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A GREAT AUK, *PINGUINIS*, FROM THE PLIOCENE OF NORTH CAROLINA (AVES: ALCIDAE)

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The Great Auk, *Pinguinis impennis*, is renowned chiefly for the sad history of its extinction, the last known individuals having been killed in 1844 (Greenway, 1958). Of the Recent species of Alcidae, *P. impennis* was the largest and the only one that was flightless. In historic times it is known to have bred on certain North Atlantic islands off Newfoundland, Iceland, and Britain, and to have wintered south to New England in the western Atlantic and to Spain in the eastern Atlantic. Remains indicating a more extensive range in the past have been found in middens in Florida and in the Pleistocene of Italy, as well as at additional localities between these sites and the known historic range (Brodkorb, 1967).

Although a number of authors have considered the Great Auk to be congeneric with the modern Razorbill, Alca torda, I agree with Salomonsen (1944) and others that impennis should be separated under the genus Pinguinis. The great modifications seen in the wing of Pinguinis are not the result of neoteny, as seen in many other flightless birds (Olson, 1973), or of "degeneration," as suggested by Greenway (1958:271), who was under the impression that the keel of the sternum of Pinguinis was as reduced as the wing. Instead, these modifications represent highly derived specializations for wing-propelled diving.

Until now there has been no fossil record of *Pinguinis* other than the Pleistocene occurrences of *P. impennis*. This lack has been remedied by the discovery, among the thousands of fossil alcid bones recovered from a phosphate mine in North Carolina (Olson and Wetmore, in press), of six specimens that pertain to an undescribed species recognizable as belonging to the genus *Pinguinis* by its short, heavy ulna. For comparison I have had the extremely large series of disassociated bones of *P. impennis* collected by Lucas (1890) on Funk Island, Newfoundland.

Pinguinis alfrednewtoni, new species Figs. 1-3

Holotype.—Right ulna lacking only the most distal portions of the condyles, National Museum of Natural History vertebrate paleontological collections, USNM 193334.

Locality.—Spoil piles at the Texasgulf phosphate mine at Lee Creek, south side of Pamlico River, near Aurora, Beaufort County, North Carolina (35°23'N; 76°47'30"W); collected in October 1973 by Roger C. Wood, et al. Horizon.—Lower part of Yorktown Formation, Chesapeake Group, Lower

Pliocenc. Strata of both Middle Miocene (Pungo River Formation) and Lower Pliocene (Yorktown Formation) age contribute fossils to the spoil at the Lee Creek mine. Most of the vertebrates are from the Yorktown Formation and the preservation of the types of *P. alfrednewtoni* is similar to that of other specimens from this level. Matrix samples from USNM 193334 and 179226 were analyzed by Dr. Thomas G. Gibson, who, on the basis of the foraminiferan fauna and sedimentary characteristics, assigned them to the lower part of the Yorktown Formation. The consensus developed elsewhere is that the Yorktown Formation is Lower Pliocene in age (Ray, in press).

Measurements of holotype.—Total length as preserved 54.1 mm (the complete length would probably not have been more than a millimeter greater), depth of proximal end 14.9, width of proximal end 5.1, greatest diameter of internal cotyla, 7.0, width of shaft at midpoint 5.3, depth of shaft at midpoint 8.3, width of distal end 6.9, depth of distal end 10.3.

Paratypes.—Distal half of left humerus USNM 179226; very worn distal third of right humerus USNM 192497; left femur abraded at the ends USNM 206362; worn right tarsometatarsus lacking the trochleae USNM 179277; very worn distal fourth of right tibiotarsus USNM 193101. All of these specimens were collected at the same locality as the holotype on various visits by USNM staff or collaborators.

Measurements of paratypes.—Humerus 179226; greatest diameter of distal end 16.7 mm, depth through internal condyle 12.7, distance from proximal end of ectepicondylar prominence to distal end of internal condyle 15.9, least width of shaft 10.3, least depth of shaft 5.4. Femur 206362; overall length 71 mm, width of proximal end 14, width of shaft at midpoint 6.4, depth of shaft at midpoint 7.4. Tibiotarsus 193101; width of distal end c. 12.5, depth through internal condyle c. 11.6. Tarsometatarsus 179277; width of proximal end 13.3, depth of proximal end 11.8, distance from proximal margin of intercotylar prominence to distal foramen 38.9, least width of shaft 6.5, least depth of shaft 5.2.

Etymology.—This species is dedicated to the memory of Alfred Newton (1829–1907). Newton was one of the principal founders of the British Ornithologists' Union and the author of A Dictionary of Birds (1896), a paragon of erudition that was said by Coues (1897) to be "by far and away the best book ever written about birds." Little has happened in the past 80 years to render this appraisal any less valid. Newton had a particular interest in the Great Auk and, even though quite lame, visited a number of its rugged former breeding places. He wrote several papers on the bird and was engaged in further work on the subject at the time of his death (Hudleston, 1909; Wollaston, 1921). It seems especially appropriate that the present species should bear his name.

