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## Journal of Systematic Palaeontology

Publication details, including instructions for authors and subscription information:  
<http://tandfprod.literatumonline.com/loi/tjsp20>

### A revision of the fossil genus *Miocepheus* and other Miocene Alcidae (Aves: Charadriiformes) of the Western North Atlantic Ocean

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Available online: 09 Mar 2010

To cite this article: Erik Wijnker & Storrs L. Olson (2009): A revision of the fossil genus *Miocepheus* and other Miocene Alcidae (Aves: Charadriiformes) of the Western North Atlantic Ocean, *Journal of Systematic Palaeontology*, 7:4, 471-487

To link to this article: <http://dx.doi.org/10.1017/S1477201909990022>

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# A REVISION OF THE FOSSIL GENUS *MIOCEPPHUS* AND OTHER MIOCENE ALCIDAE (AVES: CHARADRIIFORMES) OF THE WESTERN NORTH ATLANTIC OCEAN

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**SYNOPSIS** This study reviews and describes all known fossils of Alcidae from the Miocene of the western North Atlantic. Because the majority of alcid fossils recovered from Miocene sediments are allied with the genus *Miocepphus* Wetmore, 1940, the genus is revised here. Three new species of *Miocepphus* are described: *Miocepphus bohaskai* and *Miocepphus blowi* from the Early to Late Miocene, and *Miocepphus mergulellus* of uncertain Neogene age but probably Miocene. A new genus and species, *Pseudocepphus teres*, from the Middle and Late Miocene, has uncertain relationships within the Alcinae (a clade comprising *Miocepphus*, *Alle*, *Uria*, *Alca* and *Pinguinus*). The genus *Alca* is also reported from Late Miocene sediments. The newly recognised presence of three genera of the Alcinae in the Miocene of the North Atlantic indicates that the diversity of the subfamily was considerably greater than was evident previously. *Miocepphus* may be regarded as ancestral to modern Alcinae. The Alcinae as a group was well established in the Early Miocene, indicating that the divergence of the family Alcidae predates 20 Ma. The divergence of *Uria* and *Alca* predates 10 Ma.

**KEY WORDS** *Alca*, Calvert Formation, Choptank Formation, Eastover Formation, *Pseudocepphus*, St Mary's Formation, *Uria*

## Contents

Introduction	472
Geological setting	472
Materials and methods	474
Systematic palaeontology	474
Order Charadriiformes Huxley, 1867	474
Family Alcidae Leach, 1820	474
Subfamily Alcinae Leach, 1820	474
Genus <i>Miocepphus</i> Wetmore, 1940	474
<i>Miocepphus mcclungi</i> Wetmore, 1940	475
<i>Miocepphus bohaskai</i> sp. nov.	476
<i>Miocepphus blowi</i> sp. nov.	478
<i>Miocepphus mergulellus</i> sp. nov.	480
Genus <i>Pseudocepphus</i> nov.	481
<i>Pseudocepphus teres</i> sp. nov.	481
Genus <i>Alca</i> Linnaeus, 1758	482
<i>Alca stewarti</i> Martin <i>et al.</i> , 2001	482
<i>Alca</i> cf. <i>torda</i> Linnaeus, 1758	482
Discussion	483
Conclusions	486
Acknowledgements	486
References	487

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## INTRODUCTION

Analysis of fossil birds from the Lee Creek Mine, North Carolina, USA, documented, for the first time, an extensive view of the great diversity of the Pliocene avifauna of the North Atlantic Ocean (Olson & Rasmussen 2001). Pliocene species were shown to belong to almost exclusively modern genera, giving the avifauna a decidedly modern aspect. However, current knowledge of Miocene pelagic birds remains rather sketchy and many taxa such as gannets (*Morus*), shearwaters (*Puffinus*), auks (Alcidae) and the extinct, fossil pseudodontorns (Pelagornithidae) are in great need of revision (Olson 1985; Olson & Rasmussen 2001). Here, we review the fossil record of Alcidae from the Miocene (23–5 Ma) of the western North Atlantic, basing our study on material found mainly in place in Early, Middle and Late Miocene deposits in Maryland and Virginia and on material from Neogene spoil piles in the Lee Creek Mine in North Carolina.

The Alcidae are wing propelled diving birds confined to marine environments in the northern hemisphere. Of the six recognised divisions of the family (subfamilies or tribes: Moum *et al.* 1994; Friesen *et al.* 1996; Olson & Rasmussen 2001), the Alcinae, consisting of the genera *Miocepphus*, *Alle*, *Uria*, *Alca* and *Pinguinus*, are confined to the Atlantic Ocean, except for *Uria*. Based on mitochondrial DNA and allozyme data, Friesen *et al.* (1996) and Moum *et al.* (1994, 2002) were unable to resolve the precise interrelationships among the Alcidae due to a presumed sudden divergence caused by adaptive radiation, which Moum *et al.* (1994) thought had begun in the Middle Miocene. Their work was superseded by that of Pereira & Baker (2008) who estimated that radiation within the Alcidae began in the Paleocene (65–55 Ma) and was more gradual, although their review of the fossil record was notably deficient (e.g. they do not mention Olson & Rasmussen 2001, give the wrong part for Brodkorb's *Catalogue of Fossil Birds*, and the citation for Olson (1985) is largely erroneous).

The fossil record of the Atlantic radiation of Alcidae is extensive but is best understood for the Early Pliocene. The Lee Creek Mine produced the first fossils that were believed to belong to the lineage leading to the Dovekie (*Alle*) and the Great Auk (*Pinguinus*) (Olson 1977; Olson & Rasmussen 2001). Most characteristic of the Atlantic Pliocene however, is the striking radiation among razorbills (*Alca*) in which a minimum of four species co-existed (Olson & Rasmussen 2001). Pliocene fossils from Europe and northwest Africa substantiate the widespread nature of the radiation of *Alca* in the Atlantic and Mediterranean (Portis 1891; Martin *et al.* 2001; Sánchez-Marco 2003; Dyke & Walker 2005; Mourer-Chauviré, pers comm., 2008). The genus *Uria* (murre) has so far not been reported from the Atlantic Neogene and it has been hypothesised that *Uria* had a separate history in the Pacific from the other Atlantic Alcinae, and may have made its entry into the Atlantic as late as the Late Pleistocene (Olson & Rasmussen 2001).

The little that is written on Miocene Alcidae from the Atlantic leaves an impression of weak diversity. Olson noted 'only a few species' present in the Middle Miocene and characterised the upper Calvert Formation as 'quite depauperate' (Olson 1984, 1985), although it was later acknowledged that there was sufficient material to necessitate a revision (Olson & Rasmussen 2001). This we have undertaken here, including a complete reassessment of the genus *Miocepphus* along

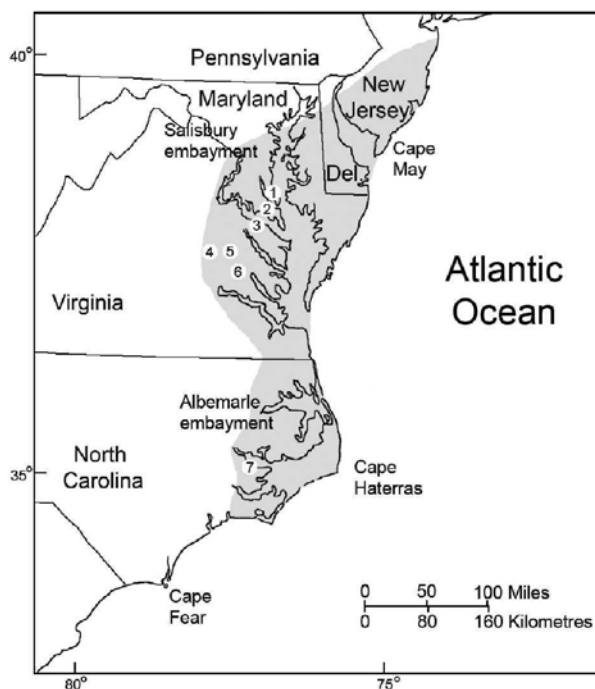
with a review of all other known fossil material of Alcidae from the Miocene of the western North Atlantic.

## GEOLOGICAL SETTING

The avian remains discussed here originated in the Salisbury and Albemarle embayments, depositional areas in which marine sediments were deposited throughout the Miocene and Pliocene. The Salisbury Embayment extends from southern New Jersey to southern Virginia and encompasses most of the contemporary Chesapeake Bay area. The Albemarle embayment lies directly to the south in eastern North Carolina (Fig. 1). The geology of the Miocene deposits of the area has been extensively discussed elsewhere (Shattuck 1904; Gibson 1983; Ward & Blackwelder 1980; Ward 1992; de Verteuil & Norris 1996). Here, we present a brief overview, based mainly on Gibson (1983) of the principal deposits with special attention to the depositional environment.

The various Miocene deposits in the Salisbury embayment that produced fossil auks represent periods in which inner shelf conditions existed and open ocean circulation prevailed. These alternated with periods in which sea levels lowered, open ocean circulation was hampered and marginal marine conditions existed. Only three fossils of Alcidae have been found so far in deposits of marginal marine conditions (lower St Mary's Formation). All other fossil Alcidae reported here were deposited in open marine environments.

The temporal placement of the various formations in the Salisbury embayment is shown in Fig. 2. The Early to Middle



**Figure 1** Map showing the presence of Miocene strata in the depositional environment of the Albemarle and Salisbury embayments. Numbers indicate fossil localities treated in this study. **1**, Calvert County; **2**, St Mary's County; **3**, Westmoreland County; **4**, Hanover County; **5**, King William County; **6**, New Kent County; **7**, Lee Creek Mine.



Miocene Eastover Formation was deposited in waters less than 30 m deep. Only a few alcid fossils have been recovered from the Choptank, St Mary's and Eastover Formations.

We also include in this study a number of fossils from the Lee Creek Mine, Albemarle embayment, in North Carolina, USA (Olson & Rasmussen 2001). These were collected from spoil piles and, therefore, their exact stratigraphical origin cannot be positively established. These specimens originated either from the Middle Miocene Pungo River Formation, which is the temporal equivalent of the upper Calvert Formation, or from the Pliocene Yorktown Formation which overlies Miocene sediments in both the Salisbury and Albemarle embayments. Deposition of both the upper Pungo River Formation as well as the Yorktown Formation took place in inner shelf conditions, with water depths of 100 m or less. For further information on the depositional environment and palaeoecology of the Albemarle embayment consult Olson & Rasmussen (2001).

## MATERIALS AND METHODS

All fossils of auks from Miocene deposits held in the Calvert Marine Museum (CMM, Solomons, Maryland, USA) and in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution (USNM, Washington, DC, USA) were examined. The holotype of *Petalca austriaca*, to which we refer in the discussion, is held in the Naturhistorisches Museum Wien (NMW, Vienna, Austria). The holotype of *Uria brodkorbi*, discussed under *Miocepphus blowi* sp. nov., is held in the Florida Museum of Natural History, Pierce Brodkorb collections (UF/PB). Osteological nomenclature follows Baumel & Witmer (1993), but for clarity of presentation several important characters of the alcid humerus are also explained in Fig. 3. Measurements were taken using digital calipers and rounded to the nearest 0.1 mm. For comparative measurements of

*Alca torda* we used specimens of the form *A. torda islandica* found in the North Sea (northwest Europe), which, according to Salomonsen (1944), are somewhat smaller than *A. torda torda* from northern Europe and America. Specimens used for measurements and comparisons are housed in the collections of the Groningen Institute of Archaeology (GIA), the Netherlands, the Natuurhistorisch Museum Rotterdam (NMR), the Netherlands and the Division of Birds (USNM). Details of specimens used are provided as "Supplementary data" available on Cambridge Journals Online: [http://www.journals.cup.org/abstract\\_S1477201909990022](http://www.journals.cup.org/abstract_S1477201909990022).

