

SHORT COMMUNICATION

FIRST ATLANTIC RECORD OF THE PUFFIN *CERORHINCA* (AVES, ALCIDAE) FROM THE PLIOCENE OF NORTH CAROLINA

N. ADAM SMITH,^{*1} STORRS L. OLSON,² and JULIA A. CLARKE^{1,3}; ¹North Carolina State University, Department of Marine, Earth and Atmospheric Sciences, Campus Box 8208, Raleigh, North Carolina 27695–8208 U.S.A., adam_smith@ncsu.edu; ²National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia 20560–0131 U.S.A., olson@si.edu; ³North Carolina Museum of Natural Sciences, 11 West Jones St., Raleigh, North Carolina 27601–1029 U.S.A., julia_clarke@ncsu.edu.

The Alcidae are pelagic, wing-propelled diving birds belonging to the order Charadriiformes and are considered to be the northern hemispherical equivalent of penguins (Storer, 1960). The Alcidae comprises 11 extant genera and 23 species of Holarctic distribution (del Hoyo et al., 1996). Fraterculini (puffins), consisting of the *Cerorhinca* and *Fratercula* has been supported as monophyletic (Strauch, 1985; Sibley and Ahlquist, 1990; Moum et al., 1994; Friesen et al., 1996) and has been proposed to be the sister-group to all other alcids (Strauch, 1985; Chandler, 1990b). Extant diversity of puffins includes three Pacific species (*Fratercula corniculata*, *Fratercula cirrhata*, *C. monocerata*) and a single species in the Atlantic (*Fratercula arctica*).

The only extant representative of *Cerorhinca*, the Rhinoceros Auklet *C. monocerata*, and all previously known fossils are from the Pacific basin (Olson, 1985d). Three fossil species of *Cerorhinca*, as well as additional material tentatively referred to *Cerorhinca* (Table 2), are known from the middle Miocene to late Pliocene of southern California and northern Mexico.

Among Pliocene material recovered from the PCS Phosphate mine in Aurora, North Carolina (Fig. 1), Olson and Rasmussen (2001) recognized remains of two species of *Fratercula*, the Atlantic Puffin *F. aff. arctica* and the Tufted Puffin *F. aff. cirrhata*. Recent re-examination of the material assigned to *F. aff. cirrhata* indicated that this material was a composite series of two distinct taxa. One complete and two proximal humeri are instead referable to *Cerorhinca*, thus providing the first record of the genus from the Atlantic basin. The remaining 29 specimens were confirmed as *F. cf. cirrhata*.

Materials and Methods—In the description, the English equivalents of the Latin osteological nomenclature of Baumel and Witmer (1993) are used. With the exception of the terms anterior and posterior substituted for cranial and caudal, respectively, the terms used for the anatomical orientation of a bird are those used by Clark (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.

Institutional Abbreviations—NCSM, North Carolina Museum of Natural Sciences, Raleigh, North Carolina; SDSNH, San Diego Natural History Museum, San Diego, California; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Geologic Setting—The PCS Phosphate Mine (formerly known as the Lee Creek Mine; Olson and Rasmussen, 2001) is located along the south shore of the Pamlico River and exposes

an unconformable sequence of middle Miocene and early Pliocene sediments, conformably overlain by Pleistocene aged sediments (Gibson, 1983). An age of 4.4 ± 0.2 Ma (early Pliocene) has been assigned to the Yorktown Fm. based on K/Ar dating of the *Orionina vaughani* assemblage zone, and correlated with planktonic foraminifera Zone N19 (Hazel, 1983). No microfossils are preserved in association with the new *Cerorhinca* remains, which could be used to precisely date the specimens. However, the preservation of the *Cerorhinca* fossils closely matches that of twelve other avian specimens (e.g., USNM 178084, 178150, 193334) referred to the Pliocene Yorktown Fm.

