8.4	78.2	–
† <i>Alca grandis</i> (USNM 336379)	–	5.3	–	71.9	9.7	15.3	10.1	–	–
† <i>Alca carolinensis</i> (NCSM 13734)	79.2	6.7	7.1	83.0	12.4	16.0	10.8	102.4	1.29
† <i>Alca olsoni</i> (USNM 454590)	77.0	6.5	6.8	87.5	8.7	16.4	11.1	104.0	1.35
† <i>Alca stewarti</i> (USNM 242238)	–	4.8	–	93.2	13.6	18.2	12.6	111.4	–
<i>Alca</i> cf. <i>torda</i> ( <i>n</i> = 4)	55.5	–	5.0	–	–	–	–	72.7	–
<i>Alca torda</i> ( <i>n</i> = 13)	60.6	5.2	5.3	62.8	8.7	12.2	8.5	78.4	1.29
<i>Uria aalge</i> ( <i>n</i> = 5)	61.6	5.7	5.6	64.0	8.3	13.1	8.8	85.0	1.38
<i>Uria lomvia</i> ( <i>n</i> = 5)	65.7	5.4	5.5	68.3	9.0	13.0	9.1	87.9	1.34
<i>Alle alle</i> ( <i>n</i> = 5)	31.9	2.7	3.1	34.1	3.1	4.5	4.9	41.5	1.30
<i>Cephus grylle</i> ( <i>n</i> = 5)	49.2	4.2	4.5	51.7	6.7	9.5	7.1	60.0	1.22
<i>Fratercula arctica</i> ( <i>n</i> = 5)	50.1	4.3	4.7	52.0	6.6	9.6	5.4	65.8	1.31

Values for *Alca torda*, *Uria aalge*, *Uria lomvia*, *Alle alle*, *Cephus grylle*, and *Fratercula arctica* are averages from Smith and Clarke (2011). Measurements of *Alca* cf. *torda* are from Wijnker and Olson (2009, table 5; humeral length is averaged). The holotype specimens of *A. ausonia*, *A. minor*, *Miocepphus mcclungi*, *Miocepphus mergulellus* and *Pseudocepphus teres* are humeri, and associated specimens that would allow for referral of radii and ulnae to those taxa are not known

*cdU* craniocaudal width of distal ulna, *cpU* craniocaudal width of proximal ulna, *dwpU* dorsoventral width of proximal ulna, *dwR* distal width of radius, *gIH* greatest length of humerus, *gIR* greatest length of radius, *glU* greatest length of ulna, *pwR* proximal width of radius, *rR:H* ratio of greatest length of radius to greatest length of humerus

–, reflects missing data owing to damage

†, denotes extinct species

<sup>a</sup> Estimated lengths that were extrapolated from the average ratio of radius to humerus length (=1.31)

extant specimens of *A. torda*, but is outside the statistically supported range of intraspecific variation expected for †*A. minor* and larger species of *Alca* (see Smith and Clarke 2011 for morphometric analysis of *Alca* forelimb dimensions).

## Discussion

Although the fossil record of Pan-Alcidae was once dominated by Pliocene material (e.g., Chandler 1990; Olson and Rasmussen 2001), recently described specimens have

increased the diversity of Miocene Pan-Alcidae known from the Pacific Ocean basin (Smith 2011a, 2013a, b) and the northwestern Atlantic Ocean basin (Wijnker and Olson 2009). The newly described remains reported here provide evidence that alcids have likely maintained their circum-polar range since at least the Late Miocene, and also represent the northernmost pre-Pleistocene fossil occurrence of an alcid from the northeastern Atlantic Ocean basin (53°18'19.14"N; Fig. 1).