## SYSTEMATIC PALAEOLOGY

Order **CHARADRIIFORMES** Huxley, 1867

Family **ALCIDAE** Leach, 1820

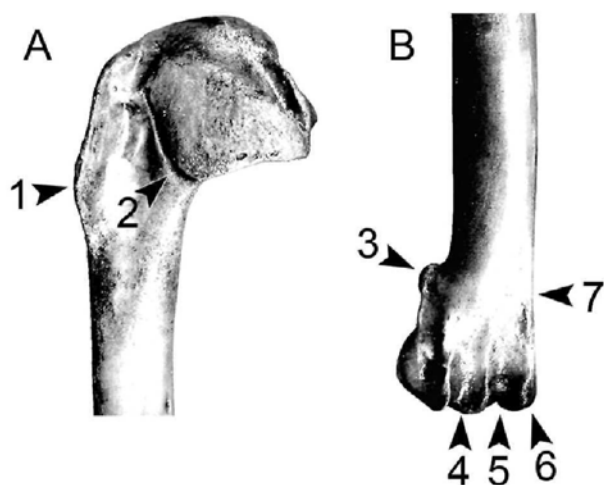
Subfamily **ALCINAE** Leach, 1820

Genus **MIOCEPPHUS** Wetmore, 1940

Although Wetmore (1940: 37) stated that *Miocepphus* 'has definite affinity with the living species of the genera *Cepphus* and *Brachyramphus*', Howard (1978: 21; 1982: 6) indicated, based partly on personal communication with Olson, that in spite of its name the affinities of *Miocepphus* do not lie with *Cepphus* but with the Atlantic Alcinae. Since the description of *Miocepphus mclungi*, fossils from different localities and ages have been referred to the same species, lineage, or genus (Olson 1984; Olson & Rasmussen 2001). All this material was re-examined, together with new elements recovered from various outcrops from Maryland and Virginia.

**ORIGINAL DIAGNOSIS.** 'Humerus... in general similar to that of modern *Cepphus* but shaft heavier and broader, more rounded, less flattened on anconal surface at proximal end; ectepicondylar process decidedly longer; deltoid crest shorter' (Wetmore 1940: 35).

**EMENDED DIAGNOSIS.** *Miocepphus* is differentiated from other Alcidae (except *Alca*, *Pinguinus* and *Alle*) by (combinations of) the following humeral characters: the fossa pneumaticipitalis is little excavated, with the head not deeply undercut; the sulcus humerotricipitalis is of equal width or narrower than the sulcus scapulo-tricipitalis. It is separated from other Alcinae (including *Alle*, *Alca* and *Pinguinus*) in having the olecranon more rounded and extending less far proximally from the ventral cotyla. It is further separated from *Alle* in having the proximal end of the corpus humeri straight rather than constricted and the dorsal margin of the crista deltopectoralis being developed as a thin ridge that is not curved anteriorly (which contrasts with *Alle* in which there is a distinct angular ridge). *Miocepphus* is separated from *Alca* and *Pinguinus* in having the neck of the coracoid more slender with the anterior margin of the neck being more acutely bent; the facies articularis clavicularis extending further anteriorly and the pointed dorsal margin being less distinctly developed than is commonly seen in *Alca* and *Pinguinus*. The humerus of *Miocepphus* differs from *Alca* and *Pinguinus* in that the sulcus nervus coracobrachialis is developed as an open groove (or exceptionally as a semi-closed duct).



**Figure 3** Frequently used characters of the alcid humerus. **A**, proximal end right humerus, anterior view. **B**, distal end left humerus, posterior view. 1, crista deltopectoralis; 2, sulcus nervus coracobrachialis; 3, processus supracondylaris dorsalis; 4, sulcus scapulo-tricipitalis; 5, sulcus humerotricipitalis; 6, processus flexorius; 7, ventral margin of the shaft.

***Miocepphus mcclungi* Wetmore, 1940**  
(Figs 4A–D; 5B)

- 1940 *Miocepphus mcclungi*; Wetmore: 35, figs 11–14.  
 1943 *Miocepphus mcclungi*; Wetmore: 604.  
 1984 *Miocepphus mcclungi* Wetmore, 1940; Olson: 219 (in part), figs 2d, e (in part).  
 2001 *Miocepphus mcclungi* Wetmore, 1940; Olson & Rasmussen: 270 (in part).

**MATERIAL EXAMINED.** USNM 16159 right humerus, holotype, face of cliff about 7 feet above beach level, 0.9 miles north of mouth of Parkers Creek, at south end of a small cove, Calvert County, Maryland. Calvert Formation, Shattuck Bed 12 (Fig. 4A);

USNM 16741 complete left humerus lacking internal tuberosity, referred to *Miocepphus mcclungi* by Wetmore (1943), 0.25 miles south of Governors Run, Calvert County, Maryland, Calvert Formation, Shattuck Bed 14. Four specimens referred to *Miocepphus mcclungi* by Olson (1984: 219): USNM 237154 proximal two thirds of right humerus, Mill Pond Creek, King William County, Virginia, lower Calvert Formation; USNM 237158 right humerus lacking proximal end, Mill Pond Creek, near Hanover Court House, King William County, Virginia, found ex-situ; USNM 237139 proximal end right humerus, roadcut where U.S. 360 crosses Pamunkey River, Hanover/King William County, Virginia, Popes Creek Sand Member, lower Calvert Formation; USNM 459974 right tibiotarsus lacking cnemial crests and condylus medialis, Grimes Landing, Pamunkey River, King William County, Virginia, Popes Creek Sand Member, lower Calvert Formation. All material (except USNM 460810) referred to *Miocepphus mcclungi* by Olson & Rasmussen (2001) from the Lee Creek Mine, North Carolina (horizon uncertain).

**NEWLY REFERRED MATERIAL.** Unless otherwise indicated, all of the following specimens come from a stretch of beach that runs from Dares Beach, Parkers Creek and Scientists Cliffs to Governors Run in Calvert County, Maryland: USNM 459981 associated complete right humerus and left ulna; USNM 237285 right coracoid; USNM 459962 left coracoid; USNM 237266 scapular end right coracoid; USNM 237165 and USNM 532553, right humeri; USNM 237269 complete right humerus lacking internal tuberosity; USNM 187664, 210541 and 529338 proximal halves right humeri; USNM 237218, 237245 and 459964 distal halves right humeri; CMM-V-1836, USNM 16741, 237262 and 25668 left humeri; USNM 237172 left humerus lacking distal articulation; USNM 237197 proximal end left humerus; USNM 237181 proximal shaft left humerus; USNM 459941 proximal two thirds of left ulna; USNM 237261 distal end left ulna; USNM 237177 distal half right femur; USNM 242233 left femur lacking proximal end. All elements from upper Calvert Formation, Plum Point Marl Member, Shattuck Beds 12 and 13 except for USNM 237269 and 187664 which are from the upper Calvert Formation, Calvert Beach Member, Shattuck Bed 14. USNM 237162 proximal two thirds of right humerus, Westmoreland State Park, Westmoreland County, Virginia, Calvert Formation; USNM 529341 proximal end right scapula and USNM 529340 proximal end left ulna, both Matadequin Creek, New Kent County, Virginia, lower Calvert Formation, Popes Creek Sand Member; USNM 237219 complete right ulna, Stratford Landing, Westmoreland County, Virginia, Calvert Formation; USNM 237268

head of left humerus including crista deltopectoralis, between Rocky Point and nuclear power plant, Calvert County, Maryland, Choptank Formation, Boston Cliffs Member, Shattuck Bed 19.

**DISTRIBUTION.** Early Miocene lower Calvert Formation to late Middle Miocene Boston Cliffs Member (Choptank Formation) of Virginia and Maryland. The species is also known from the Neogene of the Lee Creek Mine, North Carolina.

**MEASUREMENTS.** See Table 1.

**DESCRIPTION.** The scapula shows no differences from that of *Alca* apart from its smaller size. In the original description, a cross-section of the shaft of the humerus (Wetmore 1940: fig. 13) was shown as being more rounded than is actually observed in the holotype and is not consistent with any of the other material referred to the species. The sulcus scapulotricipitalis (Fig. 3) is wider than the sulcus humerotricipitalis in five out of eight humeri. The other three specimens have both sulci of even width. The ulna has the tuberculum ligamentosa collateralis ventralis placed relatively close to the ventral rim of the cotyla ventralis. In tibiotarsus USNM 459974, the crista cnemialis cranialis extends just as far distally on the shaft as the crista cnemialis lateralis. This is similar to *Alle* and fairly similar to *Alca*, whereas in *Uria* and *Cepphus* the crista cnemialis cranialis extends farther distally than the crista cnemialis lateralis. The facies articularis lateralis is laterally directed, as seen in *Cepphus*, and differs from *Alca*, in which the facies articularis lateralis is more medially placed. In medial view, the facies articularis medialis is strongly developed posteriorly in comparison with the posterior end of the shaft, thus resembling *Alle* and *Cepphus* but unlike *Alca* or *Uria* in which this posterior extension is less prominent. The pons supratendineus is missing, possibly due to incomplete ossification. The distal ends of two femora were not found to differ qualitatively from other Alcinae. Various elements, including the holotypical humerus, are shown in Fig. 4A–D. In Fig. 5B a complete humerus of *Miocepphus mcclungi* is shown in comparison with humeri of various related other species.

The lengths of the associated humerus and ulna USNM 459981 are 58.3 mm and 48.5 mm, respectively, so that the ulna in *Miocepphus mcclungi* is relatively large in comparison with the length of the humerus. In this respect *M. mcclungi* resembles Alcidae such as *Ptychoramphus*, *Aethia*, *Cepphus* and *Alle*, whereas in others (*Alca*, *Uria* and *Fratercula*) the ulna is relatively short (Table 2).

**REMARKS.** The specimen from the Choptank Formation (USNM 237268) marks the highest stratigraphical occurrence of the species. This humerus is extremely similar to the extensive material recovered from the upper Calvert Formation but has a caput that is slightly wider than in any of the other humeri of *Miocepphus mcclungi*. No differences were found and in standard measurements the proximal width (13.8 mm) falls well within the range of size variation of *M. mcclungi* (Table 1). We attribute the wide caput to intraspecific variation.

The right coracoid from Lee Creek (USNM 460810) attributed to this species by Olson & Rasmussen (2001) is very robust, with a wide neck, and the facies articularis

**Table 1** Measurements (mm) of *Miocepphus mcclungi*, *M. bohaskai* sp. nov., *M. blowi* sp. nov. and *M. mergulellus* sp. nov.