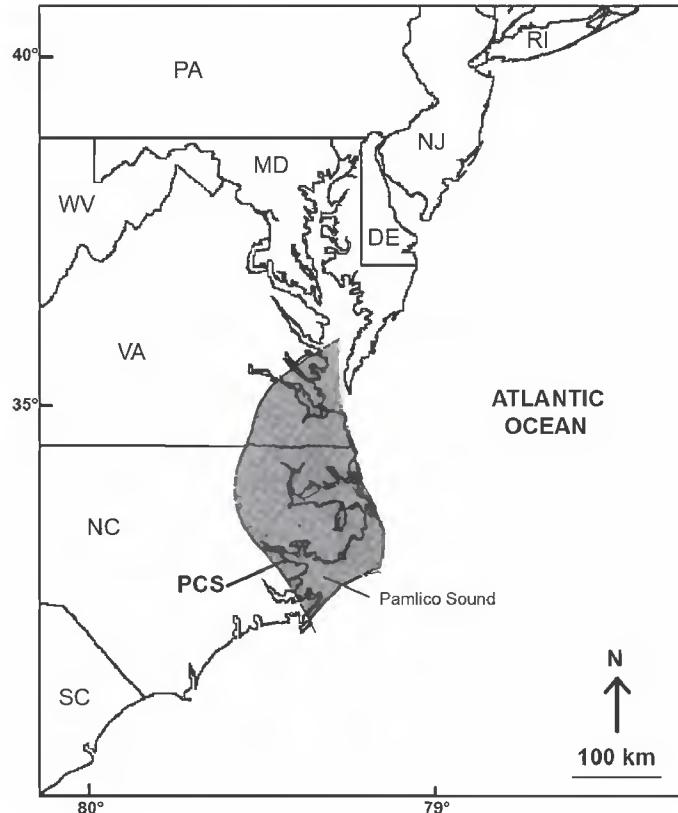


FIGURE 1. Map of eastern USA indicating the locality of PCS Phosphate mine near Aurora, NC where the specimens were collected. Shaded area denotes the subsurface extent of Unit 1 of the Yorktown Formation. (Altered from Gibson, 1983).

*Corresponding author.

on the basis of the foraminiferal assemblage derived from matrix associated with those specimens (Gibson, 1975, unpubl. data). Avian fossils from the Pungo River Fm. are also often characterized by a black phosphatic patina, which is not present in the *Cerorhinca* specimens reported here. The absence of *Fratercula* and *Cerorhinca* in coeval Miocene sediments of the Calvert Formation in Maryland, which also contain fossil alcids (Olson and Rasmussen, 2001), is also consistent with a Pliocene Yorktown Fm. provenance. However, because the *Cerorhinca* remains were not collected in-situ, the possibility that they are from the older, middle Miocene, Pungo River Fm. cannot be entirely ruled out.

SYSTEMATIC PALEONTOLOGY

AVES LINNAEUS, 1758

CHARADRIIFORMES HUXLEY, 1867

ALCIDAE VIGORS, 1825

FRATERCULINI STORER, 1960

CERORHINCA BONAPARTE, 1831

CERORHINCA sp.

Referred Material—USNM 257520, complete left humerus (Fig. 2; Table 1); USNM 459395, proximal end of right humerus (Fig. 3; Table 1); USNM 193051, proximal end of right humerus (Fig. 3; Table 1).

Comparative Material—*Cerorhinca monocerata* (USNM: 557613, 557614, 561468, 620641, 620643); *Fratercula arctica* (USNM: 18055, 18057, 18058, 224189, 621321); *Fratercula cirrhata* (USNM: 19449, 488748; NCSM: 17823, 18099, 18100); *Fratercula corniculata* (USNM: 499961, 499964; NCSM: 17835, 18083, 18388).