Diagnosis and description.—Pinguinis alfrednewtoni is separable from

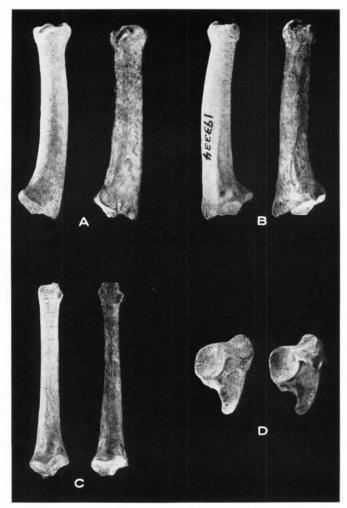


Fig. 1. Right ulnae of *Pinguinis. P. alfrednewtoni* holotype (USNM 193334) on left in each pair, *P. impennis* on right: A, External view; B, Internal view; C, Palmar view; D, Proximal view. A–C natural size; D $1.5\times$.

the Mancallinae by its proportionately longer ulna (75% of femur length vs. less than 55% in *Mancalla*) and by the characters of the humerus enumerated by Howard (1966:3). Within the Alcinae it is referable to *Pinguinis* by having the ulna shorter than the femur. The six fossil specimens all fall within the range of size variation of *P. impennis*.

The ulna of P. alfrednewtoni differs from that of P. impennis in having

the shaft more curved and decidedly less flattened, with the trailing edge more rounded. In proximal view the internal cotyla is wider and more rounded; the external cotyla is wider but not as deep as in P. impennis and does not extend as far palmarly; the olecranon is thicker, protrudes more anconally, does not curve medially at the tip, and is less sharply demarcated from the cotylae than in P. impennis by virtue of having the groove between it and the external cotyla much shallower. In external view the surface of the external cotyla is narrower and the distal tendinal groove is more nearly perpendicular (c. 70°) to the long axis of the shaft than in P. impennis (c. 45°). In palmar view the proximal radial depression is much narrower, the crest of the intermuscular line is less distinct, the carpal tuberosity and distal tendinal groove are wider and the external lip of the latter less developed than in P. impennis. In internal view the very narrow and elongate attachment of the anterior articular ligament, characteristic of *Pinguinis*, is situated much more proximally, being nearly confluent with the internal lip of the internal cotyla, and having a distinct pit at its proximal extremity, whereas in P. impennis this attachment is widely separated from the internal cotyla and the pit is absent.

The shaft of the humerus of P. alfrednewtoni, like that of the ulna, is less compressed than in P. impennis. This is best illustrated in the cross-section (Fig. 2d) of the better preserved of the two paratypic humeri (USNM 179226), where it is seen that towards the proximal end the shaft in P. alfrednewtoni is much more rounded, the medullary cavity is larger and the wall of peripheral bone much thicker. In P. impennis there is considerable variation in the degree of flattening of the shaft and particularly in the extent of the development of the crest along the proximo-anconal edge; certain individuals do not differ quite as strikingly as the one shown in Fig. 2d, while others differ more. Yet in none is the proximal end of the shaft as heavy and rounded as in P. alfrednewtoni. By contrast, the distal portion of the shaft, as seen in the poorly preserved distal fragment USNM 192497, appears to be less rounded, with thinner walls, than in P. impennis. Other differences between the humeri of P. alfrednewtoni and P. impennis are more subtle. In the former, the ectepicondylar prominence is more pointed and projects farther from the shaft, the attachment of the anterior articular ligament is smaller and does not extend as far proximally, the tricipital grooves are shallower, and the internal condyle in distal view is

The single available femur of *P. alfrednewtoni* is rather worn, but in spite of this abrasion the head appears to have been markedly smaller than in *P. impennis*. The rotular groove appears to be somewhat wider and shallower, but other consistent differences from *P. impennis* are not presently detectable.

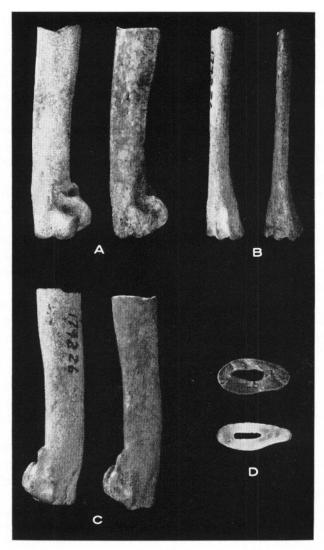


Fig. 2. Left humeri of *Pinguinis. P. alfrednewtoni* (USNM 179226) on left in each pair (above in D), *P. impennis* on right (below in D): A, Internal view; B, Anconal view; C, External view; D, Cross section through proximal portion of shaft in proximal view. A–C natural size; D $1.5\times$.