Element	<i>Miocepphus mcclungi</i>			<i>Miocepphus bohaskai</i>	<i>Miocepphus blowi</i>	<i>Miocepphus mergulellus</i>
	Size	Mean	SD	Size	Size	Size
Scapula						
Cranial diagonal	8.5	8.5	–	<b>9.8</b>	–	–
Coracoid						
Greatest length	31.8, 31.9	31.9	0.1	<b>34.4</b>	–	20.8
Medial length	29.9, 30.3	30.1	0.3	<b>33.3</b>	–	20.0
Basal width	10.5, 11.1	10.8	0.4	<b>12.4</b>	–	6.7
Humerus						
Proximal width	12.4–14.6 ( <i>n</i> = 14)	13.5	0.6	–	<b>17.9</b>	<b>10.0</b>
Greatest length	55.3–60.6 ( <i>n</i> = 11)	58.3	1.7	–	<b>78.2</b>	<b>39.6</b>
Distal width	6.8–9.4 ( <i>n</i> = 14)	8.8	0.6	9.8, <b>10.1</b> , <b>10.2</b>	<b>12.0</b>	6.0, 6.1, <b>6.2</b>
Minimum shaft width	2.6–3.4 ( <i>n</i> = 24)	3.1	0.2	<b>3.3</b> , 3.7	<b>4.2</b>	3.0, <b>3.4</b>
Ulna						
Greatest length	51.1	51.1	–	<b>55.7</b>	–	–
Proximal diagonal <sup>1</sup>	8.7, 9.0	8.9	0.2	<b>10.3</b>	–	–
Proximal width	6.0, 6.1	6.1	0.1	<b>7.2</b>	<b>8.0</b>	–
Distal diagonal <sup>2</sup>	5.6, 5.8, 6.1, 6.3	5.9	0.3	<b>6.8</b>	<b>7.3</b>	4.5
Minimum shaft width	2.9, 3.0, 3.1, 3.2, 3.5	3.1	0.2	<b>3.2</b>	–	–
Radius						
Greatest length	–	–	–	<b>53.7</b>	–	–
Distal width	–	–	–	<b>5.0</b>	–	–
Minimum shaft width	–	–	–	<b>2.2</b>	–	–
Carpometacarpus						
Greatest length	–	–	–	–	<b>42.1</b>	21.6
Proximal width	–	–	–	<b>9.2</b>	<b>10.9</b>	6.0
Femur						
Distal width	6.2, 6.4	6.3	0.2	–	–	–
Distal diagonal	6.0, 6.2	6.1	0.2	–	–	–
Minimum shaft width	2.9, 3.0	2.9	0.1	–	–	–
Tibiotarsus						
Axial length	56.1	56.1	–	–	–	–
Minimum shaft width	2.8	2.8	–	–	–	–
Proximal diagonal	5.1	5.1	–	–	–	–
Distal diagonal	5.2	5.2	–	–	–	–

All measurements of holotypes are in **boldface**. Measurements joined by a hyphen represent a range.

<sup>1</sup> Length of olecranon–processus cotylaris dorsalis; <sup>2</sup> depth of the condylus dorsalis ulnae.

extends only somewhat anteriorly. It cannot confidently be assigned to *Miocepphus* and should probably be referred to *Alca*.

**Table 2** Ratio of the greatest length of the ulna to the humerus for different species of Alcidae.

	<i>n</i>	Ratio ulna / humerus		
		Range	Mean	SD
<i>Uria lomvia</i>	20	0.76–0.81	0.78	0.01
<i>Fratercula arctica</i>	9	0.76–0.81	0.79	0.01
<i>Alca torda islandica</i>	24	0.77–0.82	0.80	0.01
<i>Miocepphus mcclungi</i>	1	–	0.83	–
<i>Alle alle</i>	19	0.80–0.85	0.83	0.01
<i>Cephus columba</i>	6	0.84–0.85	0.85	0.00
<i>Cephus grylle</i>	3	0.85–0.86	0.85	0.01
<i>Ptychoramphus aleuticus</i>	5	0.85–0.88	0.86	0.01

Note that the ratio of *Miocepphus* (USNM 459981) is similar to *Alle alle* but considerably larger than that of modern *Alca* and *Uria*.

### *Miocepphus bohaskai* sp. nov. (Figs 4E–J; 5A)

1984 '*Miocepphus*, undescribed species' Olson: 219.

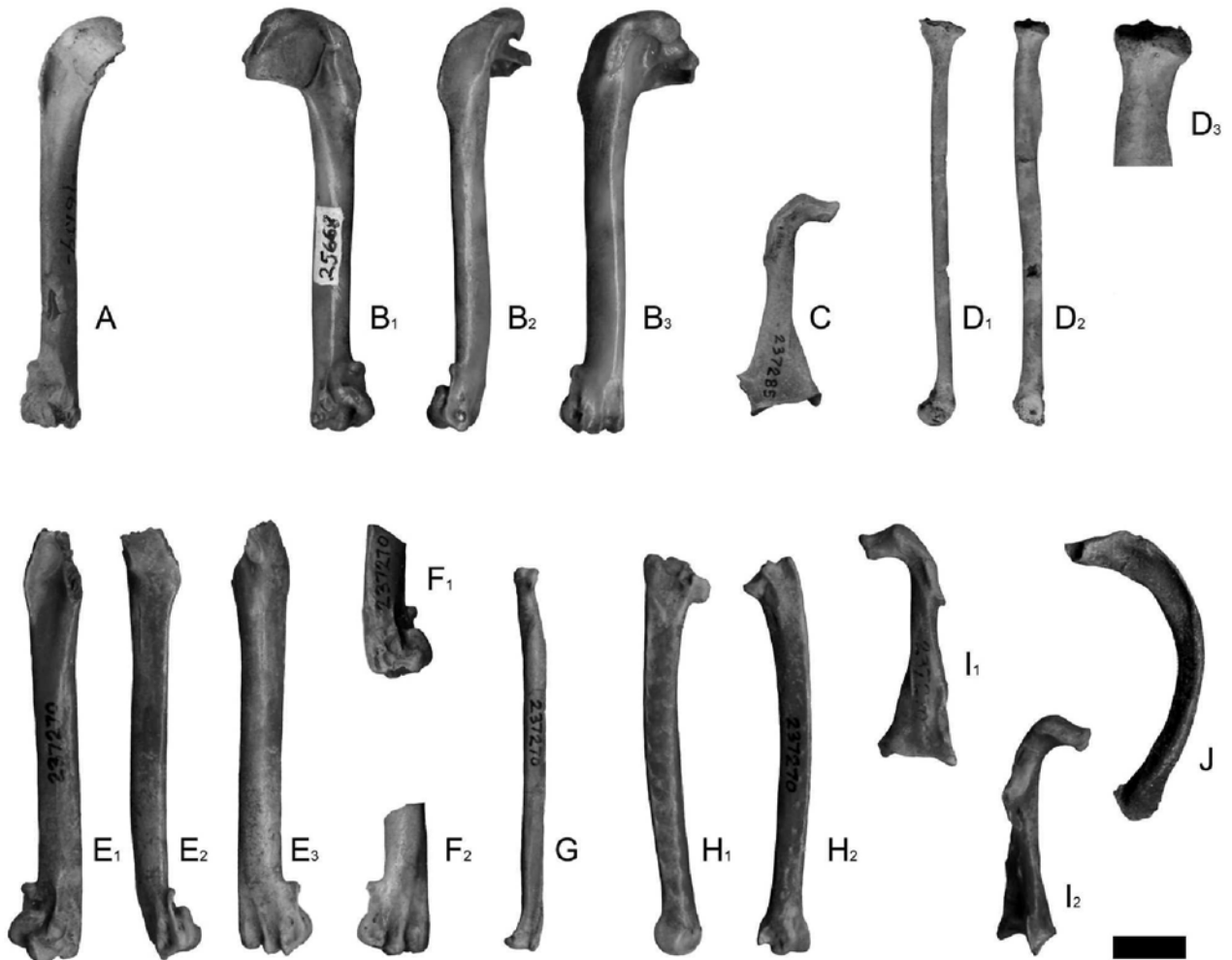
1984 *Miocepphus mcclungi* Wetmore, 1940; Olson: 219 (in part: element USNM 237142).

1984 '*Miocepphus* very similar to *M. mcclungi* Wetmore 1940' Olson: 221.

**HOLOTYPE.** USNM 237270 associated partial skeleton consisting of left coracoid lacking processus lateralis, anterior half of left scapula, furcula lacking left clavicle and extremitas omalis clavicularae of right side, right humerus lacking most of proximal end, distal end of left humerus, complete right radius and ulna and the proximal end of right carpo-metacarpus. (Figs 4E–J, 5A).

**LOCALITY AND HORIZON.** Matoka Cottages north of Calvert Beach, Calvert County, Maryland. Shattuck Bed 18, St. Leonard Member, Choptank Formation. Serravallian, late Middle Miocene.

**DISTRIBUTION.** Early Miocene lower Calvert Formation and Middle Miocene Choptank Formation of Virginia and



**Figure 4** Selected skeletal elements of *Miocepphus mclungi* Wetmore, 1940 (A–D) and *M. bohaskai* sp. nov. (E–J). *Miocepphus mclungi* Wetmore, 1940, holotype: right humerus (USNM 16159) in anterior view (A); left humerus (USNM 25668) in anterior (B<sub>1</sub>), dorsal (B<sub>2</sub>) and posterior (B<sub>3</sub>) views; right coracoid (USNM 237285) in ventral view (C); right tibiotarsus (USNM 459974) in medial (D<sub>1</sub>) and posterior (D<sub>2</sub>) views. D<sub>3</sub> is a magnification of D<sub>2</sub> showing the laterally inclined facies articularis lateralis. Associated pectoral and wing elements of *M. bohaskai* sp. nov., from the Choptank Formation, Calvert County, Maryland (holotype USNM 237270): incomplete right humerus in anterior (E<sub>1</sub>), dorsal (E<sub>2</sub>) and posterior (E<sub>3</sub>) views; distal end left humerus in anterior (F<sub>1</sub>) and posterior (F<sub>2</sub>) views; right radius in dorsal view (G); right ulna in dorsal (H<sub>1</sub>) and ventral (H<sub>2</sub>) views; left coracoid lacking processus lateralis in ventral (I<sub>1</sub>) and dorsal (I<sub>2</sub>) views; right ramus clavicularis, right lateral view (J). Scale bar = 1 cm (applies to all except D<sub>3</sub>).

Maryland and Neogene of the Lee Creek Mine, North Carolina.

**MEASUREMENTS OF HOLOTYPE.** Standard measurements given in Table 1. Additional measurement: length from distal end of the impressio musculus coracobrachialis to distal-most end of humerus is 52.3 mm.

**PARATYPE.** USNM 237142, right humerus lacking proximal end. Gravatt's Mill, near Hanover Court House, Hanover County, Virginia, lower Calvert Formation, Burdigalian, Lower Miocene.

