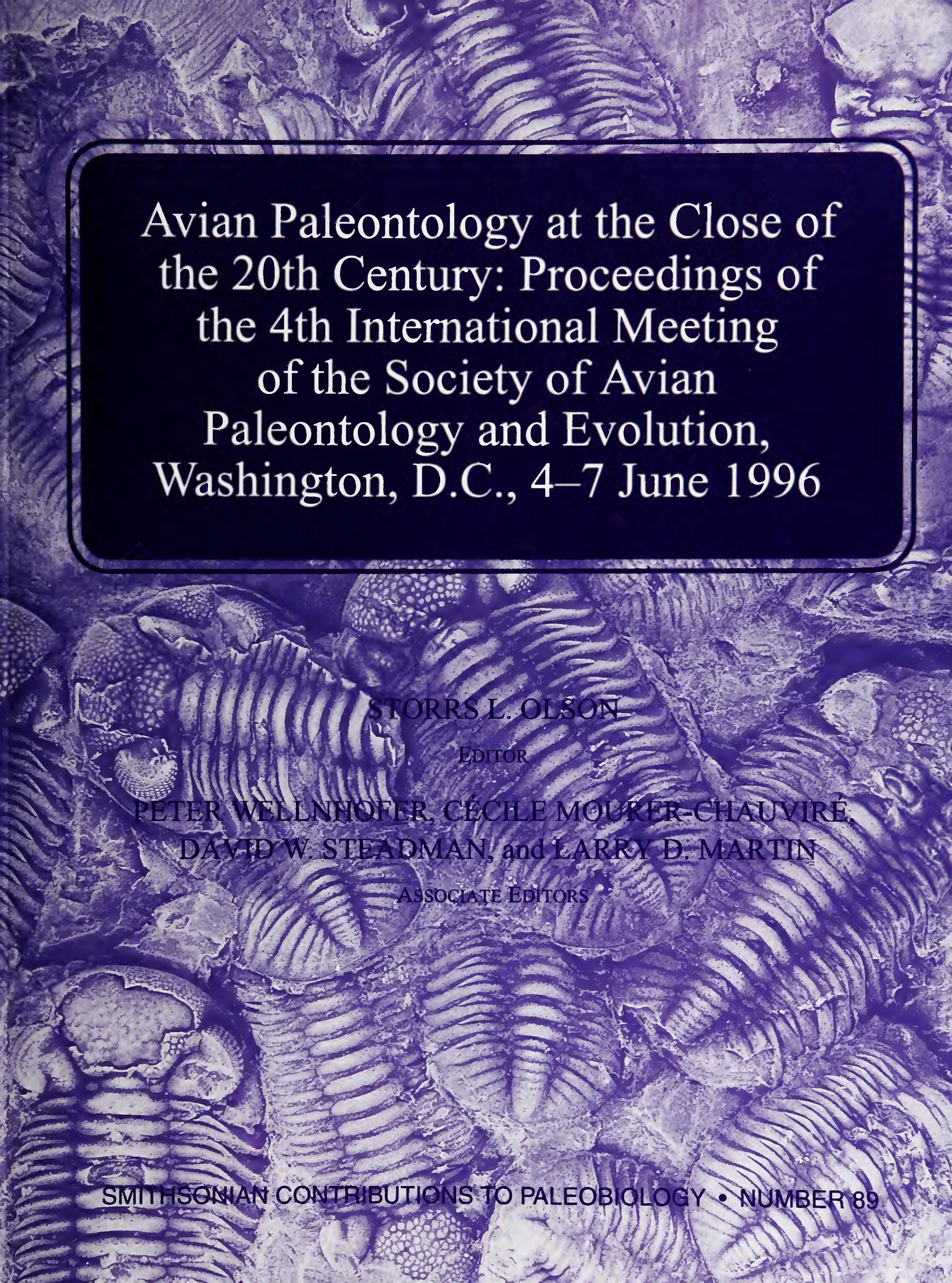

Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996

STORRS L. OLSON

EDITOR

PETER WELLNHOFER, CÉCILE MOURER-CHAUVIRÉ,
DAVID W. STEADMAN, and LARRY D. MARTIN

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SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 89

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SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 89

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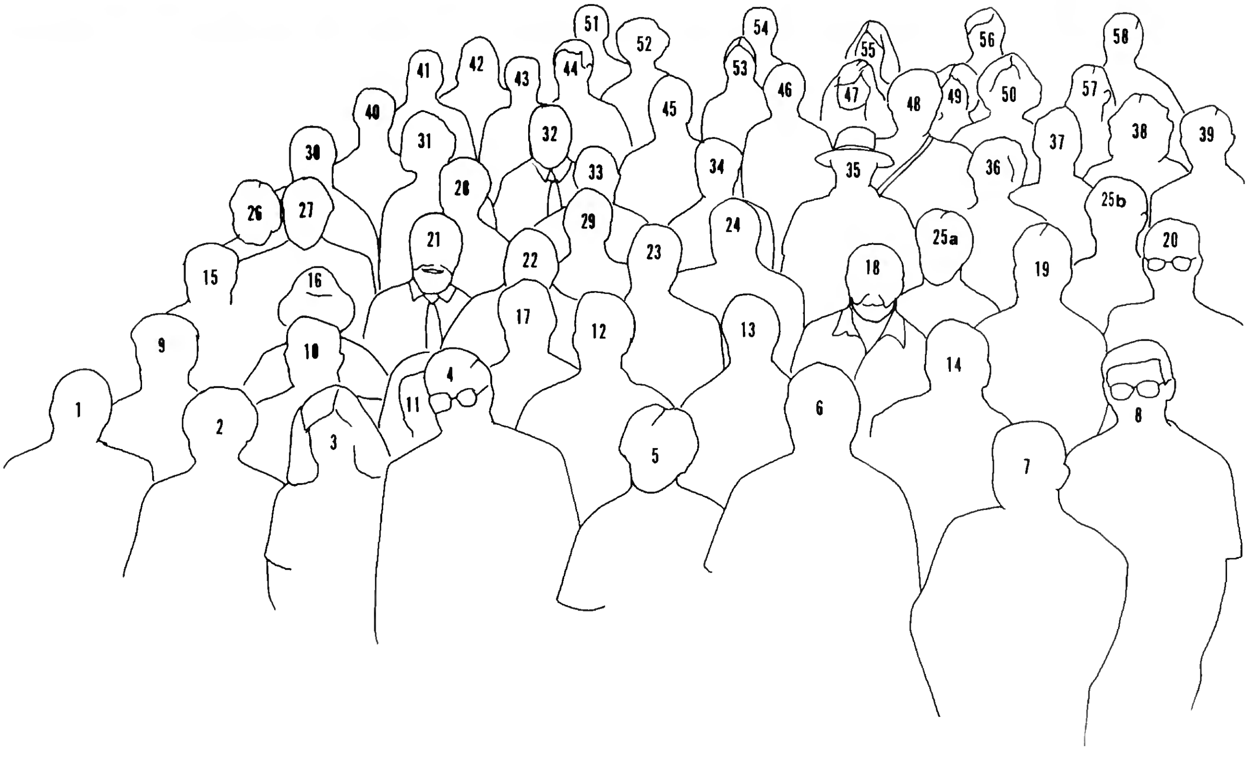
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1. Peter Wellnhofer (Munich, Germany)
2. Ingrid Wellnhofer (Munich, Germany)
3. Helen James (Washington, D.C.)
4. Storrs Olson (Washington, D.C.)
5. Cécile Mourer-Chauviré (Lyon, France)
6. Kenneth Campbell (Los Angeles, California)
7. Stefan Peters (Frankfurt, Germany)
8. Zhonghe Zhou (Beijing, China)
9. Lianhai Hou (Beijing, China)
10. John Ostrom (New Haven, Connecticut)
11. Virginia Naples (DeKalb, Illinois)
12. Lawrence Witmer (Athens, Ohio)
13. Peter Houde (Las Cruces, New Mexico)
14. Paul Bühler (Gschwend, Germany; deceased, 16 July 1996)
15. Joseph M^{c}Kee (Palmerston North, New Zealand)
16. Sylvia Hope (San Francisco, California)
17. Jean Martin (Lawrence, Kansas)
18. Gregory Paul (Baltimore, Maryland)
19. Bartomeu Seguí (Ciutat de Mallorca, Spain)
20. David Parris (Trenton, New Jersey)
21. Evgeny Kurochkin (Moscow, Russia)
22. Larry Martin (Lawrence, Kansas)
23. Herculano Alvarenga (São Paulo, Brazil)
24. Kenneth Parkes (Pittsburg, Pennsylvania)
25a. Ewan Fordyce (Dunedin, New Zealand)
25b. Hiroshige Matsuoka (Kyoto, Japan)
26. Charlie Magovern (Boulder, Colorado)
27. Luis Chiappe (Los Angeles, California)
28. Kraig Derstler (New Orleans, Louisiana)
29. Craig Jones (Dunedin, New Zealand)
30. Ralph Chapman (Washington, D.C.)
31. Diego Rassman-Gutman (Washington, D.C.)
32. Felix Dzerzhinsky (Moscow, Russia)
33. Per Ericson (Stockholm, Sweden)
34. Richard Zusi (Washington, D.C.)
35. Phil Millener (Chattanooga, Tennessee)
36. Mary Root (Albuquerque, New Mexico)
37. Marco Pavia (Turin, Italy)
38. Jorge Noriega (Diamante, Argentina)
39. Antoni Alcover (Ciutat de Mallorca, Spain)
40. Trevor Worthy (Nelson, New Zealand)
41. Walter Boles (Sydney, Australia)
42. Tom Stidham (Berkeley, California)
43. William Hilgartner (Baltimore, Maryland)
44. Richard Benson (St. Paul, Minnesota)
45. Andrzej Elzanowski (Wroclaw, Poland)
46. Darrel Tanke (Drumheller, Canada)
47. Pamela Rasmussen (Washington, D.C.)
48. Tommy Tyrberg (Kimstad, Sweden)
49. Pippa Haarhoff (Capetown, South Africa)
50. Gerald Mayr (Berlin, Germany)
51. Steven Emslie (Wilmington, North Carolina)
52. John Stewart (Cambridge, United Kingdom)
53. Jenna Boyle (Gunnison, Colorado)
54. David Steadman (Gainesville, Florida)
55. Joanne Cooper (London, United Kingdom)
56. John Becker (Edmonton, Canada)
57. Claudia Tambussi (La Plata, Argentina)
58. Alexandr Karhu (Moscow, Russia)

Registrants not shown:

Michael Braun (Washington, D.C.)
Rachel Burke (New Brunswick, New Jersey)
Sankar Chatterjee (Lubbock, Texas)
Adele Conover (Huntington, Maryland)
Alan Cooper (Washington, D.C.)
Catherine Forster (Stony Brook, New York)
Steve Gatsey (Providence, Rhode Island)
G.E. Goslow, Jr. (Providence, Rhode Island)
Michael Gottfried (Solomons, Maryland)
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ABSTRACT

Olson, Storrs L., editor. Avian Paleontology at the Close of the 20th Century: Proceedings of the 4th International Meeting of the Society of Avian Paleontology and Evolution, Washington, D.C., 4–7 June 1996. *Smithsonian Contributions to Paleobiology,* number 89, 344 pages, frontispiece, 169 figures, 49 tables, 1999.—The 32 papers collected herein reflect the great diversity and interest that the study of fossil birds has generated in recent years. The first seven papers (Mourer-Chauviré et al., Worthy and Jouventin, Seguí and Alcover, Steadman and Hilgartner, Millener, Worthy, Pavia) relate to late Quaternary birds from islands, where human intervention in the last few thousand years has caused many heretofore unrecorded extinctions. Three papers on Quaternary avifaunas of continental Europe deal with distributional changes and cultural use of birds by humans in Siberia (Potapova and Panteleyev), the utility of patterns of seabird distribution in determining former marine climatic conditions (Tyrberg), and temporal changes in morphology of ptarmigans (*Lagopus*) through the late Pleistocene (Stewart). Three papers deal with late Cenozoic raptors (Campbell et al., Tambussi and Noriega, Emslie and Czaplewski). New genera from Paleogene deposits are described by Boles and Ivison, Karhu, and Peters. Five papers deal with ancient waterfowl. Alvarenga describes the first fossil screamer (Anhimidae) from the Oligocene of Brazil. Olson provides the first fossil records of the Anseranatidae, with the description of a new species from the early Eocene of England, which is referred to *Anatalavis* from the Paleocene/Cretaceous of New Jersey. Ericson provides the means to distiguish Eocene fossils of the duck-like *Presbyornis* from the flamingo-like *Juncitarsus* and gives new records of the latter. Benson shows that the Paleocene *Presbyornis isoni* once ranged from Maryland to North Dakota, and he gives records of other Paleocene birds from North Dakota. Hope names a new, larger species of *Graculavus*, extending the range of the genus from New Jersey to the Cretaceous of Wyoming.