Differential Diagnosis—*Cerorhinca* is included in Fraterculini, a subclade within Alcidae (Storer, 1960), the monophyly of which has been supported by analyses of molecular (Sibley and Ahlquist, 1990; Moum et al., 1994; Friesen et al., 1996; Moum et al., 2002) and morphological data (Strauch, 1985; Chandler, 1990b). The humeri of the Fraterculini differ from other alcids in having a well-excavated second pneumatic fossa (Strauch, 1978, 1985; Chandler, 1990a), a condition similar to that in the nearest outgroup taxa of Alcidae (e.g., Larinae, Sterninae; Strauch, 1978; Sibley and Ahlquist, 1990), in which the second pneumatic fossa is extensively excavated. However, the condition observed in Fraterculini differs from that in the nearest outgroup taxa, in which the second pneumatic fossa is separated from the dorsal tubercle by the margo caudalis (Baumel and Witmer, 1993). In Fraterculini, the margo caudalis is absent, and the dorsal tubercle is developed as a distally extending scar (crista m. supracoracoidei; Baumel and Witmer, 1993:pg. 98), which is bordered ventrally by the steeply angled dorsal margin of the second pneumatic fossa. *Cerorhinca* differs from *Fratercula* on the basis of three distinguishing characters of the humerus: (1) the pneumatic fossa (fossa pneumotricipitalis; Baumel & Witmer, 1993) of *Cerorhinca* and *Fratercula* is divided into two separate fossae,

the second or dorsal of which is the site of origination of the dorsal head of the humerotriceps muscle (Baumel and Witmer, 1993) and is considerably less excavated in *Cerorhinca* than in *Fratercula*; (2) depression on the distal surface of the ventral tubercle deeper than *Fratercula* (Olson and Rasmussen, 2001); (3) in ventral view, the lateral margin of the ventral tubercle of *Cerorhinca* is characterized by two distinct concavities, whereas in *Fratercula*, this margin is a single concave curvature. The species level relationships among the three named extinct and one extant Pacific species of *Cerorhinca* and that represented by the Atlantic fossils will be evaluated in a broader taxonomic assessment of the validity of previously named Fraterculini species and of the phylogenetic relationships among all Alcidae species including all of the Fraterculini, (Smith, in prep.). Only the holotype specimens of the two extinct species *C. reai* and *C. minor* (Table 2) are directly comparable to the new *Cerorhinca* sp. humeri described here. *Cerorhinca dubia* is known only from associated leg elements and material identified as *Cerorhinca* sp. of Howard (1968) and Chandler (1990a) are ulnae.

DESCRIPTION

The fossils referred to *Cerorhinca* differ only slightly in morphology (Fig. 2) and size (Table 1) from specimens of the extant species *C. monocerata*. In the complete humerus USNM 257520 the proximal end of the dorsal supracondylar process contacts the shaft at a ~120° angle, whereas in *C. monocerata*, the angle is more acute at ~90°. The dorsal condyle of the fossil specimen is more rounded dorsally than that of *C. monocerata*. The ventral side of the ventral condyle of USNM 257520 is more flattened than the condition observed in *C. monocerata*. The size range observed among the new remains (Table 1) is within the range of statistically determined size variation observed in modern alcids (Bedard, 1985; Burness and Montevercchi, 1992).

All three specimens display the anteroposteriorly flattened humeral shafts characteristic of many wing-propelled divers and of all Alcidae. In posterior view the proximal ends of the new *Cerorhinca* humeri are characterized by a proximoventrally broadening dorsal tubercle (i.e., crista m. supracoracoidei), although the proximal end of the dorsal tubercle of *Cerorhinca* is less ventrally expanded than that of *F. cirrhata* (Fig 2). In contrast to other alcids (e.g., *Alca*, *Uria*) the pneumatic fossa is a deep excavation with a narrow distal margin and a broader ventral margin that merges with the base of the ventral tubercle. The brachial depression is a distinct proximally narrowing scar that extends proximally only slightly past the proximal extent of the dorsal supracondylar process.

DISCUSSION

The puffins (Fraterculini) are thought to have originated in the Pacific primarily because of their greater diversity there (Storer, 1960; Olson, 1985d). Their fossil record in the Pacific extends at

TABLE 1. Measurements of Puffin humeri (in mm).

Taxa	Specimen #	Gl	Bp	Dip	Sc	Bd	Dd
<i>Cerorhinca</i> sp.*	USNM 257520	67.2	14.9	14.1	5.7	10.5	7.5
<i>Cerorhinca</i> sp.*	USNM 459395	—	15.8	15.3	—	—	—
<i>Cerorhinca</i> sp.*	USNM 193051	—	15.6	15.4	—	—	—
<i>Cerorhinca monocerata</i>	USNM 620643	70.0	14.4	14.3	5.7	10.7	7.4
<i>Fratercula cirrhata</i>	NCSM 177823	77.0	16.0	15.8	6.0	11.5	8.3
<i>Fratercula arctica</i>	USNM 292346	67.2	14.0	13.1	4.8	9.8	6.8
<i>Fratercula corniculata</i>	NCSM 18388	69.9	15.0	14.9	5.3	10.7	7.7

Measurements according to Von den Driesch, 1976.