**MEASUREMENTS OF PARATYPE.** See Table 1.

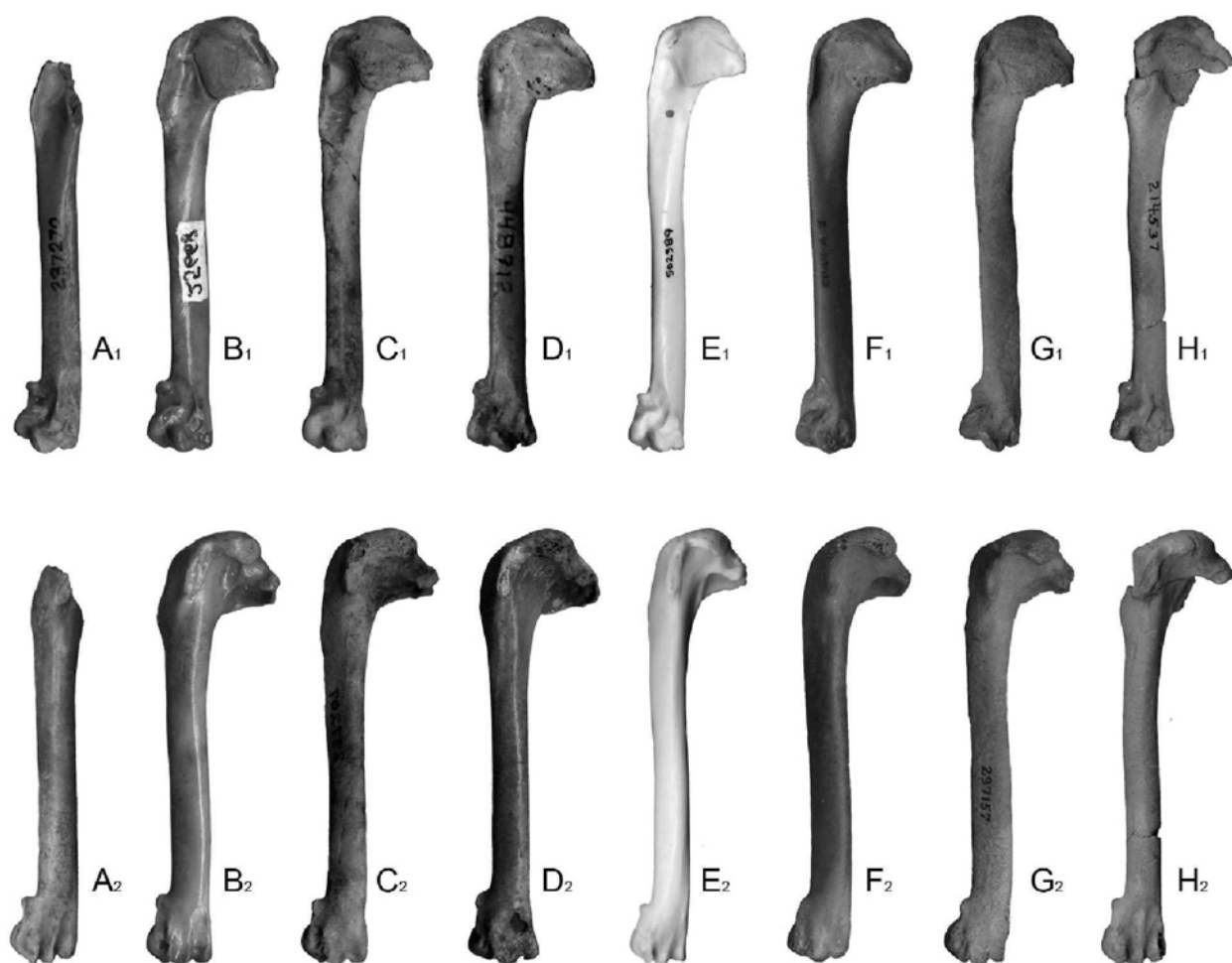
**ETYMOLOGY.** For David Bohaska of the Smithsonian Institution, the collector of the holotype and of many other fossil vertebrates from the Chesapeake area.

**DIAGNOSIS.** Distinguished from *M. mclungi* by its larger size.

**DESCRIPTION.** The scapula was not found to differ qualitatively from that of *Alca torda*. Its size is at the extreme small end of the variation observed in *A. torda islandica*. The coracoid is smaller than *A. torda islandica* in all standard measurements. Unfortunately no complete humerus is included among the material of this species. The sulcus humero- and scapulotricipitalis are of even width, but this character could only be checked in the humeri of the holotype.

The clavicle is well-preserved. The facies articularis acrocoracoidea is placed relatively anteriorly in comparison with *Alca* or *Uria*, and more resembles *Cepphus*, but has a relatively larger diameter than in any of those genera. The clavicle is typically flared along its distal margin in *Miocepphus*, unlike the slender clavicle of *Cepphus*, but much like that of *Alca* and *Uria*. The radius of *Miocepphus* may be distinguished from that of *Alca* or *Uria* by its flatness and slightly more angular posterior margin, although similarly flat radii occur in *Alca*. A rather distinct feature of the radius





**Figure 5** Proportional differences between five specimens of modern *Alca torda* and selected humeri from the Miocene and Neogene of Maryland, Virginia and North Carolina in anterior (above) and posterior (below) views. Humeri are not to scale in order to illustrate proportional differences. **A<sub>1,2</sub>**, *Miocepphus bohaskai* sp. nov. (holotype USNM 237270). **B<sub>1,2</sub>**, *M. mcclungi* (USNM 25668). **C<sub>1,2</sub>**, *M. blowi* sp. nov. (holotype USNM 237207). **D<sub>1,2</sub>**, *M. mergulellus* sp. nov. (holotype USNM 448912). **E<sub>1,2</sub>**, *A. torda torda* (Recent, female; USNM 502389). **F<sub>1,2</sub>**, *A. cf. torda* (CMM-V-8). **G<sub>1,2</sub>**, *A. cf. torda* (USNM 237157). **H<sub>1,2</sub>**, *Pseudocepphus teres* gen. et sp. nov. (USNM 214537). A<sub>2</sub>, B<sub>1</sub>, C<sub>2</sub>, D<sub>2</sub>, E<sub>2</sub>, F<sub>1</sub>, G<sub>1</sub> and H<sub>2</sub> are mirror images to facilitate comparisons.

in *Uria* and *Alca* is the presence of a distinct small, longitudinal ridge in the sulcus tendinalis near the distal articulation. This ridge is poorly developed in *M. bohaskai* and is absent in *Alle*.

The ulna is very similar to that in other Alcinae, but differs in having the olecranon less pointed and extending less proximad. The proximal end of the carpometacarpus is uninformative.

Measurements (Table 1) show that *M. bohaskai* is larger in most measurements than *M. mcclungi*. There was overlap only in the minimum width of the shaft of the humerus and ulna, which in the largest specimens of *M. mcclungi* exceed the size in *M. bohaskai*. In other measurements *M. bohaskai* is equal to, or exceeds, the average size of *M. mcclungi* by twice the standard deviation of the latter.

**REMARKS.** The '*Miocepphus*, undescribed species' of Olson & Rasmussen (2001: 270) from the Lee Creek Mine, was thought by them possibly to belong to the species here named *M. bohaskai*. This interpretation does not now appear to be

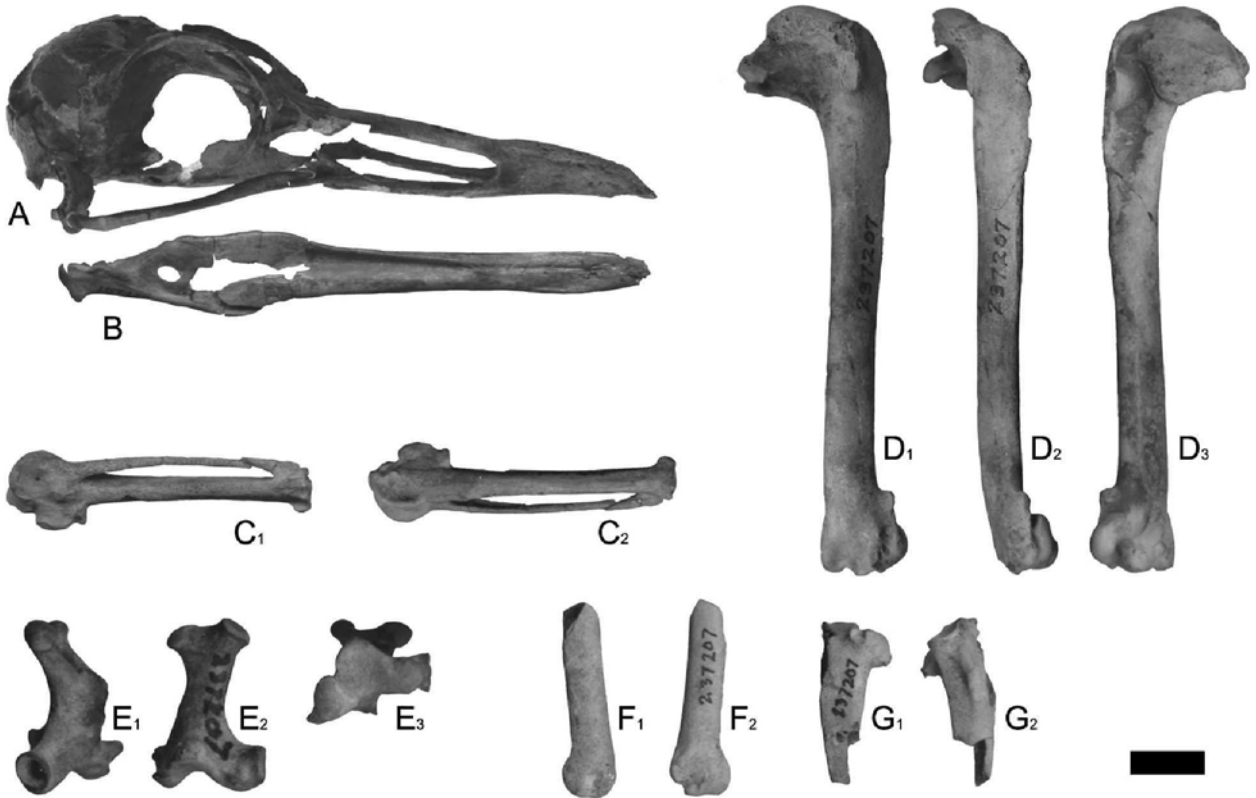
the case. Most of the Lee Creek specimens are fragmentary but in size are intermediate between *M. mcclungi* and *M. bohaskai*. The more intact humeri are now seen to be referable to a species of *Alca* smaller than *A. torda* and are almost certainly from the Lower Pliocene Yorktown Formation, which is supported by the state of preservation of most of the specimens. Hence, this material is not treated further here.

#### ***Miocepphus blowi* sp. nov. (Figs 5C; 6)**

1984 'Atlantic *Alca* group' Olson: 221.