Although quite worn, the single fragment of tibiotarsus of *P. alfrednewtoni* still shows some distinctions from its counterpart in *P. impennis*. Like that species, the tendinal bridge is not ossified, but the internal ligamental prominence is better developed and the groove on the antero-medial por-

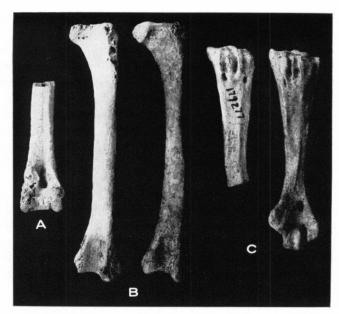


Fig. 3. Hindlimb elements of *Pinguinis*: A, Distal end of right tibiotarsus of *P. alfrednewtoni* (USNM 193101); B, Left femur of *P. alfrednewtoni* (USNM 206362) on left and *P. impennis* on right; C, Right tarsometatarsus of *P. alfrednewtoni* (USNM 179277) on left and *P. impennis* on right. All figures natural size.

tion of the shaft just proximal to the internal condyle is deeper. The most striking difference is seen in the medial view of the internal condyle; in *P. alfrednewtoni* the prominent postero-distal expansion of the rim appears to be lacking or greatly reduced, whereas it is well developed in *P. impennis*, causing the margin of the condyle to be distinctly notched.

The fragment of tarsometatarsus of *P. alfrednewtoni* is also worn and is porous proximally so as to suggest that the specimen may have been from an immature bird. In anterior view the two portions of the tubercle for M. tibialis anticus are united and are of about equal distal extent, whereas in *P. impennis* the two portions are more elongate and are separated, the lateral one extending farther distally and being well separated from the lateral proximal foramen. In proximal view the internal cotyla is deeper, does not extend as far medially, and has the postero-lateral margin more thickened and elevated than in *P. impennis*. The hypotarsus, as in *P. impennis*, consists of three calcaneal ridges and two grooves, but the internal ridge is thinner, the middle ridge is eonsiderably thicker and protrudes farther posteriorly, and the external ridge is much more distinct than in *P. impennis*.

Remarks.—Despite its eonsiderably greater age, Pinguinis alfrednewtoni

is remarkably similar in size and proportions to Recent *P. impennis*. The differences in the hindlimb of the fossil species are not obviously explained, but those seen in the wing elements indicate that the fossil form was slightly less specialized for wing-propelled locomotion than its Recent counterpart. This is evidenced mainly by the lesser degree of flattening of the humerus and ulna. Although a relatively minor feature, the angle of the distal tendinal groove of the ulna is not without significance. That this groove is more nearly parallel to the shaft of the ulna in *P. impennis* probably indicates a decreased ability to flex the distal portions of the wing, a condition that would accord with increased specialization of the wing as a rigid paddle.

It seems likely that *P. alfrednewtoni* was the direct ancestor of *P. impennis*. The only evidence possibly contrary to such a hypothesis is that the conformation of the olecranal area in *P. impennis* appears more similar to that of typical volant alcids than to *P. alfrednewtoni*. It is otherwise noteworthy that so little morphological change took place in the *Pinguinis* lineage during the 5 million years or so since the remains of *P. alfrednewtoni* were deposited.

In describing the new genus and species Australca grandis from the Middle Pliocene Bone Valley Formation in Florida, Brodkorb (1955) suggested that the supposedly reduced wing elements of this form indicated that it was approaching flightlessness and may have been ancestral to Pinguinis. It is now known that Brodkorb's A. grandis is actually a composite of at least two typically volant species of alcids (Olson and Wetmore, in press). Cranial material from Lee Creek referable to Australca appears to be morphologically intermediate between Pinguinis and the Recent genus Alca but the wing elements show no tendency towards the specializations of Pinguinis. That Pinguinis was a contemporary of Australca at Lee Creek, and occurs earlier in the fossil record than the Bone Valley specimens of A. grandis, removes any possibility that A. grandis was ancestral to Pinguinis.

The great scarcity of *Pinguinis alfrednewtoni* in the Lee Creek deposits, where thousands of alcid bones have been recovered, is probably due to one of two factors. Either the species did not occur regularly at the latitude of North Carolina, in which case its principal range was probably farther north, or it inhabited areas closer to shore than the other Lee Creek alcids. Judging from the fossil avifauna as a whole, the environment at Lee Creek during the early Pliocene was most likely open ocean at a fair distance from land (Olson and Wetmore, op. cit.).

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