The early history and evolution of birds receives great attention. Dzerzhinsky expands upon the significance of cranial morphology in paleognathous birds. Kurochkin relates the early Cretaceous genus *Ambiortus* to the Chinese *Otogornis*, which are supposed to be on a line with modern birds, as opposed to the Enantiornithes. Bochenski uses paleogeography to suggest that the Enantiornithes must antedate *Archaeopteryx.* Zhou and Martin show that the manus of *Archaeopteryx* is more bird-like than previously realized. Martin and Stewart use bird teeth to argue against dinosaurian origins for Aves, whereas Elzanowski diverges on various aspects of dinosaurian cranial morphology and that of early birds that may have evolutionary significance. Witmer, Chiappe, and Goslow present summaries of three sessions of a roundtable discussion on avian origins, early evolution of birds, and the origins of flight, which was held on June 7, the last day of the meeting, and which covered much controversial territory.

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Preface

The 4th International Meeting of the Society of Avian Paleontology and Evolution (SAPE) was held at the Smithsonian Institution, Washington, D.C., 4–7 June 1996, as an official part of the celebration of the 150th anniversary of the Smithsonian. Sessions for papers were held at the S. Dillon Ripley Center the first two days of the meeting.

A very successful workshop organized by Sylvia Hope was held during the afternoon of the second day at the National Museum of Natural History. Participants examined and compared fossils of latest Cretaceous and early Tertiary birds, resulting in numerous valuable insights and revelations.

A field trip on June 6th to the Miocene exposures of Calvert Cliffs along Chesapeake Bay was followed by a visit to the Calvert Marine Museum (CMM) at Solomon's, Maryland, and culminated with an outdoor crab feast. All of this took place under the most ideal imaginable conditions, thanks to fine weather and the careful planning of our hosts for the day at CMM.

The final day was devoted to a symposium and roundtable on Mesozoic birds and their origins, organized by Peter Wellnhofer. The roundtable brought out animated discussion of the more intractable issues that invest this subject today, but these discussions were conducted totally without rancor or animosity and in a spirit of genuine collegiality.

The SAPE meeting's tradition of international composition was fully upheld by the fourth meeting, in which there were registrants from at least 14 countries and 18 states of the United States. To maintain international participation, the Society has successfully been able to alter the venue of its quadrennial meetings among continents. At the business meeting in Washington, D.C., an offer was extended by the Institute of Vertebrate Paleontology of the Academica Sinica to hold the fifth SAPE meeting, in the year 2000, in Beijing, China. After some thoughtful discussion, the invitation was accepted.

No matter whether the 21st century begins in the year 2000 or 2001, the Washington SAPE meeting was the last to be held in a year beginning with "19." Thus, the title of this volume suggested itself. It is worth reflecting on the fact that during the last quarter of the 20th century there was probably as much or more learned about the fossil history of birds than there was throughout the rest of history. The papers that are collected herein reflect the continued vigor and diversity of this line of investigation around the world. Now the legacy of SAPE is passed to a new continent in a new century. May its light be undiminished.

ACKNOWLEDGMENTS.—The local committee on arrangements for the Washington meeting consisted of Helen James, Storrs Olson, Michael Gottfried, Pamela Rasmussen, and Ralph Chapman. That the meeting took place at all is due entirely to the persistence, optimism, and insistence of Helen James, who, through an oppressive winter of government shutdowns and dreadful weather, and with little prospect of finding sufficient funding, kept communications open and plans progressing when others only despaired.

Direct funding for the meeting came from the 150th Anniversary Program Committee and the Office of the Director, National Museum of Natural History, Smithsonian Institution. Travel subsidy for some of the participants was provided by the Office of Fellowships and Grants, Smithsonian Institution; the International Science Foundation; and the University of Kansas. Arrangements for the field trip and the crab feast were made by Michael Gottfried of the Calvert Marine Museum, cosponsor of the meeting.

In order to spread some of the burden of the editorial process for the present volume, I divided the majority of the submitted papers among four associate editors, who were responsible for reading and commenting on manuscripts and soliciting additional reviews. Of necessity, much of the task of refereeing fell largely to members of SAPE. The follow-

ing is a list of referees who commented on one or more of the papers, and I am very grateful to all of them for their help: Antoni Alcover, S. Christopher Bennett, Zygmunt Bochenski, Alan Brush, Eric Buffetaut, Kenneth Campbell, Luis Chiappe, Charles Collins, Miguel Elorza, Andrzej Elzanowski, Steven Emslie, Per Ericson, Alan Feduccia, G.E. Goslow, Peter Houde, Helen James, Dénes Jánossy, Larry Martin, Gary Morgan, Cécile Mourer-Chauviré, Storrs Olson, John Ostrom, Kevin Padian, David Parris, Steven Parry, Stefan Peters, Gregory Pregill, J.H. Reichholf, Dale Serjeantson, David Steadman, Burkhard Stephan, Tommy Tyrberg, David Unwin, Kenneth Warheit, Paul Weldon, Peter Wellnhofer, Lawrence Witmer, Trevor Worthy, Zhonghe Zhou, and Richard Zusi.

For assistance with transmission of manuscripts by electronic mail I am grateful to James Dean, Craig Ludwig, Chris Milensky, and Brian Schmidt. Mary Parrish repeatedly assisted with problems concerning illustrations and provided the outline key for the frontispiece. I also thank Sharon Jones, who cheerfully wielded her computer to render more readable several of the manuscripts that were more heavily scribbled by the editor.

Storrs L. Olson

The Avifauna of Réunion Island (Mascarene Islands) at the Time of the Arrival of the First Europeans

Cécile Mourer-Chauviré, Roger Bour, Sonia Ribes, and François Moutou

ABSTRACT

The excavations of five fossil bird localities on Réunion Island have yielded the remains of (1) five species still present on Réunion, which are mainly marine; (2) one extant species no longer on Réunion, the Greater Flamingo (*Phoenicopterus ruber* Linnaeus); and (3) 11 extinct species, namely, a night heron (*Nycticorax duboisi* (Rothschild)), an ibis (*Threskiornis solitarius* (Sélys-Longchamps)), a sheldgoose (*Alopochen kervazoi* (Cowles)), a teal (*Anas theodori* Newton and Gadow), a falcon (*Falco duboisi* Cowles), a rail (*Dryolimnas augusti*, new species), a coot (*Fulica newtonii* Milne-Edwards), a pigeon (*Nesoenas duboisi* Rothschild), a parrot (*Mascarinus mascarinus* Linnaeus), an owl (*Mascarenotus grucheti* Mourer-Chauviré et al.), and a starling (*Fregilupus varius* (Boddaert)). Representatives of extinct endemic Mascarene taxa, such as the Raphidae, *Aphanapteryx*, *Erythromachus*, and large parrots of the genera *Lophopsittacus* and *Necropsittacus*, are so far unknown from Réunion. Except for *Fulica newtonii*, which probably colonized Réunion from Mauritius, and *Dryolimnas augusti*, all the other forms appear to have had normal or nearly normal flying ability. It is possible that Réunion was colonized by the ancestors of the same forms that colonized Mauritius and Rodrigues, but these forms may have been exterminated during the very explosive events of the last phase of volcanic activity of Piton des Neiges, which took place between 300,000 and 200,000 years ago. Réunion would then have been colonized again by forms that perhaps have not had enough time to lose their ability to fly. After the arrival of the first Europeans, all the larger endemic land birds became extinct, with the exception of *Circus maillardi* Verreaux. Although most of them were not morphologically flightless, and although the topography of the island was very different, these birds became extinct on Réunion as rapidly as on the other Mascarene islands.

Introduction

The Mascarene Islands were "discovered" by Portuguese navigators as early as 1500 (North-Coombes, 1979). They were shown on more ancient maps of Arabian navigators but were uninhabited prior to the sixteenth century. Thus, Europeans were the first settlers to observe the very unusual fauna of these islands, one that was almost entirely exterminated within just two centuries.

Numerous historical accounts of Réunion have been gathered into two publications by Albert Lougnon (1970, 1992), with the oldest account being that of Samuel Castleton, who landed on the island in 1613. The parts concerning the birds are given in extenso in the books of Barré and Barau (1982) and Barré et al. (1996). Particular points of these accounts have been discussed by Cheke (1987). The most complete and detailed report is that written by Dubois (1674), also known as Sieur D.B., who spent 16 months on the island in 1671 and 1672 (English translation by Oliver, 1897). These accounts are invaluable because they make it possible to follow the demise of the endemic fauna of Réunion from the beginning of the seventeenth century to the disappearance of the two most recently extinct species, *Mascarinus mascarinus* Linnaeus, in 1834, and *Fregilupus varius* (Boddaert), between 1838 and 1858.

Fossil bird remains were found very early on Rodrigues (in 1786) and on Mauritius (in 1865), making it possible to have good knowledge of their vanished faunas. Until recently, however, the bird fauna of Réunion was known only from the accounts of early explorers. The first fossil remains were unearthed in 1974 by B. Kervazo during archaeological excavations in the Grotte des Premiers Français. Subsequently, four other fossil sites containing bird remains also were discovered. The fossil birds of the present study came from these five

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Cécile Mourer-Chauviré, Centre de Paléontologie Stratigraphique et Paléoécologie de l'Université Claude Bernard-Lyon 1, ERS 2042 du CNRS, 27–43 boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France. Roger Bour, Muséum National d'Histoire Naturelle, Laboratoire des Reptiles et des Amphibiens, 25 rue Cuvier, 75005 Paris, France. Sonia Ribes, Muséum d'Histoire Naturelle, 1 rue Poivre, 97400 Saint-Denis, La Réunion, France. François Moutou, Ministère de l'Agriculture, CNEVA, Laboratoire Central de Recherches Vétérinaires, 22 rue Pierre Curie, BP n° 67, 94703 Maisons-Alfort Cedex, France.

localities, all of them situated in the territory of Saint-Paul, on the northwest portion of the island (Figure 1). The caves are not karstic cavities but are developed inside the lava flows, or at the junction between successive lava flows.

ACKNOWLEDGMENTS.—We thank the Conseil général de la Réunion, the Conseil régional de la Réunion, and the Société Réunionaise des Amis du Muséum, whose generous cooperation made it possible to carry out excavations in the Marais de l'Ermitage, and we thank all the friends who helped us with these excavations and who provided material from other localities, in particular, Jean Jacques Argoud, Pierre Brial, Jean-Pierre and Colette Esmiol, Jean-Michel Probst, and the members of the Société d'Études scientifiques des Cavernes de la Réunion. The work at the Smithsonian Institution was made possible by a Short Term Visitor Grant from the Office of Fellowships and Grants. For the loan of comparative modern and fossil material we thank Daniel Goujet and Christine Lefèvre (Muséum National d'Histoire Naturelle, Paris), Storrs L. Olson, (National Museum of Natural History, Smithsonian Institution), Robert Prys-Jones (The Natural History Museum, London), and Janet Hinshaw (University of Michigan). We thank Alain Dubois for his advice concerning nomenclatural problems and our two referees, Storrs Olson and David Steadman, for their very constructive criticism. Steve Goodman provided unpublished measurements of Madagascan anatids. For the x-ray pictures of the two specimens of *Mascarinus mascarinus*, we thank Jean Dorst, Paris, and Herbert Schifter, Vienna. The photographs are by Noël Podevigne, and the drawings are by Arlette Armand (Centre des Sciences de la Terre, Université Claude Bernard-Lyon 1).

ABBREVIATIONS AND ACRONYMS.—The following museum acronyms are used: AMNH, American Museum of Natural History, New York; BMNH, The Natural History Museum, London (formerly, British Museum (Natural History)); FSL, Faculté des Sciences de Lyon; LAC, Laboratoire d'Anatomie Comparée du Muséum National d'Histoire Naturelle, Paris; MNHN, Muséum National d'Histoire Naturelle, Paris; MHNR, Muséum d'Histoire Naturelle, Saint-Denis, La Réunion; UCB, Université Claude Bernard-Lyon 1; USNM, collections of the former United States National Museum, now in the National Museum of Natural History, Washington, D.C.