**HOLOTYPE.** USNM 237207 associated partial skeleton consisting of skull lacking most of palate, right quadrate, lower mandible, complete right humerus with worn crista deltopectoralis, proximal and distal ends of right ulna and complete right carpometacarpus. (Figs 5C; 6)

**LOCALITY AND HORIZON.** Mattaponi River at White Oak Lodge, King William County, Virginia. Cobham Bay



**Figure 6** Associated cranial, pectoral and wing elements of *Miocepphus blowi* sp. nov., from the upper Eastover Formation, King William County, Virginia (holotype USNM 237207). Skull in right lateral view (A) and mandible in right lateral view (B). Right carpometacarpus in ventral (C<sub>1</sub>) and dorsal (C<sub>2</sub>) view. Right humerus in posterior (D<sub>1</sub>), dorsal (D<sub>2</sub>) and anterior (D<sub>3</sub>) view. Right quadratum in lateral (E<sub>1</sub>), posterior (E<sub>2</sub>) and ventral (E<sub>3</sub>) view (magnification ×2). Distal end right ulna in dorsal (F<sub>1</sub>) and ventral (F<sub>2</sub>) view. Proximal end right ulna in dorsal (G<sub>1</sub>) and ventral (G<sub>2</sub>) view. Scale bar = 1 cm.

Member, upper Eastover Formation. Messinian, Late Miocene.

DISTRIBUTION. Late Miocene (Messinian) of Virginia.

MEASUREMENTS OF HOLOTYPE. See Tables 1 and 3.

ETYMOLOGY. For the late palaeocarcinologist Warren Blow (19 October 1943 – 11 June 2007) of the Smithsonian Institution, collector of the holotype, an enthusiastic student of palaeontology of the western North Atlantic.

DIAGNOSIS. A very large species of *Miocepphus* distinguished from all other species of the genus by its larger size.

DESCRIPTION. The holotype represents an adult bird as indicated by the strongly developed supraorbital arches, which are as prominent as in adults of *Alca torda* or *Uria lomvia*, to which the skull is morphologically most similar. We, therefore, limit our comparisons to these two species. The length of the premaxilla anterior to the nostril is about two-thirds the length of the nostril, resembling *U. lomvia*, and in lateral view it is slightly expanded dorsally, forming a bulge or dertrum that ends in a slight notch above the anterior margin of the nostril. The dorsal expansion of the premaxilla is not nearly as pronounced as in *Alca*, in which it extends posteriorly to halfway between the bill tip and the os lacrimale. In *M. blowi* in dorsal view, the infranasal bars diverge gradually posteriorly, as in *Uria*, but unlike *Alca* in which the bill is

**Table 3** Cranial measurements (mm) of *Miocepphus blowi* sp. nov. and *Uria lomvia*.

element	<i>Uria lomvia</i>		<i>Miocepphus blowi</i> Size
	Range	Mean	
Cranium (n = 15, 7 males)			
Greatest length	93.7–102.9	98.4	91.3*
Condylobasal length	82.8–96.5	90.9	86.3
Greatest breadth	32.6–37.9	36.0	32.9
Smallest breadth between orbits	12.8–16.3	14.6	14.3
Greatest height	21.6–24.8	23.3	24.2
Length cranial cavity	42.8–47.6	44.9	42.7*
Length incisivum	49.4–57.0	53.6	49.7
Mandibula (n = 14, 10 males)			
Greatest length	84.8–90.8	86.3	81.0
Length symphysis	9.0–14.5	12.8	9.8

Measurements of *U. lomvia* were taken from eight adult females and seven adult males.

\*The cranium of *M. blowi* lacks the prominentia cerebellaris, because of this its length was originally a few mm longer.

laterally compressed and the infranasal bars are more nearly parallel. In ventral view, the conjunction of the quadratojugal, premaxilla and maxillopalatine is wide and penetrated

by a distinct foramen, as in *Uria* and *Alle*, but unlike *Alca* in which this area is narrow and lacks a foramen. In lateral view the quadratojugal bar is very robust in *M. blowi*, the greatest dorso-ventral depth measuring 2.4 mm, which exceeds that in *U. lomvia* and in two-thirds of the specimens of *A. torda*. It also has a small tuberosity on the ventral side just anterior to the attachment to the quadratum that is more prominent than in either *A. torda* or *U. lomvia*.

The anterior end of the cranium appears similar to that in both *Alca* and *Uria*. The posterior end is difficult to interpret because of its preservation and reconstruction but on the right side, the dorsomedial end of the fossa temporalis can be determined to be rather narrow and V-shaped, as in *Uria* but unlike *Alca* in which it is broader and more rounded (U-shaped).

The condylus caudalis of the quadrate of *M. blowi* is relatively smaller and projects less in a caudomedial direction in comparison with *Alca* or *Uria*. In addition, the incisura intercapitularis is more pronounced lateral to the capitulum oticum, which itself is bent a bit more posteriorly. When *A. torda* and *U. lomvia* are compared, the quadrate of *Alca* appears the most heavily built, *U. lomvia* is the most gracile and *M. blowi* falls in between. *Alca* appears heavy because of a rather distinct swelling on the medial side of the bone connecting the squamosal and mandibular articulations. The quadratum of *M. blowi* appears stouter than that of *Uria* because of the larger condylus lateralis and because the cotyla quadratojugal is extends more laterally. In posterior view the mediolateral width exceeds that in *U. lomvia* but the dorsoventral height is consistently smaller.

*Miocepphus blowi* is very distinct in having the retroarticular process of the mandible projecting laterally from the lateral cotyla, in contrast to *Uria* and *Alca* in which it is situated more posteriorly. In lateral view, ventral to the retroarticular process, the ventral margin of the mandibula projects as a pointed process in *M. blowi* and *Uria* whereas this area is rounded in *Alca*. *Miocepphus blowi* and *Uria* also differ from *Alca* in having a narrower processus medialis mandibulae. The fenestra caudalis mandibularis is rather small, as in *U. lomvia* and unlike the larger fenestra in *Alca* or *U. aalge*. In lateral view, the mandibula of *M. blowi* is robust, with the dorsal and ventral margins parallel. The slight anterior bulging of the symphyseal area contrasts with the very pointed mandibulae of *Uria* but does not approach the very expanded symphyseal area seen in *Alca*.

In the mandible of the holotype a distinct wide sulcus runs laterally along the side of the mandible, narrowing to a distinct, shallow groove at a point 56 mm from the posterior end of the bone and ending at the symphysis. This groove and sulcus are similar to *Uria*, whereas in *Alca torda* both the sulcus and the groove are less distinct and are not continuous. In dorsal view, the mandible, like the rostrum, shows no signs of being laterally compressed as in *Alca*.

The humerus is well preserved except for some wear on the posterior side of the caput and the crista deltopectoralis that makes it uncertain whether this crest is continuous with the dorsal margin of the shaft. The sulcus nervus coracobrachialis is an open duct and the tricipital grooves are of even width. The humerus thus agrees well with the description given in the generic diagnosis of *Miocepphus*.

In the poorly preserved ulna, the tuberculum ligamentosa collateralis ventralis is narrow and nearly rectangular in shape, contrasting with the broad, more rounded

structure in *Uria* and the wide, more triangular scar seen in *Alca*, *M. mcclungi* and *M. bohaskai*.

The carpometacarpus of *M. blowi* is distinguished from that of *Alca* and *Uria* in having the trochlea carpalis dorsalis with the distal rim extending more caudally and, thus, appearing more rounded. Apart from the appearance of being somewhat shorter and more robust than in *Alca* or *Uria*, the carpometacarpus of *M. blowi* shows no other strong points of distinction from those genera given the amount of variation in the modern taxa.

Measurements of *M. blowi* indicate no overlap with *M. bohaskai* (Table 1). Among living species, the skull of *U. lomvia* was found to be morphologically closest to *M. blowi*, which agrees in overall size with the smallest individuals of *U. lomvia* (Table 3). When compared with an individual of *U. lomvia* with a cranium of the same size, it is seen that the rostrum of *M. blowi* is much longer, whereas the humerus is about 12% shorter and decidedly more robust.

REMARKS. We have examined and compared casts and photographs of the holotype of *U. brodkorbi* Howard, 1981 (UF/PB 7960), a partial associated skeleton from the Late Miocene of California. This differs most conspicuously from *M. blowi* in lacking the swollen bill tip. Also, the proportions are different. The skulls in the two taxa are very nearly the same size (93.6 mm in *U. brodkorbi*, 91.3 mm in *M. blowi*), but the wing is considerably larger in *U. brodkorbi* (humerus 90 mm versus 78.2 mm; carpometacarpus 47.5 mm versus 42.1 mm). We consider that *U. brodkorbi* is correctly placed in the genus *Uria*. In fact, if it were a Pleistocene fossil it would probably have been referred to *U. lomvia* with very little misgiving.

### *Miocepphus mergulellus* sp. nov. (Figs 5D; 7A)

2001 *Alle* aff. *alle* (Linnaeus, 1758); Olson & Rasmussen: 279, pls 21a, c, e, g, i, k, m, o and q (in part).

HOLOTYPE. USNM 448912, complete right humerus (Figs 5D; 7A).

LOCALITY AND HORIZON. Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina. Horizon uncertain, either Middle Miocene Pungo River Formation or Early Pliocene Yorktown Formation.

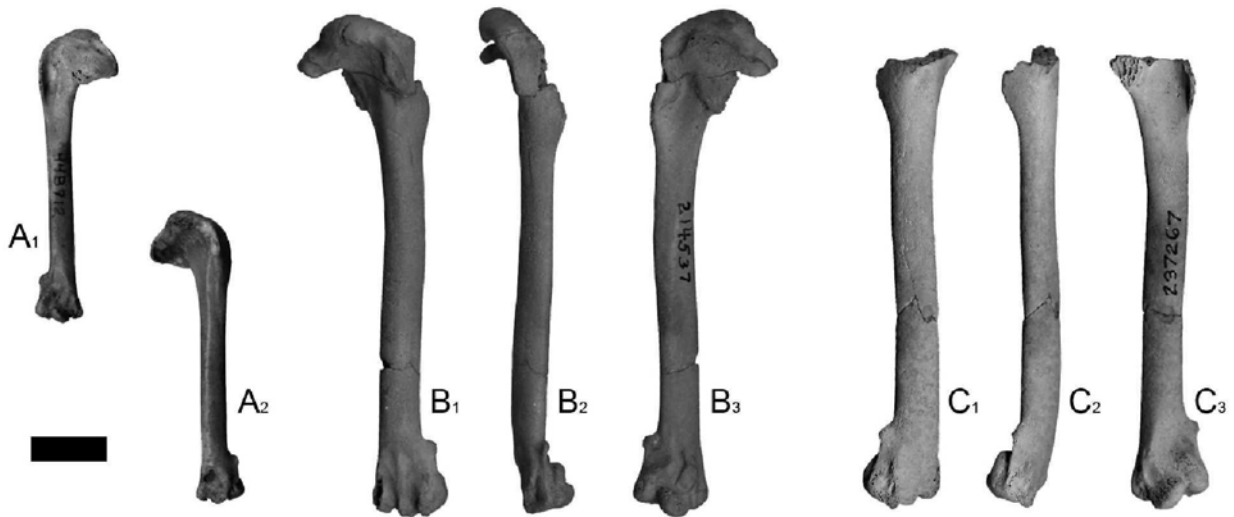
MEASUREMENTS OF HOLOTYPE. See Table 1.

PARATYPES. USNM 192856, left coracoid; USNM 430955 proximal third of shaft of left humerus with distal half of proximal end; USNM 367129, 430956, distal ends of right humeri; USNM 495585, 495601, distal ends of left humeri; USNM 430953 distal half of right ulna; USNM 430952, right carpometacarpus lacking minor metacarpal.