Compared to extant Alcidae, the fossil most closely resembles the Razorbill, *Alca torda*, which has an



exclusively North Atlantic range and is one of the most widely distributed alcids in Europe (del Hoyo et al. 1996). Several extinct species of *Alca* and related taxa have been reported from the Pliocene and Pleistocene of Europe (Table 1), including the large flightless Great Auk †*Pinguinus impennis* (Stewart 2002a, b). We consider it possible that the specimen described here represents a species on the stem lineage of *A. torda*, but such cannot be conclusively shown with the limited material at hand as the similarities (e.g., no division of the sulcus tendinosus of the distal radius) may be plesiomorphic for a more inclusive clade. The morphology of the German specimen (see “Description and comparison”) excludes it from referral to all known pan-alcid taxa other than *Alca* or *Uria*, and, although referral to *Uria* cannot be excluded, fossils of *Uria* are not known from the Atlantic Ocean basin prior to the Pleistocene (Smith and Clarke 2011). †*Alca ausonia* and †*A. stewarti* have been documented in the Pliocene of the northeastern and northwestern Atlantic Ocean basin, and additional species of *Alca* and other auks are present in the Pliocene of the northeastern Atlantic Ocean basin (Smith, unpublished data). Likewise, the ranges of extant alcid species often longitudinally span entire ocean basins (e.g., *A. torda*, *Fratercula arctica*) and although the specimen described here cannot be identified to the species level, the possibility that it represents a previously described species of Miocene auk from the northwestern Atlantic Ocean basin cannot be ruled out.

Most previously described Miocene Atlantic Ocean Alcidae were assigned to †*Miocepphus* and *Alca* (Wijnker and Olson 2009; Smith and Clarke 2011), and in size, the German auk is consistent with extant specimens of *A. torda* and †*M. bohaski* or †*M. blowi* from the early to late Miocene of the western North Atlantic Ocean basin (Table 2). However, size alone is not always a taxonomic indicator (Stewart 2002a, b), and †*Miocepphus* and the closely related extant species *Alle alle* are differentiated from other Alcinae by the lack of a division of the distal tendinal sulcus of the distal radius (Smith and Clarke 2011). SMF Av 594 is therefore not referable to †*Miocepphus*. There are no apomorphies of the ulna or radius that characterize the taxon *Alca*, and therefore an unambiguous assignment of the new fossil to that taxon is not possible. Furthermore, the fossil species of *Alca* are mainly distinguished by characteristics of the humerus (Smith and Clarke 2011), which complicates identification of the new fossil. However, autapomorphies of the radius and ulna of †*A. carolinensis* and †*A. olsoni* (Smith and Clarke 2011) are absent in the German specimen, which is not referable to those taxa on the basis of morphology or size (Table 2). Wijnker and Olson (2009) reported fossils from the Miocene of the western Atlantic Ocean basin which they referred to *Alca* cf. *torda*, and there remains a possibility

that those fossils belong to the same species as the German fossil. In addition to humeri, Wijnker and Olson (2009) referred a radius to *Alca* cf. *torda*, but the radius was not figured, and we were unable to perform direct comparisons between the German and western Atlantic fossils. In size, however, the *Alca* cf. *torda* remains from the western Atlantic Ocean basin are comparable to the German specimen (see Wijnker and Olson 2009, table 5; Table 2).