In the listing of material, the following abbreviations are used: d., distal; j., juvenile; l., left; p., proximal; r., right; s., shaft.

Fossil Localities

Grotte des Premiers Français (Grande Caverne).—This is a very large cavity, situated 1.5 km from the center of Saint-Paul. Details concerning the stratigraphy and the location of excavations have been given by Kervazo (1979) and Bour (1979, 1980a). The bird material comes from layers 4 and 5 of pit number 2, in the most northeastern cave, which now includes a statue of the Virgin Mary. The top of layer 4 was situated about 80 cm below the floor of the cave at the time of the excavation, and layers 4 and 5 together were 25 cm thick. These layers did not include any trace of human occupation or any remains of introduced mammals; therefore, the vertebrate material can be considered as having been deposited prior to the occupation of the island by humans.

In this cave, as well as in Grotte "au sable," most of the bird remains belong to the two species of shearwater, *Puffinus pacificus* Gmelin and *P. lherminieri* Lesson. The remains come from all growth stages, from very young individuals, the bones of which are simple sticks without articulations, to fully grown adults. With the exception of a single bone of *Fregilupus varius*, no passerine remains were found. The sediments were not sieved (Kervazo, pers. comm., 1996), but a large number of very small bones, such as pedal phalanges of shearwaters, were collected, and, if there had been passerine remains, they would have been collected. The shearwater remains probably come from individuals that were nesting in burrows in the vicinity of the cave; the sediments of their nesting site might have been washed into the cave during a cyclonic episode. The other vertebrate remains probably come from animals that took refuge in the cave during such an episode (Bour, 1979).

Bird material from this site was first described by Cowles (1987, 1994). All this material is in the MNHN and has the prefix LAC.

Grotte de l'Autel.—This cave was discovered in 1980 by R. Bour and F. Moutou (Bour, 1980a). It is situated along the N1 road, 2 km south of Saint-Gilles, to the south of and a little higher up than a shrine dedicated to Saint Expédit. It is a small cavity, about 2.50 m long, 1.20 m wide, and 1 m high at its highest part. The sediment, completely removed in 1980, was not sieved.

Grotte "au sable."—This cave also was discovered and excavated in 1980 by R. Bour and F. Moutou (Bour, 1980a); it was excavated again in 1987 by F. Moutou, R. Mourer, and C. Mourer-Chauviré. It is situated close beside the N1 road, to the north and at the same level as the Saint Expédit shrine. Its dimensions are about 2 m^2 and 1.50 m high at its highest part. Its sediment also was completely excavated in 1987 and was sieved with 1.5 mm mesh screens. Very tiny lizard bones were found, which are smaller than those of recent endemic passerines, as well as isolated mouse teeth. It is therefore likely that the absence of passerines actually reflects their absence in the deposits and is not an artifact of collecting. The vertebrate remains from Grotte de l'Autel and Grotte "au sable" are probably contemporaneous with the occupation of the caves by the first settlers, from the middle of the seventeenth century, because they include some bones of introduced mammals.

All the material from Grotte de l'Autel and Grotte "au sable" is in the UCB and has the prefix FSL.

Marais de l'Ermitage.—This swamp is situated a little further to the south of the above-mentioned sites, along the N1 road, between Saint-Gilles and La Saline-les-Bains, at the locality of l'Ermitage-les-Bains. The first fossil bones were dis-

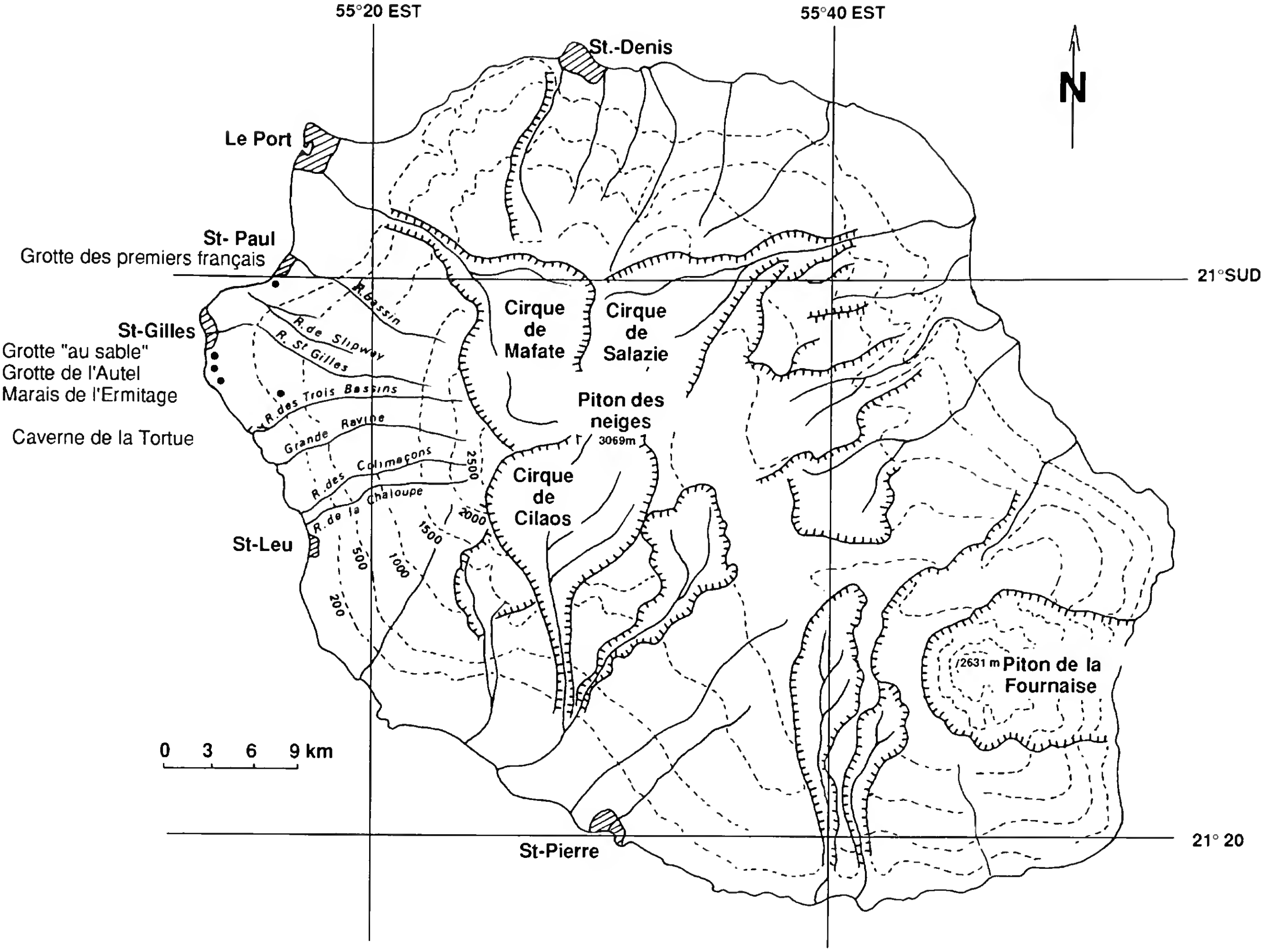


FIGURE 1.—Map of Réunion Island showing the five localities in the northwest where fossil birds have been recovered. Contour intervals are in meters.

covered in 1989–1990, during earthworks for the construction of the Jardin d'Eden. Excavations have been carried out in this same swamp, to the south of the Jardin d'Eden, under the responsibility of the Muséum d'Histoire Naturelle de La Réunion, since 1992, and are still conducted every year. The area excavated so far is about 80 m^2 The filling of the swamp consists of about 80 cm of organic soil with very few fossils. This overlies a layer 30 to 40 cm deep made up of countless bones and shell fragments of the large, extinct land-tortoise *Cylindraspis borbonica* Bour, mixed with volcanic rocks and blocks of coral. Among this extraordinary accumulation of tortoise remains occur very rare bird and bat bones. The fossiliferous layer rests on marine sediments made up of coralline sands, fragments of corals, and marine molluscs. A very few remains of domestic mammals, introduced by humans, have been found associated with the extinct tortoises, although most remains of domestic mammals are found in the upper sediments.

The sediments of the marsh were systematically sieved using 2.5 mm and 1.5 mm mesh screens, and very small bones of juvenile *Cylindraspis borbonica* as well as tiny bones of bats were found. Here also, the absence of passerines probably reflects their absence in the sediments.

Radiocarbon dates have been obtained for material from the Marais de l'Ermitage. The first one, on several bones of *Cylindraspis borbonica*, yielded an age of 915±120 BP (Lyon 5551); interval in real years after calibration: 883–1273 AD (confidence interval 90%). Two other dates on single bones by the accelerator (AMS) method, gave the following results:

Bone of *Cylindraspis borbonica*, from the base of the filling: 1755±40 BP (OxA-5994 (Lyon 201)). Interval in real years after calibration: 186–391 AD (confidence interval 95%).

Bone of *Sus scrofa* Linnaeus, introduced by humans, from the fossiliferous layer, associated with bones of *Cylindraspis borbonica:* 365±35 BP (OxA-5993 (Lyon 200)). Interval in real years after calibration: 1458–1633 AD (confidence interval 95%). This date agrees very well with historical accounts indicating that pigs were released on the island in or before 1629 (Lougnon, 1970, 1992).

The three dates obtained for the Marais de l'Ermitage indicate that the remains of tortoises, birds, and bats accumulated over a period of at least 1400 years, from about 300 AD to about 1700 AD.

All the bird material from Marais de l'Ermitage is in MHNR and has the prefix MHN-RUN-FE-O.

Caverne de la Tortue.—This cave is situated in the territory of Saint-Paul, near Chemin Bruniquel, between the localities of La Saline, the upper village, and La Saline-les-Bains, on the ocean side, approximately halfway between Ravine de la Saline, at the northwest, and Ravine Tabac, at the southeast, at an altitude of about 250 m above sea level. It is a complex cavern, including several galleries, and extends over a maximum length of 322 m (Brial, 1996). The entrance is through the roof of a tunnel, the floor being situated 5 m below. The bird remains were collected on 23 March 1996 by Jean-Michel Probst and Pierre Brial, in Salle des Tortues Géantes. They were situated on the surface of the floor, along the walls, and associated with remains of the extinct tortoise (*C. borbonica*), introduced mammals (*Capra hircus* Linnaeus, *Lepus nigricollis* Cuvier, *Rattus* sp., *Tenrec ecaudatus* (Schreber)), and molluscs (Brial, 1996). The bones are poorly preserved and appear recent. The tortoise disappeared from this part of the island between 1717 and 1732 (Bour, 1980a), and *Lepus nigricollis* was introduced between 1868 and 1887 (Cheke, 1987), so the age of the animal remains is unknown. The material is in MHNR and has the prefix MHN-RUN-CT.

A list of species identified in the different localities is given in Table 1.

Systematic Paleontology

Family PROCELLARIIDAE

Genus *Puffinus* Brisson

Puffinus pacificus (Gmelin, 1789)

Wedge-tailed Shearwater

MATERIAL.—Grotte des Premiers Français: Very numerous remains from all parts of the skeleton, corresponding at least to 5 individuals (4 adults, 1 juvenile) in layer 4 and to 43 individuals (21 adults, 22 juveniles) in layer 5.

Grotte "au sable": Very numerous remains, corresponding at least to 14 individuals (5 adults, 9 juveniles): 330549–330571, 330589–330590, 330592–330595, 330598, 330600– 330627, 330639–330641, 330644, 330647–330650, 330653–330660, 330665–330667, 330669, 330671–330683, 330700–330711, 330727–330729.

Grotte de l'Autel and Grotte "au sable": Very numerous remains, corresponding at least to 7 individuals (5 adults, 2 juveniles): 330763–330800.

Marais de l'Ermitage: l. p. ulna, 1836; l. d. ulna, very abraded, 1919; r. d. tarsometatarsus, 1835; 2 l. tarsometatarsi, 1833, 1834; pedal phalanx, 1837.

Caverne de la Tortue: r. p. humerus, 28; fragment of r. carpometacarpus, 29; l. tarsometatarsus, 30.