The paradigm includes all of the specimens referred to *Alle* aff. *alle* by Olson & Rasmussen (2001) except for humeri USNM 206572, 367158 and 430954, which we believe are referable to other species of small Alcidae and may be either Miocene or Pliocene in age. Hence we have not considered them further in the present context.

MEASUREMENTS OF PARATYPES. See Table 1.

ETYMOLOGY. From the Latin *mergus*, meaning a diver, and a double diminutive suffix *-ulus* + *-ellus*, indicative of the extremely small size of the species.



**Figure 7** Humeri of *Miocepphus mergulellus* sp. nov. (A) and *Pseudocepphus teres* gen. et sp. nov. (B, C). Holotype right humerus of *M. mergulellus* sp. nov., from the Neogene of the Lee Creek Mine, North Carolina (holotype USNM 448912) in anterior (A<sub>1</sub>) and posterior (A<sub>2</sub>) view. Holotype humerus (USNM 214537) of *P. teres* gen. et sp. nov., in posterior (B<sub>1</sub>), dorsal (B<sub>2</sub>) and anterior (B<sub>3</sub>) view. Paratype (USNM 237267) in posterior (C<sub>1</sub>), dorsal (C<sub>2</sub>) and anterior (C<sub>3</sub>) view. Scale bar = 1 cm.

**DIAGNOSIS.** The species agrees well in most characters with other species of *Miocepphus* but is much smaller (even smaller than modern *Alle alle*). The coracoid has a distal notch in place of the procoracoid foramen and the processus flexorius of the humerus projects quite strongly ventrally.

**DESCRIPTION.** This species differs from *Alle alle* in its slightly smaller size and in having a coracoid with a smaller procoracoid process, the neck of the coracoid being shorter and, in medial view, thinner at the level of the glenoid facet, while the coracohumeral surface is more pointed. The humerus is distinguished from that of *Alle* in having the proximal end of the humeral shaft wide rather than constricted; the distal edge of the bicipital crest more nearly perpendicular to the axis of the shaft and slightly notched at the juncture with the shaft; the crista deltopectoralis in dorsal view more prominent and rounded; and the distal third of the shaft much less flattened, without a ridge on the ventral margin.

**REMARKS.** The previous assignment of this species to *Alle* by Olson & Rasmussen (2001) was based mainly on size and the absence of a procoracoid foramen. The last condition may be size-related, however, as the procoracoid foramen is absent in all the genera of small alcids except *Synthliboramphus* (*sensu lato*). The morphology of the humerus, however, is extremely close to that of *M. mcclungi* and *M. bohaskai* (see Fig. 5). In fact, apart from the coracoid, there would be little other than size to suggest an affinity with *Alle*.

The stratigraphical horizon of the fossils of *M. mergulellus* has not been determined, but inasmuch as all the rest of the known history of *Miocepphus* is in the Miocene, the presumption would be that they originated in sediments of the Pungo River Formation and would be equivalent in age to the Calvert Formation to the north, a presumption that is supported by their excellent state of preservation. This tiny species is extremely rare at the Lee Creek mine (9 specimens out of tens of thousands of alcid bones recovered so far) and this rarity may explain why the species has not yet been found in deposits of the Chesapeake region.

### Genus *PSEUDOCEPPHUS* nov.

**TYPE SPECIES.** *Pseudocepphus teres* sp. nov.

**ETYMOLOGY.** From the Greek *pseudo*, meaning false, plus *Cepphus*, the living genus of guillemots or tysties, from the Greek *kepphos*, a waterbird mentioned by Aristotle.

**DIAGNOSIS.** Differs from all other genera of Alcidae except *Cepphus* in having the shaft of the humerus terete rather than flattened. Differs from *Cepphus* in having the sulcus scapulo-tricipitalis wider than the sulcus humerotricipitalis, whereas the opposite is true in *Cepphus*; and the processus supracondylaris dorsalis is much more pronounced and angular than in *Cepphus*. In all these characters *Pseudocepphus* resembles *Alca* and *Miocepphus*. The sulcus nervus coracobrachialis in *Pseudocepphus* is a closed duct.

#### *Pseudocepphus teres* sp. nov. (Figs 5H; 7B, C)

**HOLOTYPE.** USNM 214537, right humerus lacking parts of bicipital and pectoral crests (Figs 5H; 7B, C).

**LOCALITY AND HORIZON.** One mile east of Oakville, on Patuxent River at Cat Creek, St Mary's County, Maryland. About 1 m above beach level in thick grey clay with many remains of marine mammals, turtles and shark's teeth. Shattuck Bed 14 or 15 of the Calvert Formation, Langhian, Middle Miocene.

**DISTRIBUTION.** Middle Miocene Calvert Formation and Upper Miocene St Mary's Formation in Calvert and St Mary's counties, Maryland.

**MEASUREMENTS OF HOLOTYPE.** See Table 4.

**PARATYPES.** USNM 459967, abraded right humerus lacking most of proximal end; half a mile south of Governors Run, Calvert County, Maryland; USNM 459969, proximal end of right humerus lacking internal tuberosity and bicipital crest,

**Table 4** Measurements (mm) of *Pseudocepphus teres* gen. et sp. nov.

Element	<i>Pseudocepphus teres</i>	
	Size	Mean
Humerus		
Greatest length	<b>67.5</b>	67.5
Distal width	<b>10.2+</b> , 10.7, 10.6	10.6
Maximum shaft width	5.6, <b>5.7</b> , 5.7	5.7
Minimum shaft width	3.6, <b>3.6</b> , 3.9	3.7

Measurements from the holotype are in **boldface**.

three-quarters of a mile south of Governors Run, Calvert County, Maryland. Both USNM 459967 and USNM 459969 from upper Calvert Formation, Calvert Beach Member, Shattuck Bed 14.

USNM 23726, left humerus lacking most of proximal end; Chancellors Point, St Mary's County, Maryland, Windmill Point Member, St Mary's Formation; Tortonian, early Late Miocene.

MEASUREMENTS OF PARATYPES. See Table 4.

ETYMOLOGY. From the Latin *teres*, rounded, cylindrical, in reference to the cross-sectional shape of the shaft of the humerus.

DIAGNOSIS. As for the genus.

DESCRIPTION. In most humeral characters *Pseudocepphus* resembles *Miocepphus* and *Alca*, the distinctively terete shaft of the humerus being the main point of difference. In size *Pseudocepphus teres* was slightly larger than *Cephus columba* and considerably larger than *C. grylle*. It was similar in size to *M. bohaskai* but in that species the distal end is rotated dorsally so that the ventral epicondyle does not project beyond the line of the shaft and the ventral surface above the epicondyle is much broader and more flattened. The crista deltopectoralis extends further distally from the tuberculum dorsale than *Miocepphus* or *Alle*. *Pseudocepphus* has the sulcus nervus coracobrachialis as a closed duct, resembling *Alca*.

REMARKS. The holotypical humerus of *Cephus olsoni* Howard, 1982 from the Late Miocene of California shows all of the characters typical of *Cephus* and does not have the alcine features of *Pseudocepphus*. The flattened shaft of the humerus of typical alcids is a specialisation for wing-propelled diving, so the terete condition in *Cephus* and *Pseudocepphus* is presumably the primitive state and not indicative of relationship. *Pseudocepphus* may possibly represent an early offshoot of the Atlantic radiation of Alcinae that includes *Alca* and *Miocepphus*.

### Genus *ALCA* Linnaeus, 1758

*Alca* has a very extensive record in the Atlantic Tertiary, with four species having been recognised in Pliocene deposits. Moreover, Olson & Rasmussen (2001) showed that this number is most probably an underestimate. The species named thus far are extremely similar in morphology and can only be separated by size except when remains of the bill have been found, as in the case of *Alca grandis* (*A. anti-*

*qua* auct.). Two species are here recognised from Miocene deposits.

### *Alca stewarti* Martin *et al.*, 2001 (Fig. 8B–E)

1984 *Australca* sp. Olson: 221.

1985 *Australca* sp. Olson: 185.

2001 *Alca stewarti* Martin *et al.*: 54.

2001 'Alca, undescribed species' Olson & Rasmussen: 278.

2005 *Alca stewarti* Martin *et al.* 2000 [sic]; Dyke & Walker: 236.

MATERIAL EXAMINED. USNM 242238 partial associated skeleton consisting of left coracoid, anterior portion of the sternum with most of the carina, right humerus, right ulna, proximal and distal end of right radius. Claremont Manor Member, Eastover Formation, Westmoreland County, Virginia.

MEASUREMENTS. See Table 5.

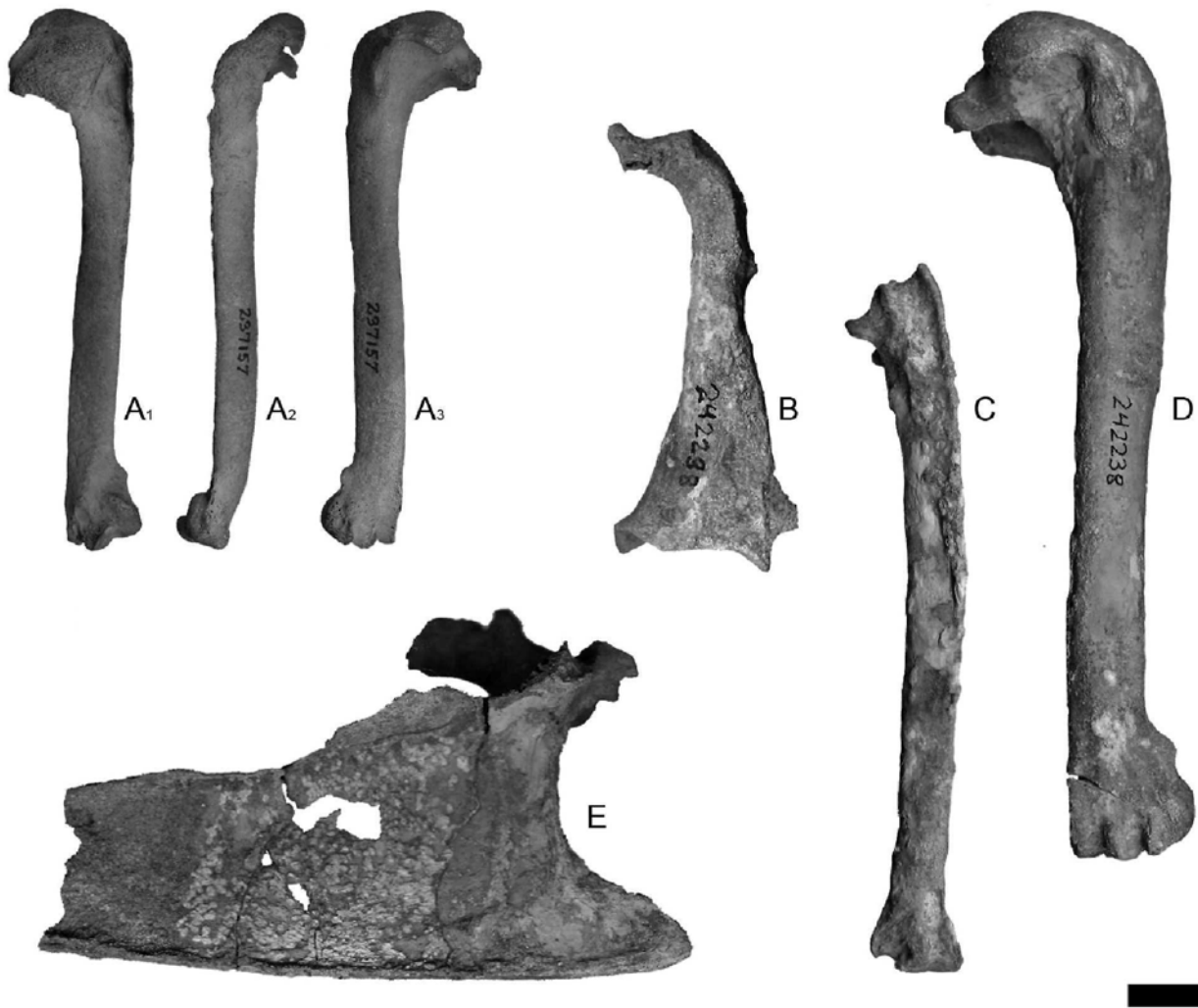
REMARKS. This partial skeleton can be referred to *A. stewarti* because of its very large size and the lack of qualitative characters separating it from *Alca*. It confirms the proportional similarity between *A. stewarti* and *A. torda*, although the former is some 50–60 % larger (see Table 5). The coracoid is relatively small and the ulna relatively long. We do not know whether the small coracoid and rather long ulna is attributable to individual variation or indicates a structural difference between the species. Otherwise, the only noticeable qualitative difference from *A. torda* is the more rounded cross-section of the humeral shaft.