*Denotes fossil specimens.

Abbreviations: **Bd**, breadth of the distal end; **Bp**, breadth of proximal end; **Dd**, distal diagonal; **Dip**, diagonal of proximal end; **Gl**, greatest length; **Sc**, smallest breadth of corpus (shaft).

TABLE 2. Published specimens referred to *Cerorhinca*.

Taxa	Material	Provenience	Age	Reference
<i>Cerorhinca dubia</i>	associated legs	California	Middle Miocene	Miller, 1925
<i>Cerorhinca</i> sp.	proximal ulna	California	Late Miocene	Howard, 1968
<i>Cerorhinca minor</i>	wing elements	Mexico	Middle Pliocene	Howard, 1971
<i>Cerorhinca reai</i>	wing elements	California	Late Pliocene	Chandler, 1990a
<i>Cerorhinca</i> sp.	right ulna	California	Late Pliocene	Chandler, 1990a

least as far back as the middle Miocene (Miller, 1925), whereas in the Atlantic there are no records from the Miocene (Olson and Rasmussen, 2001). The occurrence of *Cerorhinca* in the Atlantic documented here, in addition to previously reported Fraterculini taxa (Miller, 1925; Howard, 1968, 1971; Chandler, 1990a) indicates that the diversity of puffins was as great in the Atlantic in the early Pliocene as it is in the Pacific today. This diversity has been proposed to have been achieved rapidly during the mid Miocene to early Pliocene, presumably indicating an influx of three separate lineages of puffins (*Cerorhinca* plus two *Fratercula*) from the Pacific through a northern passage between the oceans (Olson and Rasmussen, 2001), although a southern route of dispersal cannot be ruled out as the Panamanian Seaway remained open until ~2.5 Ma (Warheit, 2002). Just as climate changes in the middle Miocene (~11–16 mya) are proposed to have influenced the initial diversification of alcids (Warheit, 2002), major oceanographic changes in the late Pliocene (~2.9

Ma) due in part to closure of the Panamanian Seaway and the onset of severe glacial cycles in the North Atlantic (Bartoli et al., 2005), the smallest of the world's ocean basins (Briggs, 1970), also may have played a role in the evolutionary history of the Alcidae. Factors such as changing salinities, temperatures, current patterns, and the faunal turnover of pelagic invertebrates associated with these factors, caused the Atlantic to become a much less hospitable place for many organisms (Bartoli et al., 2005). The drop in sea level in southern parts of the North Atlantic, estimated at ~85 m by Krantz (1991), would have resulted in a regression of the shoreline many kilometers away from the once near-shore breeding grounds of puffins. Additionally, the formation of ice on more northern shores associated with the onset of glaciation would have obstructed the traditional breeding grounds of puffins along the Atlantic coast (Olson and Rasmussen, 2001). Although extant Pacific *Fratercula* and *C. monocerata* both forage for fish and small invertebrates at similar depths, the range of *C. monocerata* does not extend as far north as that of *F. corniculata* or *F. cirrhata*, and extends further south (del Hoyo et al., 1996). Extreme climate changes associated with the final closing of the Panamanian Isthmus led to dramatic faunal shifts to the south during the middle Pliocene (Bartoli et al., 2005). These climate changes, linked with a preference for warmer waters, may have contributed to the extinction of *Cerorhinca* in the Atlantic.

Extinctions and retractions in range were also rampant during the Pleistocene and overall diversity of seabirds in general and alcids in particular was greatly reduced (Emslie, 1998; Olson and Rasmussen, 2001). To the growing list of North Atlantic disappearances recognized by ornithologists, we can now add *Cerorhinca*. The biogeographical implications of this discovery will



FIGURE 2. Comparison of Fraterculini humeri in posterior view. A, *Cerorhinca* sp. (USNM 257520); B, *Cerorhinca monocerata* (USNM 620643); C, *Fratercula cirrhata* (USNM 459395). **Anatomical Abbreviations:** dt, dorsal tubercle; pf1, pneumatic fossa one; pf2, pneumatic fossa two.