TABLE 1.—List of the bird species found in the different fossil localities. The numbers correspond to the minimum numbers of individuals.

Species	Grotte des Premiers Français	Grotte de l'Autel	Grotte "au sable"	Marais de l'Ermitage	Caverne de la Tortue
Puffinus pacificus	48	7[*]	14	2	1
Puffinus lherminieri	28	4[*]	11	–	–
Phaethon lepturus	1	1	–	–	–
Nycticorax duboisi	1	1		2	–
Threskiornis solitarius	1	2	–	3	–
Phoenicopterus ruber	–	–	–	8	–
Alopochen (M.) kervazoi	2	2	1	3	–
Anas theodori	–	–	–	1	–
cf. *Aythya sp.*	–	–	–	1	–
Falco duboisi	2	1	–	–	–
Dryolimnas augusti, new species	–		–	–	2
Fulica newtonii	1	1	–	3	–
Numenius phaeopus	1	–	–	–	–
Nesoenas duboisi	1	1	–	–	–
Streptopelia picturata	–	–	1	–	–
Mascarinus mascarinus	1	1	2	–	–
Mascarenotus grucheti	1	2	1	1	–
Fregilupus varius	1	–	–	–	–
Total	89	23	30	24	3

[*] Combined collections from Grotte de l'Autel and Grotte "au Sable."

Puffinus lherminieri Lesson, 1840

Audubon's Shearwater

MATERIAL.—Grotte des Premiers Français: Very numerous remains from all parts of the skeleton, corresponding at least to 1 adult in layer 4 and to 27 individuals (14 adults, 13 juveniles) in layer 5.

Grotte "au sable": Very numerous remains, corresponding at least to 11 individuals (2 adults, 9 juveniles): 330572–330588, 330591, 330596–330597, 330599, 330628–330638, 330642–330643, 330645–330646, 330651–330652, 330661–330664, 330668, 330670, 330684–330699, 330712–330726.

Grotte de l'Autel and Grotte "au sable": Very numerous remains, corresponding at least to 4 individuals (2 adults, 2 juveniles): 330745–330762.

REMARKS.—The high proportion of juveniles indicates that both species of *Puffinus* were probably nesting in these cavities or their surroundings. *Puffinus pacificus* now nests at Réunion only on a small islet, accessible only with difficulty for humans or introduced mammals, whereas *P. lherminieri* nests in numerous parts of the island (Jouanin, 1987). In the three caves, *P. pacificus* is more numerous than *P. lherminieri,* but at present *P. lherminieri* is much more common on the island.

Two other species of Procellariidae, *Pseudobulweria aterrima* (Bonaparte) and *Pterodroma baraui* (Jouanin), now nest on Réunion, at high altitudes. Subfossil remains of *P. baraui* have been found in the Caverne à Cotte, at about 1800 m elevation (Jouanin and Gill, 1967). In our fossil localities, which are situated at low elevation, we did not find remains that can be attributed to either of these species. The limited fossil evidence therefore suggests that they may always have nested at higher elevations than *Puffinus.*

Family PHAETHONTIDAE

Genus *Phaethon* Linnaeus

Phaethon lepturus Daudin, 1802

White-tailed Tropicbird

FIGURE 4*t*

MATERIAL.—Grotte des Premiers Français: Part of skull, 1993-51.

Grotte de l'Autel: l. coracoid, 330515 (Figure 4*t*).

REMARKS.—The internal length of the coracoid is 39.0 mm, which falls within the range of variation of modern *P. lepturus* (36.2–40.1, $n=10$) and is clearly smaller than in the other two species, *P. rubricauda* Boddaert, the Red-tailed Tropicbird (47.0–53.9, $n=24$), and *P. aethereus* Linnaeus, the Red-billed Tropicbird (47.0–50.4, $n=7$). *Phaethon lepturus* still nests on Réunion.

Family ARDEIDAE

Genus *Nycticorax* Forster

Megaphoyx Hachisuka 1937b:148 [type by original designation, *Ardea megacephala* Milne-Edwards, 1874].

Each of the three Mascarene islands sustained an extinct species of *Nycticorax.* The first of these species was described from Rodrigues by Milne-Edwards (1874) under the name *Ardea megacephala.* Günther and Newton (1879) showed that the Rodrigues heron belonged in the genus *Nycticorax* and that, although its size was not very different from a large modern *N. nycticorax* (Linnaeus), its wing bones were proportionally shorter and its femur, tarsometatarsus, and pedal phalanges proportionally longer. Actually, when compared with typical *N. nycticorax nycticorax,* the wings are not very short, but the femora, tibiotarsi, and tarsometatarsi are wider, longer, and more robust (Cowles, 1987). Newton and Gadow (1893) described a second, Mauritian species, *Butorides mauritianus,* which is smaller than *N. megacephalus,* and then Rothschild (1907) described a third species, from Réunion, under the name of *Ardea duboisi.* Rothschild placed the three species in the genus *Ardea* but wrote (1907:115): "From the short, stout legs and general build, I am inclined to think that all three of these Herons belong to the genus *Nycticorax.*" Later, other authors (Lambrecht, 1933; Hachisuka, 1953; Brodkorb, 1963) placed the three species in different genera, and it was Cowles (1987) who first formally united them in the genus *Nycticorax.*

Nycticorax duboisi (Rothschild, 1907), new combination

Réunion Night Heron

FIGURE 4*a–h*

"Butors ou Grands Gauziers" Dubois, 1674:169.
Ardea duboisi Rothschild, 1907:114 [based on birds described by Dubois (1674) from Bourbon (=Réunion Island)].
Megaphoyx duboisi.—Hachisuka,1953:175.
Nycticorax n. sp. Cowles, 1987:94.
Nycticorax borbonensis Cowles, 1994:90, fig.1d,e [new synonymy; holotype, distal half of left tibiotarsus MNHN, LAC 1993-35, from bed 4, Grotte des Premiers Français (Grande Caverne), Réunion Island].

MATERIAL.—Grotte des Premiers Français: Holotype of *N. borbonensis* (see below).

Grotte de l'Autel: r. scapula, 330516.

Marais de l'Ermitage: r. scapula, 1866; l. p. coracoid, 1831; l. d. humerus, 1826; r. ulna, 1828; l. p. ulna, 1832; r. femur, 1827; 2 r. d. tibiotarsi, 1829, 1830; r. tarsometatarsus, 1916; 2 l. d. tarsometatarsi, 1865, 1917.

DESCRIPTION AND COMPARISONS.—The material from Réunion agrees perfectly with the genus *Nycticorax.* The different species of this genus show much variation in size, the largest being *N. caledonicus* (Gmelin), which lives in Indonesia, Australia, New Zealand, New Caledonia, and in some Pacific archipelagos (Mayr and Cottrell, 1979). The remains of *N.*

duboisi are larger than the largest individuals of *N. nycticorax* or *N. caledonicus* in the USNM collection.

The supratendinal bridge is incompletely ossified in the three tibiotarsi of *N. duboisi.* The condition is unknown in *N. mauritianus,* whereas in *N. megacephalus* the supratendinal bridge is completely ossified (Milne-Edwards, 1874, pl. 14: fig. 7). The dimensions of Mascarene *Nycticorax* are given in Table 2. Most of the remains of *N. duboisi* are larger than those of either *N. megacephalus* or *N. mauritianus* (Figure 4*i–j*), except for the tarsometatarsus, which is almost the same size as in *N. megacephalus,* and the femur, which is smaller in most dimensions than that in *N. megacephalus.*

The ratio-diagram (Figure 2) shows the differences in the relative proportions of the bones in the three Mascarene species, compared with the modern species *N. nycticorax* and *N. caledonicus.* In *N. mauritianus* and *N. megacephalus* the wings (humeri, ulnae, carpometacarpi) are considerably reduced, and the legs (particularly the femora) are longer than in modern species. In contrast, *N. duboisi* is larger than living species, but the proportions are almost the same. The tarsometatarsus is slightly longer than in *N. nycticorax* or *N. caledonicus,* but only two are available, and for one of them the length is estimated. The ratio-diagram clearly demonstrates that the Rodrigues and Mauritius species had a reduced flying ability, whereas the Réunion form had a flying ability quite similar to that of living species.

By the proportions of the tarsometatarsus, which is short and thick, the Mascarene night herons are more similar to *Nycticorax nycticorax* than to other congeners, particularly *N. cale-*

TABLE 2.—Dimensions (mm) of the long bones of *Nycticorax duboisi,* from Réunion, *N. megacephalus,* from Rodrigues, and *N. mauritianus,* from Maritius. (a=data from Milne-Edwards (1874), Günther and Newton (1879), and material at MNHN; b=data from Newton and Gadow (1893) and from material at MNHN; c=from base of glenoid facet to top of acromion; d=from the most internal part to the most external part; est.=estimated; *n*=number of specimens.)

Measurement	*N. duboisi*		*N. megacephalus*	*N. mauritianus*
	Mean (*n*)	Range	Range (a)	Range (b)
Scapula				
length art. part (c)	11.10 (2)	10.2–12.0	–	–
width art. part (d)	12.65 (2)	12.4–12.9	–	–
width shaft	4.90 (2)	4.7–5.1	–	–
depth shaft	2.90 (2)	2.8–3.0	–	–
Coracoid				
internal length	–	–	est. 53.0–57.0	est. 45.5
width midshaft	–4.8 (1)	–	–	4.3
depth midshaft	~5.4 (1)	–	–	4.2
Humerus				
total length	est. 137 (1)	–	114–119	–
distal width	18.4 (1)	–	16.5–16.8	–
width midshaft	8.1 (1)	–	6.9–7.0	–
depth midshaft	7.2 (1)	–	5.9	–
Una				
total length	est. 155 (1)	–	121	111–112
proximal width	13.5 (1)	–	–	–
proximal depth	11.5 (1)	–	–	–
distal width	~10.3 (1)	–	–	–
depth ext. cond.	~9.0 (1)	–	–	–
width midshaft	6.20 (2)	6.2–6.2	–	–
depth midshaft	5.65 (2)	5.6–5.7	–	–
Femur				
total length	est. 85 (1)	–	86–90	79.3
distal width	14.8 (1)	–	15.0	13.8
distal depth	14.2 (1)	–	–	11.7
width midshaft	6.6 (1)	–	6.2	6.4
depth midshaft	6.2 (1)	–	–	5.8
Tibiotarsus				
total length	~144.5 (2)	~139–~150	136–140	–
distal width	12.87 (3)	12.4–13.2	13.0	–
distal depth	13.2 (1)	–	–	–
width midshaft	6.80 (3)	6.8–6.8	6.0	–
depth midshaft	6.03 (3)	5.9–6.1	–	–
Tarsometatarsus				
total length	est. 97.55 (2)	95.1–est. 100	93–95.5	79.5–87
proximal width	~13.5 (1)	–	13.7–14.0	12.7–12.8
proximal depth	~13.5 (1)	–	13.5	12.4–12.6
distal width	14.2 (1)	–	13.5–13.8	11.7–12.1
distal depth	7.35 (2)	7.2–7.5	7.4	7.1–7.3
width midshaft	6.53 (3)	6.4–6.8	6.0–6.5	5.8–5.9
depth midshaft	4.73 (3)	4.4–5.0	5.0	4.7–4.8

donicus. In the case of *N. megacephalus* and *N. mauritianus,* however, the robustness of the tarsometatarsus is probably accentuated by the reduced flying ability (Table 3).

The Réunion night heron had green feet and had gray plumage flecked with white, a description that fits very well with the juvenile plumage of *Nycticorax nycticorax.*

REMARKS.—Cowles (1994) thought that the species name *Ardea duboisi,* created by Rothschild (1907), was a nomen nudum, but actually this name, published with a description, is valid. It has been used several times (Hachisuka, 1953; Greenway, 1967) and therefore must be retained, in conformity with the law of priority. Many other accepted scientific names of Mascarene birds are based on similar descriptions.

The description given by Dubois is as follows: "Bitterns or Great throats, large as big capons [domestic fowl, *Gallus gallus* (Linnaeus)], but fat and good [to eat]. They have grey plumage, each feather tipped with white, the neck and beak like a heron and the feet green, made like the feet of the 'Poullets d'Inde' [domestic turkey, *Meleagris gallopavo* (Linnaeus)]. That lives on fish" (Barré and Barau, 1982:30, our translation). Dubois' words "Butors ou Grands Gauziers" were left in French by Ol-

TABLE 3.—Robustness index of the tarsometatarsus in different modern and extinct species of the genus *Nycticorax.* (Robustness index = midshaft width × 100 / total length; *n*=number of specimens.)