*Alca stewarti* was originally described from ulnae and humeri from the Early Pliocene of Belgium (Martin *et al.* 2001) with additional specimens of the same elements from the type locality being referred later (Dyke & Walker 2005). Olson & Rasmussen (2001) reported additional material as an unnamed species of *Alca* from the Early Pliocene of the Lee Creek Mine. The fossil of *A. stewarti* from the Late Miocene of Virginia described here represents the earliest known occurrence of the species.

This associated skeleton was previously reported on by Olson (1984, 1985) under the genus *Australca*. The specimen was later referred to as an undescribed species of *Alca* by Olson & Rasmussen (2001), whose paper had gone to press before the original description of *A. stewarti* was available, as despite its printed date of 2000, the paper by Martin *et al.* was not actually published until 2001 (Dyke & Walker 2005: 236). Following rule 21.2 of the ICZN (1999), a publication date of 2001 is used here because we have evidence of the description of *A. stewarti* having been published after the date cited in the original publication.

### *Alca cf. torda* Linnaeus, 1758 (Figs 5F, G; 8A)

MATERIAL EXAMINED. USNM 237157, left humerus, Chancellors Point, St Mary's County, Maryland, Windmill Point Member, St Mary's Formation. CMM-V-8, left humerus and CMM-V-3230, right radius, Chesapeake Ranch Estates Beach, Calvert County, Maryland; Little Cove Point Member, St Mary's Formation. USNM 237140, distal two-thirds of right humerus, Westmoreland State Park, Westmoreland County, Virginia, Eastover Formation.



**Figure 8** Pectoral and wing elements of *Alca* cf. *torda* Linnaeus, 1758 (A) and *Alca stewarti* Martin *et al.*, 2001 (B–E). Left humerus of *A.* cf. *torda* (USNM 237157) from St Mary's Formation, St Mary's County, Maryland: anterior (A<sub>1</sub>), dorsal (A<sub>2</sub>) and posterior (A<sub>3</sub>) views. Associated pectoral and wing elements of *A. stewarti* (USNM 242238): left coracoid in ventral view (B); right ulna in ventral view (C); right humerus in posterior view (D); sternum in right lateral view (E). Scale bar = 1 cm.

**MEASUREMENTS.** See Table 5.

**DESCRIPTION.** These fossils belong to a rather large auk the size of *A. torda* with a humerus that is proportionately more similar to *Alca* and *Uria* than to the stout, straight humeri of *Miocepphus*. There are, however, a few slight differences from *A. torda*: the shaft of the humerus seems not quite as flat, the head is larger and the sulcus nervus coracobrachialis is open, although this could perhaps be due to wear. In concurrence with the humeral morphology of *Alca* the shaft has a slight sigmoid curve; the angular processus supracondylaris dorsalis is prominent (broken in CMM-V-8); the distal rim of the caput humeri in distal view is less pointed than in *Uria* and is more similar to *Alca*. As for other species, comparison of this material to others is facilitated by Fig. 5, in which humeri of various species of auks are compared. In the radius there is a well developed longitudinal ridge in the distal end of the sulcus tendinalis, which is similar to modern *Alca* and different from *Miocepphus*. The relative size of the radius in

comparison with both humeri points to very modern wing proportions (see Table 5).

**REMARKS.** Most measurements fall well within the range of modern *A. torda islandica* (Table 5). Numerous specimens of similar size from Early Pliocene deposits in North Carolina were referred to '*Alca* aff. *torda*' by Olson & Rasmussen. More detailed study of all of these specimens is needed to determine whether they really belong to the same lineage as the modern species or represent one or more different lineages.

## DISCUSSION

Our revision greatly increases the diversity of Alcidae in the Miocene of the western North Atlantic based on fossils from Maryland, Virginia and North Carolina. The previously monotypic genus *Miocepphus* is augmented by two species

**Table 5** Measurements (mm) of modern *Alca torda islandica*, *A. cf. torda* from the St Mary's Formation (Maryland) and Eastover Formation (Virginia) and *A. stewarti* from the Eastover Formation (VA).

element	<i>Alca torda islandica</i> (n = 23)		<i>Alca cf. torda</i> Size	<i>Alca stewarti</i> Size
	Range	Mean		
<b>Coracoid</b>				
Greatest length	37.1–40.9	38.4	–	57.3
Medial length	34.4–37.7	35.4	–	56.5
Width sternal facet	12.6–15.2	13.8	–	23.3
<b>Humerus</b>				
Greatest length	69.5–76.8	73.7	70.6, 74.7	111.7
Proximal width	15.3–16.8	15.9	15.3, 16.6	25.1
Distal width	10.3–11.2	10.7	9.9, 10.0	17.0
Maximum shaft width	6.1–7.3	6.6	6.2, 6.8, 7.0	9.8
Minimum shaft width	3.2–3.6	3.4	3.7, 3.7, 3.9	6.1
<b>Ulna</b>				
Greatest length	55.3–61.6	58.6	–	93.3
Proximal diagonal <sup>1</sup>	10.9–12.0	11.5	–	18.3
Proximal width	7.1–7.9	7.4	–	11.9
Minimum shaft width	3.3–3.8	3.5	–	5.8
Distal diagonal <sup>2</sup>	6.6–7.6	7.1	–	10.5
<b>Radius</b>				
Greatest length	54.1–59.7	56.9	55.5	–
Distal width	4.7–5.5	5.2	5.0	–
Maximum shaft width	3.1–3.6	3.3	3.5	–
Minimum shaft width	2.1–2.5	2.3	2.3	–

<sup>1</sup> Length of olecranon–processus cotylaris dorsalis; <sup>2</sup> depth of the condylus dorsalis ulnae.

that are larger than the type species *M. mcclungi*, and one that is much smaller, being among the smallest species of the family. The latter had previously been referred to the living genus *Alle*. A new genus and species, *Pseudocepphus teres*, is described as occupying an uncertain position within the Alcinae. Two Late Miocene species are referred to the modern genus *Alca*.

Based on material described in this paper and elsewhere and on previously published molecular data, we present the following hypothesis of the phylogenetic relationships. Figure 2 proposes a phylogenetic tree of the Alcinae including most fossil and modern species, based on characters given in Table 6. The circled numbers correspond to those in the following text.

The name *Pseudocepphus teres* reflects the primitive rounded shaft of the humerus. The earliest possible common ancestor of *Pseudocepphus* and the oldest species of *Miocepphus* (*M. mcclungi* and *M. bohaskai*) would have to be no younger than Early Miocene (Aquitainian: Fig. 2, no. 1). It is difficult to say whether *Pseudocepphus teres* should be interpreted as being the most primitive of the Alcinae. Most characters it has in common with *Miocepphus* cannot be regarded as synapomorphies because the proportionately stout humerus, the well developed crista deltopectoralis, the straight ventral margin of the humeral shaft extending distally to the processus flexorius and the angular processus supracondylaris dorsalis can all also be found in several other Pacific genera of Alcidae. The only exception is the even width of the sulcus humero- and scapulo-tricipitalis. *Pseudocepphus* might well represent a new offshoot of the basal alcid radiation. *Pseudocepphus* has an apomorphy in the sulcus coracobrachialis, which is closed to a duct, a character that within the Alcinae is only found in *Alca* and *Pinguinus*.

Although Moum *et al.* (1994) estimated the onset of diversification of the Alcidae to have occurred between 20 and 14 Ma, Pereira & Baker (2008) put this event much earlier, in the Paleocene (65–55 Ma). They also dated the split between the Alcinae and other subfamilies to the Oligocene, between 34 and 23 Ma. This is in much better accordance with the occurrence of two species of *Miocepphus* in the Popes Creek Sands, which indicates that the split between *Miocepphus* (Alcinae) and other subfamilies took place before 20 Ma.

Both *M. mcclungi* and *M. bohaskai*, survived into the late Middle Miocene Choptank Formation. *Miocepphus blowi* in the St Mary's Formation and upper Eastover Formation extends the range of the genus into the latest Miocene. Although the stratigraphical context of most fossils from the Lee Creek Mine is uncertain, a Middle Miocene origin for the specimens of *M. mcclungi* from that locality seems likely (Olson & Rasmussen 2001).

The interrelations between the species of *Miocepphus* are uncertain (Fig. 2, no. 2). *Miocepphus mcclungi* and *M. bohaskai* lived contemporaneously, but the relationship of the largest member of the genus, *M. blowi*, to the older species remains an open question. It may have been part of an initial radiation of *Miocepphus* that split off some time before 20 Ma and has remained undetected in earlier deposits, or it may be the Late Miocene derivative of one of its Middle Miocene congeners.

The precise relationships between *Miocepphus*, *Alle* and the closely related *Uria* and *Alca* are also equivocal (Fig. 2, no. 3). Moum *et al.* (1994) and Friesen *et al.* (1996) indicated that *Alca*, *Uria* and *Alle* diverged rapidly and shared a common ancestor at supposedly 10 Ma (Moum *et al.* 1994). Pereira & Baker (2008), however, place this divergence much earlier, not long after the divergence of the Alcinae in the

**Table 6** Humeral characters used for the construction of the phylogeny presented in Fig. 2. The various characters are discussed throughout the text.