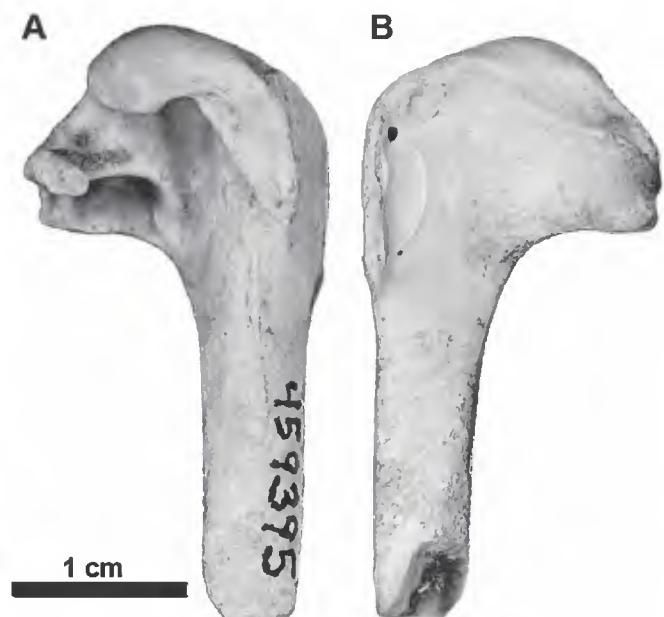


FIGURE 3. Proximal ends of right humeri. A, posterior view (USNM 459395); B, anterior view (USNM 193051).

become clearer only after the phylogenetic relationships among all extant and extinct Fraterculini species have been resolved.

Acknowledgments—We thank V. Schneider and B. Browning for access to comparative material at the NCSM, M. Florence and J. Dean for collections assistance at USNM, PCS Phosphate Mine for allowing continued collection of fossils from this important site, and dedicated amateurs such as P.J. Harmatuck and R. Douglas who have donated hundreds of specimens for study. A grant from the Smithsonian Institution Office of Fellowships to N. Adam Smith is gratefully acknowledged.