Species	Mean	Range	*n*
Nycticorax nycticorax nycticorax	6.25	5.60–6.59	11
Nycticorax caledonicus	5.87	5.49–6.20	4
Nycticorax melanolophus	5.44	–	1
Nycticorax (Gorsachius) leuconotus	5.02	–	1
Nycticorax megacephalus	6.57	6.32–6.99	3
Nycticorax mauritianus	7.23	7.17–7.29	2
Nycticorax duboisi	~6.77	6.73– ~6.80	2

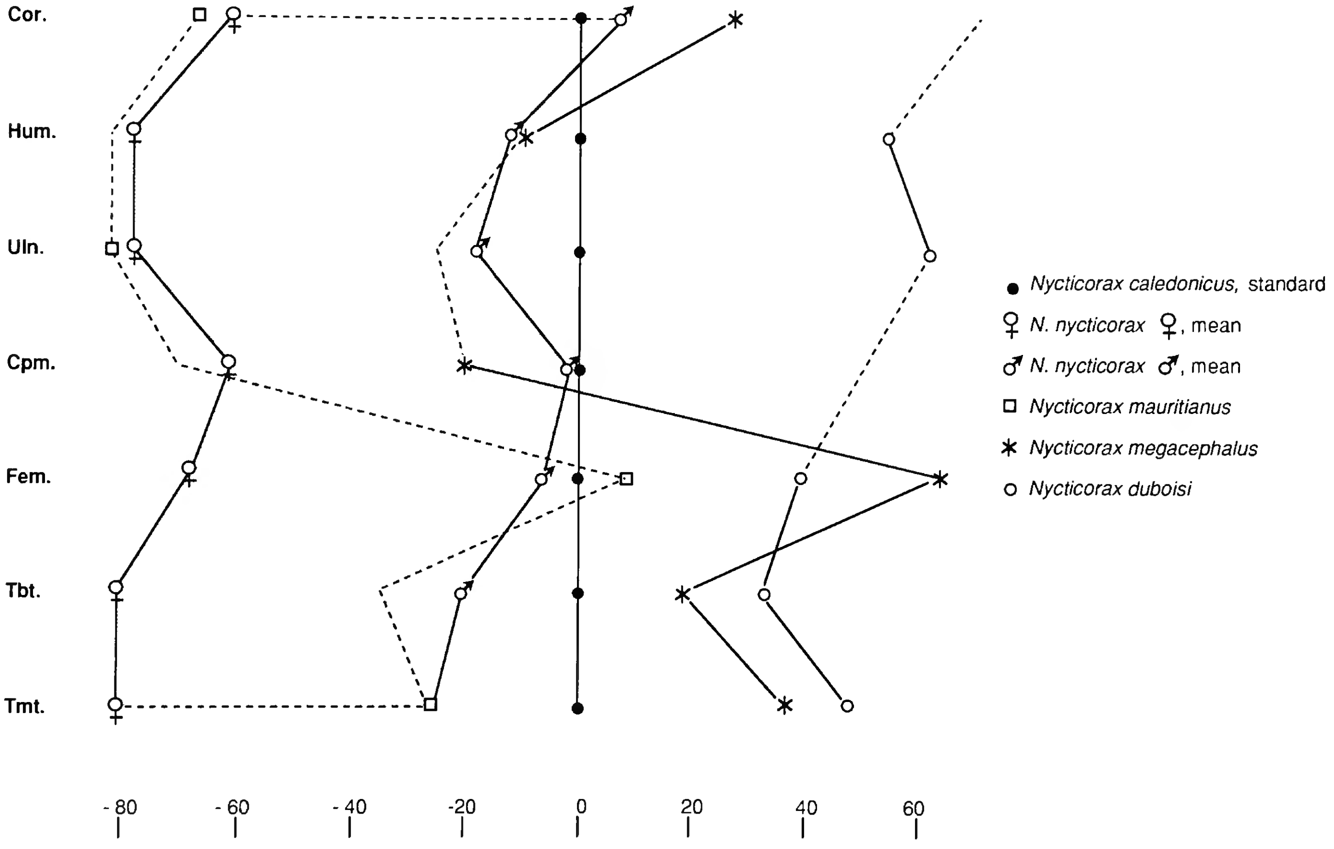


FIGURE 2.—Ratio-diagram of the dimensions of the main long bones of the three species of *Nycticorax* of the Mascarenes. The standard is a male *N. caledonicus* from New Caledonia (USNM 561542). For *N. nycticorax* the dimensions are the means of three females (USNM 292037, 319467, 430526) and nine males (USNM 289884, 292036, 430527, 432698, 488680, 489903, 499390, 501991, 610609). For *N. megacephalus* the data are from Milne-Edwards (1874), and for *N. mauritianus* the data are the means of the dimensions given by Newton and Gadow (1893) plus those of the fossil material in the MNHN collection. Coracoid measurement is of internal length; for other bones, measurement is of total length. When measurements are not known, successive points are united by dashed lines. (Cor.=coracoid, Cpm.=carpometacarpus, Fem.=femur, Hum.=humerus, Tbt.=tibiotarsus, Tmt.=tarsometatarsus, Uln.=ulna.)

iver (1897) but afterward were translated into English by Rothschild (1907:114) as "Bitterns or Great Egrets." The word *gosier,* in old French *gauzier,* does not mean "egret" but "throat," and the words *grand gosier* designated both pelicans and the "argalas" of India (*Leptoptilus dubius* (Gmelin)).

Family THRESKIORNITHIDAE

Genus *Threskiornis* Gray

Apterornis Sélys-Longchamps, 1848:293 [not *Apterornis* Owen, 1848:1, a senior homonym; type by subsequent designation of Gray, 1855:154, *Apterornis solitarius* Sélys-Longchamps, 1848]. [New synonymy.]

Ornithaptera Bonaparte, 1854:139 [new name for *Apterornis* Sélys-Longchamps, 1848, not *Apterornis* Owen, 1848:1]. [New synonymy.]

Borbonibis Mourer-Chauviré and Moutou, 1987:419 [type by original designation, *Borbonibis latipes* Mourer-Chauviré and Moutou, 1987]. [New synonymy.]

Threskiornis solitarius (Sélys-Longchamps, 1848), new combination

Réunion Ibis

FIGURES 4*k–s*, 7*a–e*

Apterornis solitarius Sélys-Longchamps, 1848:293 [based on birds described by Tatton in S. Castleton, 1613 (1625), D.B. (=Dubois), 1671–1672 (1674), and Abbé Carré, 1667 (1699), from Bourbon (=Réunion Island)].

Didus apterornis Schlegel, 1854:244 [based on birds described by Tatton in S. Castelton, 1613 (1625) and in Abbé Carré, 1667 (1699), from Bourbon (=Réunion Island)].

Ornithaptera borbonica Bonaparte, 1854:2 [based on birds described by Tatton in S. Castleton, 1613 (1625) and in Abbé Carré, 1667 (1699), from Bourbon (=Réunion Island)].

Victoriornis imperialis Hachisuka, 1937a:71 [based in part on descriptions of the Reunion Ibis by Tatton in S. Castleton, 1613 (1625) and in W.Y. Bontekoe, 1646, but mainly on illustrations by Holsteyn and Withoos that likely pertain to the dodo (*Raphus*) of Mauritius, so that the disposition of the name must depend on future lectotypification].

Borbonibis latipes Mourer-Chauviré and Moutou, 1987:419 [holotype, right juvenile tarsometatarsus, FSL 330512 (UCB), Grotte de l'Autel, Saint-Gilles, commune of Saint-Paul, Réunion Island].

MATERIAL.—Grotte des Premiers Français: r. d. j. tarsometatarsus, 1993-37.

Grotte de l'Autel: r. coracoid, 330510; l. p. coracoid, 330527; r. carpometacarpus 330511; r. d. j. tibiotarsus, 330513; r. j. tarsometatarsus, 330512; r. d. j. tarsometatarsus, 330514; metatarsal I, 330536; j. pedal phalanx 1 of digit I, 330530; j. pedal phalanx 1 of digit II, 330529; j. pedal phalanx 1 of digit III, 330532; j. pedal phalanx 2 of digit III, 330533; j. pedal phalanx 1 of digit IV, 330535.

Marais de l'Ermitage: Anterior part of mandible, 1872; l. quadrate, 1913; sacrum, 1918; fragment of pelvis, r. side, 1912; l. scapula, 1909; l. p. humerus, 1908; r. p. ulna, 1806; ulna, s., 1910; p. radius, 1871; 3 d. radii, 1808, 1875, 1911; r. carpometacarpus, 1809; 3 r. d. tibiotarsi, 1804, 1805, 1807; l. tibiotarsus, 1867; l. d. tibiotarsus, 1868; r. and l. tarsometatarsi, same individual, 1801, 1803; r. j. tarsometatarsus, 1870; l. tarsometatarsus, 1802; l. j. tarsometatarsus, 1869; 2 pedal phalanges 1 of digit II, 1873, 1874.

REMARKS.—It had generally been thought that a representative of the family Raphidae (Columbiformes), equivalent to the Mauritius Dodo (*Raphus cucullatus* (Linnaeus)) or to the Rodrigues Solitaire (*Pezophaps solitaria* (Gmelin)), used to live on Réunion. For the following reasons, however, we believe that the "solitaire" described by the early explorers was an ibis and not a dodo (Mourer-Chauviré et al., 1995a, 1995b). First, although the early accounts speak of a solitaire, we did not find any remains of dodo-like birds. On the other hand, we found relatively abundant remains of an ibis, which had never been mentioned in the historical reports. This begged the question, was the solitaire of Réunion an ibis? Second, the morphological and behavioral characteristics given by eyewitnesses agree better with an ibis than with a dodo. Dubois said that the solitaire had a beak like a woodcock (*Scolopax*) but larger, and Feuilley mentioned that "their food is but worms and filth taken on or in the soil" (Cheke, 1987:39).

The first taxonomic authors to refer to the solitaire of Réunion (Strickland and Melville, 1848; Sélys-Longchamps, 1848; Bonaparte, 1854; Schlegel, 1854) regarded it as different from the Mauritius Dodo. Schlegel, although placing it in the same genus, presented a restoration that was quite different from the dodo, showing a bird with a longish beak, probably reflecting Dubois' description of it being like a woodcock. Nevertheless, from the time when paintings of a white dodo were considered to depict the Réunion solitaire (Newton, 1869), this bird was regarded as a species of Raphidae. Storer (1970) was the only person to suggest that it could have belonged to a different family. In addition, as pointed out by Cheke (1987:39), "none of the existing paintings ascribed to Réunion birds has supporting documentation."

DESCRIPTION AND COMPARISONS.—We previously indicated that the Réunion Ibis, then described under the new name of *Borbonibis latipes,* was more closely related to the genus *Geronticus* (Mourer-Chauviré and Moutou, 1987). Now, with more fossil remains and more comparative material, we conclude that this was an error.