Character	Character states	Species											
		<i>Pseudocepphus teres</i>	<i>Miocepphus mcclungi</i>	<i>Miocepphus bohaskai</i>	<i>Miocepphus blowi</i>	<i>Miocepphus mergulellus</i>	<i>Alle alle</i>	<i>Alca cf. torda</i>	<i>Alca torda</i>	<i>Alca stewarti</i>	<i>Pinguinus impennis</i>	<i>Uria aalge</i>	<i>Uria lomvia</i>
Proximal end shaft	0 = not constricted; 1 constricted	0	0	0	0	0	1	0	0	0	0	0	0
Sulcus scapulotricipitalis	0 = wider or equally wide as sulcus humerotricipitalis; 1 = narrower	0	0	0	0	0	0	0	0	0	0	1	1
Processus supracondylaris dorsalis	0 = angular; 1 = reduced	0	0	0	0	0	0	0	0	0	0	1	1
Processus flexorius	0 = in line with ventral margin; 1 = bends dorsally	0	0	0	0	0	0	0	1	1	1	0	0
Sulcus nervus coracobrachialis	0 = open; 1 = closed to duct	1	0	0	0	0	0	?	1	1	1	0	0
Proximal and distal articulations	0 = relatively large; 1 = relatively small	0	0	0	0	0	0	0/1	1	1	1	1	1
Crista deltopectoralis	0 = well developed; 1 = strongly reduced	0	0	0	0	0	0	1	1	1	1	1	1
Shaft	0 = flattened; 1 = extremely flattened	0	0	0	0	0	0	1	1	1	1	1	1
Shaft	0 = rounded; 1 = flattened	0	1	1	1	1	1	1	1	1	1	1	1

Oligocene, which is much more likely given that the genera *Alca* and *Uria* were in existence by the Late Miocene and the assumption would be that the lineage leading to *Alle* was present by then as well. *Alle* shares more characters with *Miocepphus* than with other modern Alcinae. Among others, *Alle* retained the open sulcus nervus coracobrachialis, the stout humeral proportions (Fig. 5), similar wing proportions (Table 2) and a well-developed crista deltopectoralis.

Unfortunately, the age of *M. mergulellus* is problematic. When thought to be on the lineage of modern *Alle alle* it was assumed to be Early Pliocene (Olson & Rasmussen 2001) but now that its affinities are seen to be with *Miocepphus*, which is otherwise known only in the Miocene, we must consider the likelihood that the specimens were derived from the Middle Miocene Pungo River Formation. Rarity and very small size may account for it never yet having been found in any deposits of the Chesapeake Group in Virginia and Maryland. Whether *M. mergulellus* is part of a lineage leading to *Alle alle*, as hypothesised by Olson & Rasmussen (2001) is not known. Its characters do not contradict such a hypothesis.

The presence of *Alca cf. torda* in the St Mary's Formation places the split between *Alca*, *Uria* and *Miocepphus* at a minimum of 10 Ma. This is substantiated by the occurrence of *U. brodkorbi* (Howard, 1981) at about the same time in the early Late Miocene of the Pacific (Becker 1987).

Shared characters of *Alca* and *Uria* that appear to be derived relative to *Miocepphus* are the reduction of the humeral crista deltopectoralis, the proportionately more slender humerus and the proportionately shorter ulna with a longer, more pointed olecranon. Related to these adaptations for improved diving abilities are changes in coracoid morphology in which the facies articularis clavicularis forms an anteriorly pointed extension. We note that these characters could be the result of convergent evolution rather than being synapomorphies.

The divergence between *Alca* and *Uria* can also be discerned in humeral characters: *Alca* differs from *Uria* in having the sulcus nervus coracobrachialis as a closed duct, the ventral margin of the distal articulation bending slightly but distinctively dorsad. The species identified herein as *Alca cf. torda* appears to represent a part of this lineage. *Uria* diverged from its common ancestor with *Alca* by a reduction of the processus supracondylaris dorsalis, the widening of the sulcus humerotricipitalis and the extension of the flattening of the proximal dorsal margin of the humeral shaft further distad.

The spread of an auk related to *Miocepphus* or *Alca* to the Pacific in the Late Miocene is suggested by the report of *Alca* sp. in the Clarendonian (or possibly older, see Becker 1987) of Laguna Hills, California (Howard 1968), although this was based only on a poorly preserved coracoid and a humerus lacking the proximal end. Howard (1981) noted that the humerus most closely resembled *Alca* in the tricipital grooves and the curvature of the anconal (= posterior) contour of the shaft near the distal end, but is shorter and stouter than in *A. torda*, characters strongly reminiscent of *Miocepphus*. The split between *Uria* and *Alca* at 10 Ma (Fig. 2, no. 3) may have occurred earlier. Thus, 10 Ma is a minimum age.

The radiation of *Alca*, of which no fewer than four species were reported from the Early Pliocene of the Lee Creek Mine (Olson & Rasmussen 2001), can be placed in the Tortonian because both the smallest (*A. cf. torda*) and largest (*A. stewarti*) were present by the early Messinian (Fig. 2, no. 4), although the onset of this radiation was probably earlier.

*Miocepphus*, in the form of *M. blowi*, survived to be contemporaneous with *Alca* during the Late Miocene. Possibly the success of *Alca* and *Uria* was fuelled by the new or more accessible food resources that became available because of their improved diving abilities, as both are more specialised than *Miocepphus*. Because of its size, *M. blowi* may have



closely resembled the common ancestor of *Uria* and *Alca*. As mentioned, the uncertain relationships of *Alle* may mean that the placement of *Alle alle* and *M. blowi* in Fig. 2 should, in fact, be reversed, putting the origin of *Alle* deep within the *Miocepphus* lineage.

The data presented here provide a few implications for the timing of divergences within the Alcidae. Accepting the refutation of Eocene records of Alcidae (Olson 1985), the oldest supposed auk is *Petalca austriaca*, which was described from the Late Oligocene of Austria by Mlikovsky (1987). Examination by Olson of digital photographs of the holotype slab and counterslab (NMW 1980/25) strongly suggested that this taxon does not belong in the Alcidae and is more likely to belong to the Gaviidae. Further comparisons of the type material by U. Göhlich and C. Mourer-Chauviré confirmed that the specimen was incorrectly assigned to the Alcidae so that we give it no further consideration.

The occurrence of *M. mclungi* and *M. bohaskai* in the Lower Miocene provide the earliest occurrences of auks to date, as no certain alcid fossils predating the Miocene have been recognised so far. Because *Miocepphus* clearly pertains to the Alcinæ, a split between the Alcinæ and other lineages must have taken place before 20 Ma.

## CONCLUSIONS

The notion of a depauperate alcid fauna in the Miocene of the Atlantic can no longer be maintained, as it is now evident that the radiation of *Alca* in the Early Pliocene was preceded by a diverse fauna belonging to a completely extinct radiation of Alcidae in the Early to early Late Miocene. Furthermore, the great radiation of *Alca* in the Early Pliocene, as evident at the Lee Creek Mine, probably had a history extending back into the Late Miocene. Unfortunately, alcid material from Late Miocene deposits is very scarce in comparison to material from Middle Miocene and Early Pliocene deposits. We can only await the discovery of more material to find out more about the exact timing of the extinction of *Miocepphus* but its contemporaneity with *Alca* cf. *torda* may point to a gradual rather than a sudden change in faunal composition.

The radiation of *Alca* in the Late Miocene, and the modern aspect of the alcid fauna of the Early Pliocene presents a strong parallel with the evolution of whales in the Neogene of the Atlantic. The Middle and the early Late Miocene were dominated by extinct taxa whereas modern Mysticeti (baleen whales) first appear in the Late Miocene. In the Pliocene the cetacean fauna is dominated by modern taxa and a rapid onset of a high diversity of Delphinidae (oceanic dolphins). The Late Miocene evolution of Mysticeti and radiation within Delphinidae is coincident with the establishment of a cold bottom current in the Atlantic as a result of the formation of the west Antarctic ice sheet and the closure of the Tethys, which limited the influx of warm water from the Mediterranean. The expected steeper temperature gradients in the North Atlantic may have triggered radiation events within various groups of marine life (Whitmore 1994). It may be hypothesised that the radiation of the genus *Alca* is linked to these events.

The Miocene fossil record of Alcids in the north Pacific shares some conspicuous similarities to the Atlantic

record. The first appearance of auks in the Pacific lies in the Middle Miocene, somewhat postdating the first Atlantic (Early Miocene) occurrence of auks. Modern genera (*Aethia*, *Cerorhinca* and *Uria*) first appear around the early Late Miocene following the establishment of a cold upwelling system near the Californian coast (Warheit 1992).

We face a large gap between the first alcid fossils (Early Miocene) and the presumed onset of alcid evolution in the Paleocene and the gradual establishment of different genera during the Eocene and Oligocene (Pereira & Baker 2008). The sudden appearance of modern genera in the Late Miocene Pacific and Atlantic may be artificial rather than reflecting radiation events. We suspect the absence of a better fossil record for auks may be due to the general lack of fossil birds from marine deposits in more northern areas where alcids may have evolved and spread between oceans. The reiterated idea of a subtropical or temperate origin of Alcidae (e.g. Bédard 1985; Pereira & Baker 2008) and the idea of early alcids spreading through southern routes appears contrary to the adaptive advantage of wing propelled diving (Ainley 1977), which is highest in polar or subpolar regions. Revision of fossils of other groups of pelagic birds, such as Sulidae or Pelagornithidae, may eventually provide further understanding of the faunal turnover from the archaic Middle Miocene to the modern fauna of the Pliocene.

## ACKNOWLEDGEMENTS

For assistance with fossils we are indebted to Mark Florence, Department of Paleobiology, National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA and to Stephen Godfrey, Calvert Marine Museum (CMM), Solomons, Maryland, USA. Many collectors donated material that was studied for this paper. Special thanks in this respect are owed to W. L. Ashby, E. Ashby, D. J. Bohaska and N. L. Riker for numerous donations. Further thanks go to J. Bell, W. Blow, D. Carver, R. Childers, W. Counterman, D. Domning, E. Eshelman, R. Eshelman, G. Fonger, R. Foos, W. F. Foshag, C. Gasbarre, P. Heater, J. M. Hooper, R. M. A. Ison, J. Kaltenbach, A. C. Myrick Jr, A. Norden, H. Philyaw, L. M. Schoonover, M. Tynes, R. E. Weems, D. Williams and J. Westgate. For lending casts of the holotype of *Uria brodkorbi* we thank D. W. Steadman and R. Hulbert, Florida Museum of Natural History, Gainesville, Florida, USA (UF). N. A. Smith kindly supplied photographs of the specimen as well. For kindly supplying photographs of the holotype of *Petalca austriaca* and for reporting the results of her examination of the specimen with C. Mourer-Chauviré we thank U. Göhlich, Naturhistorisches Museum Wien, Austria (NMW). This study was made possible by grants awarded by the Molengraaff fund and the A. M. Buytendijk fund. The article greatly benefited from help and comments by J. de Vos of the National Museum of Natural History (Naturalis), Leiden, the Netherlands, T. Heijerman of the department of Biosystematics of Wageningen University, the Netherlands and D. Bohaska, Smithsonian Institution, Washington, DC, USA. For assistance in the collections of the Groningen Institute for Archaeology, we thank W. Prummel, and likewise we acknowledge the help of K. Moeliker and H. van de Es of the Natuurhistorisch Museum Rotterdam.

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