As detailed above, the German specimen can be differentiated from all other Pan-Alcidae except Alcini (i.e., the clade including *Alca*, †*Pinguinus*, *Alle*, †*Miocepphus*, and *Uria*). The specimen does not display any of the derived features associated with flightlessness that are present in †*Pinguinus* (e.g., relatively short and highly curved radius) and we consider it most probable that that it represents a species of *Alca* or a taxon on the stem lineage of the (*Alca* + †*Pinguinus*) clade. Alternatively it could represent *Uria* or a taxon on the stem lineage of the (*Uria* + *Alle* + †*Miocepphus*) clade. However, given that the specimen is not referable to †*Miocepphus* or *Alle*, and given that the (†*Miocepphus* + *Alle* + *Uria*) lineage split from the (*Alca* + †*Pinguinus*) lineage at least 20 Mya (Wijnker and Olson 2009; Smith and Clarke 2011), we consider the latter hypothesis less likely because fossil records of *Uria* from the Atlantic Ocean basin are restricted to the Pleistocene (†*Uria affinis* Marsh 1872) and †*Miocepphus* is restricted to the northwestern Atlantic Ocean basin (Wijnker and Olson 2009). Brodkorb (1960) hypothesized that most avian species-level cladogenic events date to the Pleistocene and that “almost no avian species are known to cross epochal lines” (Brodkorb 1960:47). In contrast, Wetmore (1952) expressed “a firm belief [...] that our living kinds had their evolution both as genera and as species in the Miocene and Pliocene periods” (Wetmore 1952: 63). The former view is not supported by current knowledge of the fossil record. For example, just within Alcidae, Pliocene records are known for the extant species *A. torda*, *U. lomvia*, *F. arctica* and *F. cirrhata* (Olson and Rasmussen 2001; Smith et al. 2007; Smith and Clarke 2011; Olson in press). However, diagnosis of morphologically cryptic, fragmentary and isolated avian fossils is problematic (discussed by Stewart 2002a, b; Tyrberg 2002). Regardless of the taxonomic affinities of the new specimen, it nonetheless represents an extension of both the temporal range of Pan-Alcidae in the northeastern Atlantic Ocean basin, and the geographic range of Miocene pan-alcids in general.

Extant alcids often partition habitat by size (Ainley 1990), and examples of extinct alcid faunas that are characterized by a range of small to large species have been previously documented (Wijnker and Olson 2009; Smith and Clarke 2011; Smith 2011a). Size-based habitat partitioning in extant alcids occurs in relation to several life

history traits including nesting preference, foraging depth and prey choice (Ainley 1990). Although direct data on size-based habitat partitioning are largely lacking for extinct pan-alcids, the size range of coeval extinct pan-alcid species is greater than that of extant alcids when considering the flightless Great Auks (†*Pinguinus*) and Lucas Auks (†*Mancallinae*). These data suggest that similar partitioning schemes have been in place among Pan-Alcidae since at least the Late Miocene. Although Old World Alcinae today exhibit some variation in size and morphology, it is notable that from the Miocene and Pliocene of Europe only *Alca*-like forms of a size comparable to *Alca torda* or larger have so far been reported. The sample size of fossils from the northeastern Atlantic Ocean basin is currently too small to discern if an actual difference in body sizes existed between opposite sides of the Atlantic Ocean basin in the past or if this apparent difference is an artifact of relative undersampling.

Whether the diversity of auks in the Miocene of Europe paralleled that of the northwestern Atlantic Ocean basin will have to be shown by future studies. As far as the current fossil record indicates, auks appear to have been numerically less abundant in the northeastern Atlantic Ocean basin than in contemporaneous deposits of the northwestern Atlantic Ocean basin. At least 15 species of pan-alcids are known from the Miocene and Pliocene of the northwestern Atlantic Ocean basin (Smith 2011a), whereas only †*A. ausonia* and †*A. stewarti* are definitively known to date from the northeastern Atlantic Ocean basin. Furthermore, with respect to the quantity of alcid specimens recovered, remains from the rich early Pliocene deposits of the western Atlantic Ocean basin (e.g., ~8,000 specimens reported from the Yorktown Formation and equivalents; Olson and Rasmussen 2001; Smith and Clarke 2011) far outnumber remains recovered from coeval deposits of the eastern Atlantic Ocean basin (<100 specimens total; reviewed by Smith 2011b). Sampling effort and exposed strata of appropriate age are roughly equivalent between the northwestern and northeastern Atlantic Ocean basins, and, thus, the significant difference in quantity of specimens recovered can be almost entirely attributed to the mining efforts that have exposed late Miocene and early Pliocene sediments of the Yorktown Formation in North Carolina (see Ray 1983). Further collecting effort is warranted to evaluate the potential for increased pan-alcid diversity from the Miocene and Pliocene of the northeastern Atlantic Ocean basin.

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