The remains of the Réunion Ibis have been compared with specimens of the different extant genera of Threskiornithidae in the USNM collection, and they agree perfectly with the genus *Threskiornis.* They are most similar to the Sacred Ibis, *T. aethiopicus* (Latham), and to the Straw-necked Ibis, *T. spinicollis* (Jameson), from Australia, which is sometimes ascribed to a separate genus, *Carphibis.* The ratio-diagram of total bone length (Figure 3) shows that the curve obtained for *T. solitarius* is practically identical to that of *T. aethiopicus* and is parallel to that of *T. spinicollis.*

Various skeletal dimensions of *Threskiornis* are given in Table 4. The differences between *T. solitarius,* on the one hand, and *T. aethiopicus* and *T. spinicollis* on the other, are mainly in robustness. The total length of the bones as yet known of *T. solitarius* is almost the same as in a large male of *T. aethiopicus* and is slightly greater than in *T. spinicollis,* although the

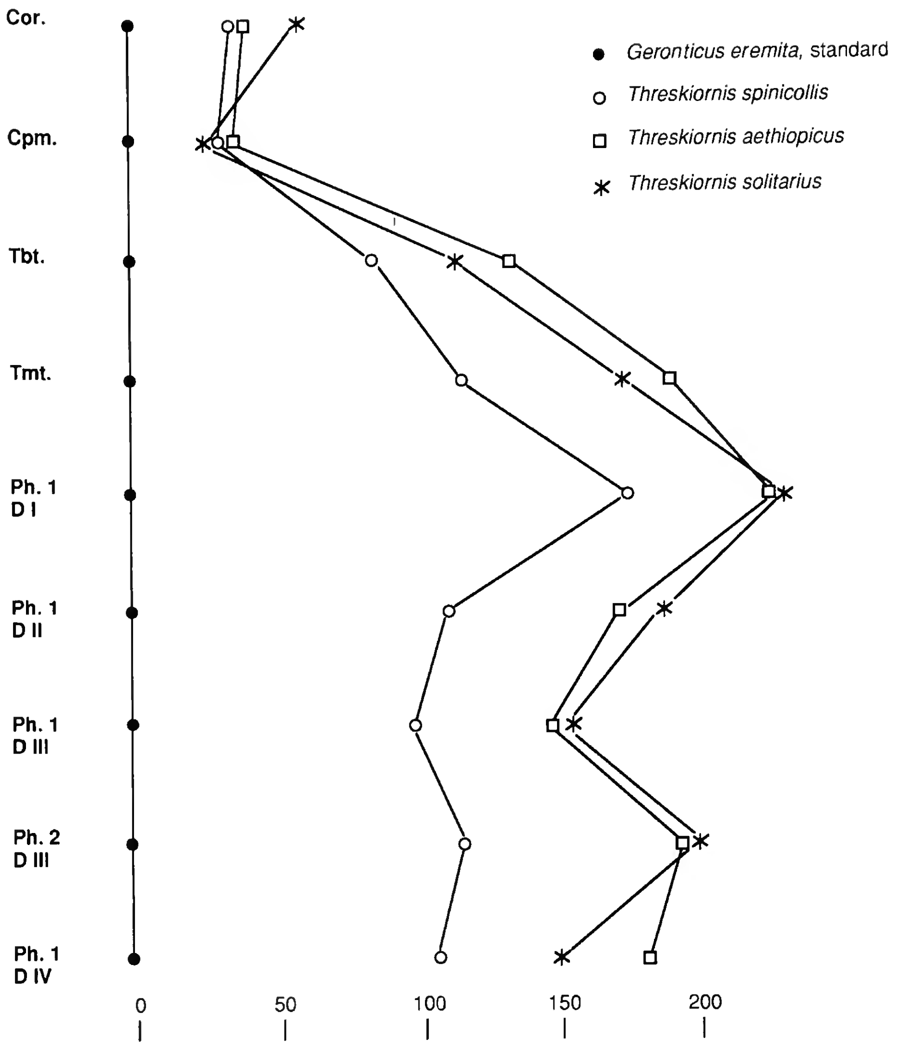


FIGURE 3.—Ratio-diagram of dimensions of long bones of *Threskiornis solitarius* compared with those of a male *T. aethiopicus* (USNM 558412), and of *T. spinicollis* (mean of two males, USNM 347785, 429720). The standard is a *Geronticus eremita* (UCB Lyon 1974-1). Coracoid measurement is of internal length; for other bones, measurement is of total length. When measurements are not known, successive points are united by dashed lines. (Cor.=coracoid, Cpm.=carpometacarpus, DI–DIV=digits I–IV, Ph.=pedal phalanx, Tbt.=tibiotarsus, Tmt.=tarsometatarsus.)

width and depth of the proximal and distal ends and of the shaft are almost always larger than in those two species. This indicates that the Réunion Ibis must have been of comparable size but was much heavier. The quadrate (Figure 4*s*, Table 4) is much stronger than in living forms; thus, the head of the bird must have been larger. The two mandiblular rami are wider at the level of the symphysis (Figure 4*n–o*), and the bill must have been more robust.

In *Threskiornis solitarius* the acrocoracoid is wider on the anterior face (Figure 7*k–l*). Only a proximal part of the humerus is known (Figure 4*p*), i.e., where the head forms a lobe above the capital groove; the distal outline of this area is much more rectilinear in *T. aethiopicus*. The two known carpometacarpi have an accessory foramen at the distal part of the symphysis between the alular and the major metacarpals (Figure 4*q*), and this foramen is absent in *T. aethiopicus*. The pisiform apophysis is preserved on only one specimen; it projects further internally than it does in *T. aethiopicus* or *T. spinicollis*. The alular metacarpals and the pisiform apophyses end in rough protuberances, as can be seen in birds that use their wings to fight. In *T. solitarius* the minor and major metacarpals are fused over a longer distance, at both proximal and distal extremities, than in *T. aethiopicus*, but the same is true in *T. spinicollis*. On the tarsometatarsus, the trochleae are more splayed and are disposed on a less-curved line than in *T. aethiopicus*. The tarsometatarsi of *T. solitarius* (Figure 7*c–e*) look very


92
MHN-RUN-FE-O-1826
A
B
C
92
D
MAD 6563
I
E
F
MHN-RUN-FE-O-1911
G
MAD 7080
J
P
330 511
Q
1950
R
K
MHN-RUN-FE-O 1909
M
L
N
O
H
T
S

FIGURE 4 (opposite).—Fossils of herons, ibis, and tropicbird from the Mascarene Islands. *Nycticorax duboisi: a,* left humerus, Marais de l'Ermitage, 1826, palmar view; *b,* right ulna, Marais de l'Ermitage, 1828, internal view; *c,* right tibiotarsus, Marais de l'Ermitage, 1829, anterior view; *d,* right femur, Marais de l'Ermitage, 1827, posterior view; *e,* left tarsometatarsus, distal part, Marais de l'Ermitage, 1865, anterior view; *f,* right tarsometatarsus, Marais de l'Ermitage, 1916, anterior view; *g,* same, posterior view; *h,* right scapula, Grotte de l'Autel, 330516, dorsal view. *Nycticorax mauritianus: i,* left femur, Mare aux Songes, MNHN MAD-6563, posterior view; *j,* right tarsometatarsus, Mare aux Songes, MNHN MAD-7080, anterior view. *Threskiornis solitarius: k,* right coracoid, Grotte de l'Autel, 330510, anterior view; *l,* same, posterior view; *m,* left scapula, Marais de l'Ermitage, 1909, ventral view; *n,* mandible, anterior part, Marais de l'Ermitage, 1872, right lateral view; *o,* same, dorsal view; *p,* left humerus, proximal part, Marais de l'Ermitage, 1908, anconal view; *q,* right carpometacarpus, Grotte de l'Autel, 330511, internal view; *r,* right ulna, proximal part, Marais de l'Ermitage, 1806, palmar view; *s,* left quadrate, Marais de l'Ermitage, 1913, posterior view. *Phaethon lepturus: t,* left coracoid, Grotte de l'Autel, 330515, posterior view. All figures are natural size.

much like those of a specimen of *T. spinicollis* (USNM 429720), in which the tarsometatarsi are shorter, with more splayed trochleae than in another individual of the same species examined, although in *T. solitarius* the trochleae are still more splayed. Indices for the tarsometatarsus (Table 5) show that its distal part is proportionally wider, and its shaft width proportional to depth is greater, in *T. solitarius* than in *T. aethiopicus* or *T. spinicollis.*

The various pectoral elements so far known, with one exception, do not indicate any reduction in flying ability; the coracoid is elongated and the proximal parts of the humerus and ulna are very robust. The only possible indication of a reduction in flying ability is the occurrence of an accessory foramen in the symphysis between the alular and the major metacarpal (Mourer-Chauviré et al., 1995b). To our knowledge this foramen exists only in flightless forms. It is present in *Palaeotis weigelti* Lambrecht, a flightless fossil ratite from the Eocene of Germany, and it also is regularly present in *Struthio,* in the Spheniscidae, and occasionally in *Rhea* (Houde and Haubold, 1987). It also exists in *Sylviornis neocaledoniae* Poplin, a giant, flightless, extinct galliform from New Caledonia (Poplin and Mourer-Chauviré, 1985).

The ibis of Réunion was probably much heavier than the living members of the genus *Threskiornis.* It was perhaps flightless in its behavior, but, apart from this accessory foramen, this had not yet led to osteological consequences.

Family PHOENICOPTERIDAE

Genus *Phoenicopterus* Linnaeus

Phoenicopterus ruber Linnaeus, 1758

Greater Flamingo

MATERIAL.—Marais de l'Ermitage. *Male-sized fossils:* Articular part of l. mandible, 1906; r. p. tarsometatarsus, 1840; r. s. tarsometatarsus, 1904; l. j. tarsometatarsus, 1907; l. d. tarsometatarsus, 1842. *Female-sized fossils:* r. s. humerus, 1856; l. d. humerus, 1877; r. d. ulna, 1878; l. p. ulna, 1905; r. carpometacarpus, 1880; r. p. tibiotarsus, 1898; r. d. tibiotarsus, 1839; r. d. tibiotarsus, 1900; l. d. tibiotarsus, 1897; 3 l. d. tibiotarsi (2 j.), 1838, 1847, 1899; l. d. tarsometatarsus with medullary bone, 1902; r. d. tarsometatarsus, 1901; 5 l. d. tarsometatarsi, 1844, 1860, 1861, 1862, 1903. *Male- or female-sized fossils:* l. quadrate, 1887; fragment of sternum, 1854; fragment of pelvis, 1855; r. scapula, 1876; l. scapula, 1852; 3 s. ulna, 1845, 1849, 1879; p. radius, 1843; 2 d. radii, 1848, 1881; l. d. carpometacarpus, 1864; r. s. tibiotarsus, 1857; l. s. tibiotarsus, 1846; 2 l. d. tibiotarsi, 1858, 1859; r. s. tarsometatarsus, 1863; r. d. j. tarsometatarsus, 1841; 6 fragments of tarsometatarsi, 1851, 1882–1886; j. pedal phalanx, 1853.

REMARKS.—The size and shape of the fossils correspond to *Phoenicopterus ruber,* the Greater Flamingo, and differ from *Phoeniconaias minor* Geoffroy Saint-Hilaire, the Lesser Flamingo. Among the tarsometatarsi of female size, one that is broken into two pieces shows a deposit of medullary bone inside the shaft. Such medullary bone tissue develops in practically all the bones of the skeleton of a female bird 10 to 14 days before egg laying. It constitutes a reserve of calcium that is used during the laying period to produce the eggshell, and it is very quickly resorbed as soon as egg laying is over (Simkiss, 1967; Rick, 1975). The presence of medullary bone indicates that Greater Flamingos formerly nested on Réunion, probably at or near the spot where the Marais de l'Ermitage is now, which, on some old maps of the island, is shown as a pond that persisted at least until the eighteenth century. The flamingo material also includes bones from juveniles.

Greater Flamingos are mentioned several times in historical accounts on Réunion (Lougnon, 1970, 1992), and Feuilley indicated that there were 3000 to 4000 of them in 1704 on the Etang du Gol (Barré and Barau, 1982). They disappeared between 1710 and 1730 (Cheke, 1987). They also have been found as fossils on Mauritius (the distal end of an ulna from Mare aux Songes is in the MNHN, MAD 6573), whence the resident population disappeared around 1758 (Cheke, 1987).

Family ANATIDAE

Genus *Alopochen* Stejneger

Alopochen (*Mascarenachen*) *kervazoi* (Cowles, 1994), new combination

Kervazo's Egyptian Goose

FIGURE 7*f–n*

MATERIAL.—Grotte des Premiers Français. *Holotype:* Fragment of rostrum, 1993-19. *Paratypes:* Sternum, 2 anterior parts, 1993-22, 1993-24; sternum, posterior part, 1993-25; furcula, 1993-21; cervical vertebra, 1993-27; r. carpometacarpus, with thickened bony knob, 1993-20; l. carpometacarpus, 1993-

TABLE 4.—Dimensions (mm) of different bones of the extinct Réunion Ibis, *Threskiornis solitarius,* modern *T. aethiopicus* (USNM, MNHN, and UCB), and modern *T. spinicollis* (USNM). (a=proximal width measured without external tubercle; *n*=number of specimens.)