LITERATURE CITED

- Bartoli, G., M. Sarnthein, M. Weinelt, H. Erlenkeuser, D. Garbe-Schonberg, and D. W. Lea. 2005. Final closure of Panama and the onset of northern hemisphere glaciation. *Earth and Planetary Science Letters* 237:33–44.
- Baumel, J. J., and L. M. Witmer. 1993. *Osteologia*; pp. 45–132 in J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge (eds.), *Handbook of avian anatomy: nomina anatomica avium*, 2nd ed. Publications of the Nuttall Ornithological Club 23: 45–132.
- Bedard, J. 1985. Evolution and characteristics of the Atlantic Alcidae; pp. 1–53 in Nettleship and Birkhead (eds.), *The Atlantic Alcidae*. Academic Press, London.
- Bonaparte, C. L. 1831. in R. Jameson (ed.) *American Ornithology*, Edinburgh, Constable, 4v.
- Briggs, J. C. 1970. A faunal history of the North Atlantic Ocean. *Systematic Zoology* 19:19–34.
- Brodkorb, P. 1967. Catalogue of fossil birds: Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). *Bulletin of the Florida State Museum, Biological Sciences* 11:99–220.
- Burness, G. P., and W. A. Monteverchi. 1992. Oceanographic-related variation in the bone sizes of Great Auks. *Polar Biology* 11:545–551.
- Chandler, R. M. 1990a. Fossil birds of the San Diego Formation, late Pliocene, Blanca, San Diego County California, II. pp. 73–161 in *Recent Advances in the Study of Neogene Fossil Birds*, Ornithological Monographs 44.
- Chandler, R. M. 1990b. Phylogenetic analysis of the alcids. Ph.D. dissertation, University of Kansas, Lawrence Kansas 133 pp. (unpublished).
- Clark, G. A., Jr. 1993. *Termini situm et directionem partium corporis indicantes*. pp. 1–5 in J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge (eds.), *Handbook of avian anatomy: nomina anatomica avium*, 2nd ed. Cambridge, MA: Nuttall Ornithological Club.
- del Hoyo, J., et al. (eds.) 1996. *Handbook of the Birds of the World*. Vol 3. Hoatzins to Auks. Lynx Edicions, Barcelona, Spain. 821 pp.
- Emslie, S. D. 1998. Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida peninsula. *Ornithological Monographs* 50:1I3 pp.
- Friesen, V., A. Baker, and J. Piatt. 1996. Phylogenetic relationships within the Alcidae (Charadriiformes: Aves) inferred from total molecular evidence. *Molecular Biology and Evolution* 13:359–367.
- Gibson, T. G. 1983. Stratigraphy of Miocene through lower Pleistocene strata of the United States central Atlantic coastal plain. *Smithsonian Contributions to Paleobiology* 53:35–80.
- Hazel, J. E. 1983. Age and correlation of the Yorktown (Pliocene) and Croatan (Pliocene and Pleistocene) Formations at the Lee Creek Mine. *Smithsonian Contributions to Paleobiology* 53:81–199.
- Howard, H. 1968. Tertiary birds from Laguna Hills, Orange County, California. *Los Angeles County Museum Contributions to Science* 142:1–21.
- Howard, H. 1971. Pliocene avian remains from Baja California. *Los Angeles County Museum Contributions to Science* 217:1–17.
- Huxley, T. 1867. On the classification of birds: and on the taxonomic value of the modifications of certain of the cranial bones observable in the class. *Proceedings of the Zoological Society of London* x: 415–472.
- Krantz, D. E. 1991. A chronology of Pliocene sea-level fluctuations: the U.S. middle Atlantic coastal plain record. *Quaternary Science Review* 10:163–174.
- Linnaeus, C. 1758. *Systema Naturae*. Edition X. *Systema naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*.
- Miller, L. 1925. Avian remains from the Miocene of Lompoc California. *Carnegie Institution Washington, Contributions to Paleontology* 349:107–117.
- Moen, S. M. 1991. Morphologic and genetic variation among breeding colonies of the Atlantic Puffin (*Fratercula arctica*). *Auk* 108: 755–763.
- Moum, T., S. Johansen, K. E. Erikstad, and J. F. Piatt. 1994. Phylogeny and evolution of the auks (subfamily Alcinae) based on mitochondrial DNA sequences. *Proceedings of the National Academy of Sciences* 91:7912–7916.
- Olson, S. L. 1985d. The fossil record of birds. pp. 79–252 in D.S. Farmer and J. King (eds.), *Avian Biology* 8, Orlando, Florida: Academic Press.
- Olson, S. L. and P. Rasmussen. 2001. Miocene and Pliocene birds from the Lee Creek Mine, North Carolina. *Smithsonian Contributions to Paleobiology* 90:233–365.
- Shufeldt, R. W. 1901. On the osteology and systematic position of the Alcae. *American Naturalist* 35:541–551.
- Sibley C. G. and J. E. Ahlquist. 1990. *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. Yale University Press, New Haven, Connecticut. 976 pp.
- Storer, R. W. 1960. Evolution in the diving birds, pp. 694–707 in *Proceedings of the Twelfth International Ornithological Congress*.
- Strauch, J. 1978. The Phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. *Transactions of the Zoological Society of London* 34:263–345.
- Strauch, J. G. 1985. The phylogeny of the Alcidae. *Auk* 102:520–539.
- Warheit, K. I. 2002. The seabird fossil record and the role of paleontology in understanding seabird community structure, pp. 17–55 in E. A. Schrieber and J. Burger (eds.), *Biology of Marine Birds*. CRC Press, Boca Raton, Florida.
- Vigors, N. 1825. Observations on the natural affinities that connect the families of birds. *Transactions of the Linnaean Society of London* I:4:395–517.
- Von den Driesch, A. 1976. A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bulletin* 1:137 pp.

Submitted January 18, 2007, accepted May 20, 2007.