Measurements	*T. solitarius*		*T. aethiopicus*	*T. spinicollis*
	mean (*n*)	range	range (*n*)	range (*n*)
Quadrate				
length from squamosal articulation to mandibular articulation	18.9 (1)	–	15.0–15.5 (4)	–
Mandible				
width at level of symphysis	6.4 (1)	–	4.7–6.3 (4)	–
dorsoventral length at same level	5.2 (1)	–	5.0–6.8 (4)	–
Coracoid				
maximum length	~58.2 (1)	–	51.5–59.0 (12)	55.8–57.0 (2)
internal length	53.5 (1)	–	46.2–52.3 (12)	49.6–51.8 (2)
proximal width	15.8 (1)	–	12.1–14.4 (12)	13.1–13.7 (2)
proximal depth	13.9 (1)	–	11.3–13.0 (12)	12.3–12.3 (2)
head width	8.5 (1)	–	5.6–7.0 (12)	6.0–7.5 (2)
sternal-facet length	~25.2 (1)	–	19.4–23.4 (12)	20.0–23.0 (2)
sternal-facet depth	5.4 (1)	–	4.2–5.9 (12)	4.7–6.0 (2)
midshaft width	9.2 (1)	–	6.7–9.0 (12)	8.5–8.8 (2)
midshaft depth	7.8 (1)	–	5.4–6.3 (12)	6.3–6.4 (2)
Humerus				
proximal width	32.3 (1)	–	26.4–30.0 (12)	28.2–30.4 (2)
Ulna				
proximal width	14.6 (1)	–	12.2–13.8 (12)	14.2–14.2 (2)
proximal depth	13.6 (1)	–	11.7–13.5 (12)	13.1–13.5 (2)
midshaft width	7.1 (1)	–	5.6–6.6 (12)	6.3–6.7 (2)
midshaft depth	7.2 (1)	–	5.7–6.7 (12)	6.2–6.8 (2)
Carpometacarpus				
total length	73.95 (2)	73.0–74.9	64.3–75.6 (12)	73.6–75.2 (2)
proximal width	8.8 (1)	–	6.5–7.5 (12)	7.4–7.4 (2)
proximal depth	17.95 (2)	17.3–18.6	14.6–17.0 (12)	16.6–17.2 (2)
distal width	8.6 (1)	–	6.2–7.7 (12)	7.3–8.1 (2)
distal depth	11.3 (1)	–	9.19–10.3 (12)	9.2–9.7 (2)
width metacarpale majus	5.65 (2)	5.5–5.8	4.8–5.5 (12)	5.1–5.7 (2)
depth metacarpale majus	5.0 (2)	4.8–5.2	3.9–4.6 (12)	4.2–4.8 (2)
Tibiotarsus				
total length	144.5 (1)	–	129.5–156.0 (12)	133.4–137.0 (2)
proximal width	16.0 (1)	–	12.6–15.5 (12)	13.5–15.0 (2)
proximal depth	21.6 (1)	–	16.4–19.1 (12)	18.0–18.8 (2)
distal width	15.78 (6)	15.0–16.1	11.8–14.4 (12)	12.8–14.1 (2)
distal depth	15.80 (3)	15.2–16.6	12.3–14.7 (12)	13.3–14.0 (2)
midshaft width	9.63 (4)	9.1–10.3	6.4–8.0 (12)	7.0–7.5 (2)
midshaft depth	6.45 (4)	6.3–6.6	4.6–6.5 (12)	5.5–6.0 (2)
Tarsometatarsus				
total length	105.10 (6)	103.4–106.9	89.1–115.2 (12)	89.0–96.7 (2)
proximal width (a)	17.85 (6)	17.2–18.5	13.4–16.5 (12)	14.9–16.4 (2)
proximal depth	17.83 (3)	17.0–18.4	12.1–14.7 (12)	13.5–14.2 (2)
distal width	20.72 (5)	19.4–21.3	13.7–16.2 (12)	15.3–16.5 (2)
distal depth	13.90 (4)	13.7–14.5	10.1–12.5 (12)	11.5–12.2 (2)
midshaft width	7.98 (6)	7.2–8.4	5.3–6.7 (12)	6.0–6.8 (2)
midshaft depth	5.65 (6)	5.5–5.8	4.3–5.4 (12)	5.0–5.1 (2)
Metatarsal I				
total length	16.8 (1)	–	13.4–15.8 (12)	15.0–15.8 (2)
width distal articulation	7.3 (1)	–	4.2–5.6 (12)	4.5–5.2 (2)
Pedal phalanges				
phalanx 1 digit I				
total length	27.4 (1)	–	25.5–29.4 (12)	24.0–24.3 (2)
proximal width	7.4 (1)	–	4.4–5.4 (12)	5.3–5.5 (2)
phalanx 1 digit II				

TABLE 4.—Continued.

Measurements	*T. solitarius* mean (*n*)	*T. solitarius* range	*T. aethiopicus* range (*n*)	*T. spinicollis* range (*n*)
total length	29.97 (3)	29.5–30.8	24.7–30.8 (12)	25.1–25.6 (2)
proximal width	7.40 (3)	7.3–7.5	4.9–6.4 (12)	5.6–5.9 (2)
phalanx 1 digit III				
total length	29.7 (1)	–	24.3–31.2 (12)	25.6–27.2 (2)
proximal width	8.2 (1)	–	5.5–5.8 (12)	6.4–6.6 (2)
phalanx 2 digit III				
total length	25.3 (1)	–	21.9–26.4 (12)	20.1–22.0 (2)
proximal width	5.9 (1)	–	4.2–5.4 (12)	4.9–5.1 (2)
phalanx 1 digit IV				
total length	20.8 (1)	–	19.0–24.1 (12)	18.0–19.8 (2)
proximal width	7.4 (1)	–	5.0–6.5 (12)	5.7–6.2 (2)

23; phalanx 1 of the major digit of wing, 1993-26. *Additional Specimen:* r. d. radius, 1993-54.

Grotte de l'Autel: Cranium, 330525; sternum, anterior part and fragment, 330523; l. coracoid, 330519; l. scapula, 330524; r. humerus, 330517; l. p. ulna, 330518; 2 r. carpometacarpi, 330520, 330522; l. femur, 330526; r. tarsometatarsus, 330521.

Grotte "au sable": Fragment of furcula, 330735; sacrum, r. lateral part of pelvis, l. lateral part of pelvis from same bone, 330730–330732; d. radius, 330733; phalanx 1 of major digit of wing, 330736; phalanx 2 of major digit of wing, 330734.

Marais de l'Ermitage: Sacrum, 1914; fragment of pelvis (without number); 2 l. anterior scapulae, 1825, 1889; 2 l. coracoids, 1822, 1888; r. s. humerus, 1821; r. d. ulna, 1892; r. d. carpometacarpus, 1891; l. p. carpometacarpus, 1823; l. s. carpometacarpus, 1890; r. d. tibiotarsus, 1824; r. s. j. tibiotarsus, 1820; l. d. j. tibiotarsus, 1915; r. d. j. tarsometatarsus, 1893.

REMARKS.—The new genus and species *Mascarenachen kervazoi* was created by Cowles (1994) for an extinct sheldgoose from Réunion. Comparison of a larger quantity of material from the Grotte de l'Autel and Marais de l'Ermitage, in addition to that from the Grotte des Premiers Français, shows that the Réunion form is very close to the living *Alopochen aegyptiacus* (Linnaeus), the Egyptian Goose, which lives in many parts of Africa. Extinct species of *Alopochen* also are known from Madagascar and Mauritius.

Cowles (1994) gave two sets of characteristics in the diagnosis of the genus *Mascarenachen.* First, the bill is shorter and is dorsoventrally deeper at the level of the cranial junction than in other Tadorninae, and the rostral tip forms a true semicircle, whereas in the other Tadorninae it is more pointed and forms a semiellipse (Figure 7*g*). Second, the sternal carina has an almost straight, not concave, anterior margin and a pronounced ventral manubrial spine.

Dubois described the geese of Réunion as being "wild geese, slightly smaller than European geese. They have the same feathering, but with the bill and the feet red. They are very good [to eat]" (Barré and Barau, 1982:30, our translation). This description applies well to a goose related to *A. aegyptiacus,* which has a pink bill and bright pink legs and feet (Brown et al., 1982).

TABLE 5.—Tarsometatarsus distal width and shaft indices in the extinct Réunion Ibis *Threskiornis solitarius* and in modern *T. aethiopicus* and *T. spinicollis.* (Distal-width index=distal width × 100/ total length; shaft index=width midshaft × 100/ depth midshaft; *n*=number of specimens.)

Species	Distal width index mean (*n*)	Distal width index range	Shaft index mean (*n*)	Shaft index range
T. solitarius	19.92 (4)	19.81–20.04	141.33 (5)	129–151
T. aethiopicus	14.65 (11)	13.70–15.94	125.45 (11)	119–137
T. spinicollis	17.18 (2)	15.82–18.54	127.00 (2)	118–136

COMPARISON WITH LIVING FORMS.—After examining 11 specimens of *A. aegyptiacus* in the USNM and MNHN collections, we found the cranium and all the elements of the post-cranial skeleton of *Mascarenachen* to be morphologically very similar to those in the genus *Alopochen*, although differing from those in all the other genera of Tadorninae. The premaxilla of the Réunion sheldgoose differs from all specimens of *A. aegyptiacus,* however, by its shorter length (Table 6) and by the semicircular shape of the tip. The rostrum is longer and anteriorly sharper in *A. aegyptiacus.* In the Réunion sheldgoose, the part of the nasal above the nostrils bulges; the nostrils are not narrow and elongated, as in *A. aegyptiacus,* but are more rounded. The dorsal outline of the premaxilla is almost straight, whereas in *A. aegyptiacus* it is clearly upturned at the tip. The premaxilla also is much deeper than in *A. aegyptiacus.*

The anterior carinal margin of the sternum is almost straight in the specimen described by Cowles (MNHN LAC-1933-22), but it is strongly concave in specimen UCB FSL-330523 (Figure 7*n*), which also possesses a ventral manubrial spine that is narrow but very projecting. The shapes of the anterior carinal margin and of the ventral manubrial spine are highly variable in *A. aegyptiacus;* some individuals have a straight anterior margin, others a slightly incurved one, and still others a deeply incurved one. Likewise, some individuals have a very projecting ventral manubrial spine, others a very short one, and others no ventral manubrial spine at all.

TABLE 6.—Dimensions (mm) of the skull and long bones of the extinct *Alopochen* (*Mascarenachen*) *kervazoi*, from Réunion, modern *A. aegyptiacus* (USNM), and extinct *Alopochen sirabensis* (MNHN), from Madagascar. (a=maximal width of frontal at level of processus supraorbitalis of prefrontal bone; b=minimal width of frontal above orbits; c=cranium width at level of insertion of postorbital processes; d=bill length, from frontonasal hinge to tip of premaxillae; e=bill depth, from dorsal surface at frontonasal hinge to ventral surface at proximal end of maxillary; f=sternum-keel depth, from dorsal surface of sternum to ventral tip of keel; g=pelvis length, from first synsacral vertebra to last synsacral vertebra; h=length of anterior scapula, from base of glenoid facet to top of acromion; *n*=number of specimens.)

Measurement	*A. (M.) kervazoi*		*A. aegyptiacus*		*A. sirabensis*	
	mean (*n*)	range	mean (*n*)	range	mean (*n*)	range
Skull						
frontal width (a)	25.3 (1)	–	24.17 (7)	21.8–26.3	–	–
frontal width (b)	13.0 (1)	–	12.58 (8)	11.1–14.2	–	–
cranium width (c)	30.7 (1)	–	30.46 (8)	29.4–32.3	–	–
bill length (d)	45.1 (1)	–	50.91 (8)	47.6–54.1	–	–
bill depth (e)	18.6 (1)	–	19.16 (8)	17.5–21.0	–	–
ratio e x 100 : d	41.2 (1)	–	37.66 (8)	34.3–39.9	–	–
Sternum						
keel depth (f)	37.20 (2)	36.7–37.7	37.17 (9)	34.1–40.2	–	–
Pelvis						
length (g)	100.6 (1)	–	104.71 (9)	99.0–112.0	–	–
Coracoid						
maximum length	~63 (1)	–	67.71 (9)	62.0–75.1	–	–
internal length	56.90 (3)	53.7–60.0	60.56 (11)	55.0–65.6	63.11 (16)	56.7–68.3
proximal width	13.8 (1)	–	14.17 (9)	12.4–16.0	–	–
proximal depth	12.03 (3)	11.1–13.0	13.71 (9)	12.2–15.1	–	–
sternal-facet length	23.5 (1)	–	25.30 (9)	23.7–27.9	–	–
sternal-facet depth	5.4 (1)	–	6.10 (9)	5.0–7.3	–	–
midshaft width	6.87 (3)	6.2–7.4	7.52 (10)	6.5–8.8	7.34 (16)	6.6–7.9
midshaft depth	4.97 (3)	4.6–5.2	5.33 (9)	4.6–6.2	–	–
Scapula						
anterior length (h)	14.70 (3)	14.2–15.5	17.11 (9)	15.7–19.0	–	–
Humerus						
total length	126.0 (1)	–	134.10 (11)	122.8–148.4	140.26 (30)	127.3–152.4
proximal width	25.7 (1)	–	28.79 (10)	25.7–32.7	–	–
proximal depth	14.2 (1)	–	14.86 (10)	13.2–16.4	–	–
distal width	19.2 (1)	–	20.63 (10)	18.3–22.5	–	–
distal depth	10.9 (1)	–	11.63 (10)	10.5–12.5	–	–
midshaft width	9.65 (2)	9.0–10.3	9.62 (10)	8.6–11.0	10.07 (30)	8.8–11.8
midshaft depth	8.25 (2)	8.0–8.5	8.89 (9)	8.1–10.0	–	–
Ulna						
total length	~119 (1)	–	128.92 (11)	118.1–144.1	128.56 (10)	119.5–139.1
proximal width	13.1 (1)	–	13.80 (10)	11.8–15.4	–	–
proximal depth	11.9 (1)	–	12.53 (10)	11.5–13.7	–	–
distal width	12.3 (1)	–	12.01 (10)	10.6–13.5	–	–
depth external condyle	10.8 (1)	–	11.47 (9)	10.2–12.7	–	–
midshaft width	6.65 (2)	6.3–7.0	7.13 (10)	6.4–7.9	6.96 (10)	6.3–7.5
midshaft depth	6.50 (2)	6.0–7.0	6.84 (9)	5.9–7.5	–	–
Carpometacarpus						
total length	72.35 (4)	70.7–75.7	79.06 (10)	72.0–86.0	80.69 (21)	73.2–90.0
proximal width	7.70 (4)	7.4–8.2	8.21 (10)	7.2–9.0	–	–
proximal depth	19.80 (4)	18.3–22.4	22.61 (11)	19.3–27.4	–	–
distal width	9.05 (4)	8.6–9.5	9.76 (9)	8.8–10.6	–	–
distal depth	6.23 (4)	5.8–6.5	6.92 (9)	6.3–7.5	–	–
width metacarpale majus	6.07 (7)	5.3–6.5	6.06 (9)	5.5–6.7	6.52 (21)	5.9–7.1
depth metacarpale majus	4.78 (6)	4.2–5.3	5.09 (8)	4.5–6.0	–	–
Phalanx 1, major wing digit						
total length	31.60 (2)	30.9–32.3	–	–	–	–
Phalanx 2, major wing digit						
total length	24.1 (1)	–	26.06 (7)	24.1–28.1	–	–
Femur						

TABLE 6.—Continued.

Measurement	*A.* (*M.*) *kervazoi*		*A. aegyptiacus*		*A. sirabensis*	
	mean (*n*)	range	mean (*n*)	range	mean (*n*)	range
total length	69.0 (1)	–	71.04 (11)	65.0–78.0	72.64 (12)	66.8–78.4
proximal width	18.8 (1)	–	17.31 (10)	14.9–20.6	–	–
proximal depth	11.8 (1)	–	12.01 (10)	11.0–13.7	–	–
distal width	16.9 (1)	–	17.60 (10)	15.5–20.1	–	–
distal depth	12.6 (1)	–	13.38 (10)	12.1–15.0	–	–
midshaft width	6.9 (1)	–	7.24 (10)	6.4–7.9	8.03 (12)	7.3–9.0
midshaft depth	7.8 (1)	–	7.70 (9)	6.1–9.0	–	–
Tibiotarsus						
total length	–	–	133.30 (11)	124.2–146.2	136.97 (19)	123.7–144.8
proximal width	–	–	14.52 (9)	12.8–17.0	–	–
proximal depth	–	–	17.42 (9)	16.0–18.7	–	–
distal width	–		14.01 (10)	12.6–15.6	–	–
distal depth	–	–	15.33 (10)	13.7–17.6	–	–
midshaft width	6.0 (1)	–	7.44 (10)	6.5–8.3	7.55 (19)	6.2–8.7
midshaft depth	5.8 (1)	–	6.14 (9)	5.3–6.9	–	–
Tarsometatarsus						
total length	80.5 (1)	–	86.42 (11)	77.0–96.6	86.03 (17)	76.5–94.3
proximal width	14.8 (1)	–	15.25 (10)	14.3–16.1	–	–
proximal depth	13.4 (1)	–	13.23 (10)	12.1–14.6	–	–
distal width	~16 (1)	–	16.17 (10)	14.6–18.7	–	–
distal depth	~11 (1)	–	11.96 (9)	10.9–13.4	–	–
midshaft width	5.95 (2)	5.2–6.7	6.13 (10)	5.3–7.0	6.01 (17)	5.3–7.3
midshaft depth	5.30 (2)	4.8–5.8	5.90 (10)	5.2–6.6	–	–

Humerus UCB FSL-330517 (Figure 7*i*) also shows a slight difference compared with *A. aegyptiacus.* On the anconal face, below the head, and on the medial side of the pneumatic fossa, there is a proximodistally elongated depression that does not exist in *A. aegyptiacus.* Moreover, on this humerus, the pneumatic foramen, which opens at the bottom of the pneumatic fossa, has a small surface compared with that of the fossa, whereas in *A. aegyptiacus* the pneumatic foramen occupies all the surface of the pneumatic fossa.

On the whole, because of the great similarities between the Réunion sheldgoose and the living Egyptian goose, we think that *Mascarenachen* must be considered a subgenus, and that the Réunion form can be designated as *Alopochen* (*Mascarenachen*) *kervazoi* (Cowles), new combination. This subgenus includes only the type species, *kervazoi.*

Although the size of *A. aegyptiacus* is highly variable (Table 6), the mean dimensions of *A.* (*M.*) *kervazoi* are smaller than those of *A. aegyptiacus.* The size of the Réunion sheldgoose either is at the lower limit of variation in *A. aegyptiacus* or is slightly smaller.

COMPARISON WITH FOSSIL FORMS.—An extinct sheldgoose, *Chenalopex sirabensis,* was described by Andrews (1897) from Holocene deposits in Madagascar. Because *Chenalopex* is a synonym of *Alopochen,* it is now known as *Alopochen sirabensis* (Brodkorb, 1964). It varies widely in size, so Andrews divided the material into two sets that he attributed to males and females. In a large amount of material at MNHN, the size of the bones also varies according to the locality, the material from Antsirabé being larger than that from Ankazoabo. We present measurements of specimens from both sites (Table 6) without trying to separate males and females. Bones of *A. sirabensis* on average are larger than those of living *A. aegyptiacus* and are thus distinctly larger than *A.* (*M.*) *kervazoi.*

Another extinct species, *Sarkidiornis mauritianus,* was described by Newton and Gadow (1893). The holotype is a left carpometacarpus with a very projecting alular metacarpal ending in a callosity. Andrews (1897) showed that this bone corresponded to the genus *Chenalopex* and did not differ from the species *Chenalopex sirabensis* that he was describing from Madagascar (although the former name has priority). The length of this carpometacarpus (77 mm) is within the variation of *A. sirabensis* (Table 6) and is slightly larger than the largest individuals of *A.* (*M.*) *kervazoi.* The Réunion form shows some characteristics that are probably related to insularity (see below). The Mauritian form also may be an endemic insular form. With more fossil material from Mauritius, it might be possible to discern distinctive characteristics compared with the Madagascar and Réunion forms.

The ratio-diagram (Figure 5) drawn for the species *Alopochen aegyptiacus, A. sirabensis,* and *A.* (*M.*) *kervazoi* shows a slight lessening of flying ability in *A. sirabensis* compared with *A. aegyptiacus,* as indicated by shortening of the ulna and carpometacarpus and by the slight lengthening of the femur. The curve of *A.* (*M.*) *kervazoi* closely parallels that of *A. sirabensis,* but it also shows a slight reduction of the ulna and carpometacarpus and a slightly longer femur. For comparison, an-

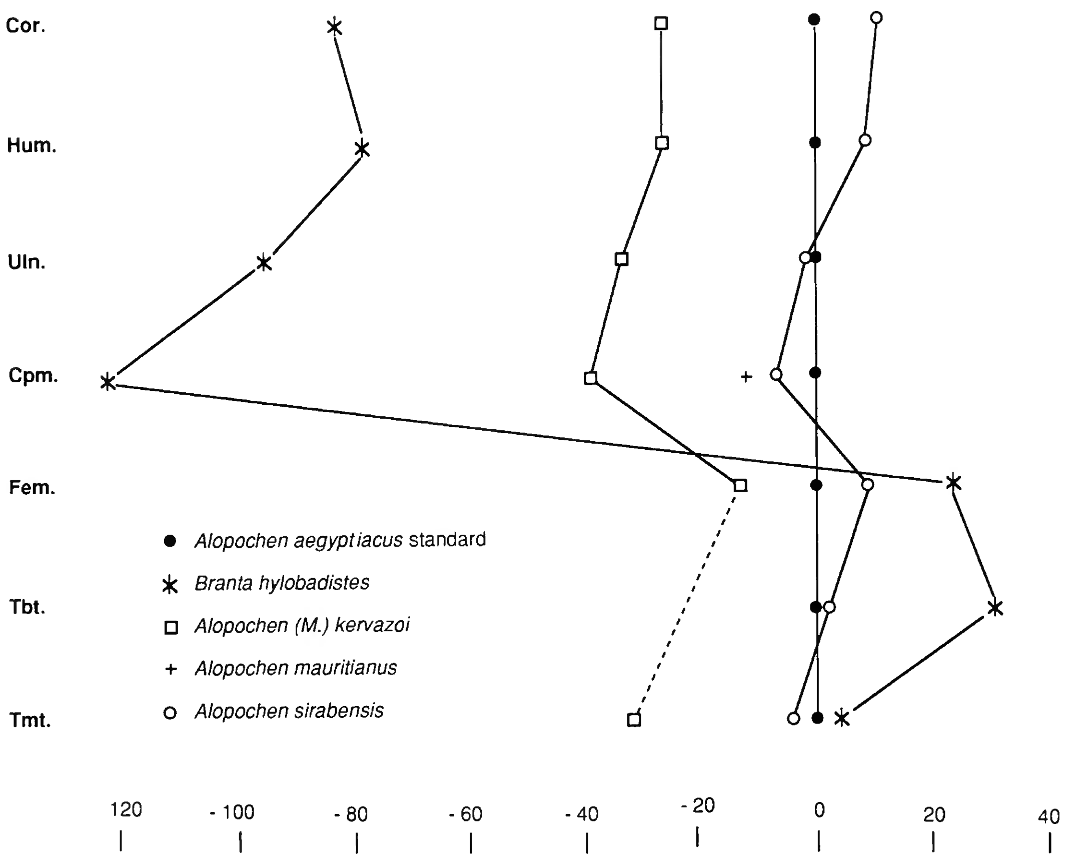


FIGURE 5.—Ratio-diagram of the mean dimensions of the long bones of *Alopochen* (*Mascarenachen*) *kervazoi*, compared with those of *Alopochen sirabensis, A. mauritianus,* and *Branta hylobadistes* (USNM 322632, see Olson and James, 1991). The standard is the mean of the dimensions of 11 *A. aegyptiacus* (USNM 19003, 291415, 346399, 346854, 430829, 431686 431687, 488145, 488713; MNHN-LAC 1874-154, 1911-39). Coracoid measurement is of internal length; for other bones, measurement is of total length. When measurements are not known, successive points are united by dashed lines. (Cor.=coracoid, Cpm.=carpometacarpus, Fem.=femur, Hum.=humerus, Tbt.=tibiotarsus, Tmt.=tarsometatarsus, Uln.=ulna.)

other extinct species of goose, *Branta hylobadistes* Olson and James (1991) from the Hawaiian Islands, shows a much more reduced flying ability, with a considerable shortening of the carpometacarpus and lengthening of the femur (Olson and James, 1991). Thus, it can be concluded that *A.* (*M.*) *kervazoi* had only slightly reduced flying ability compared with the continental form *A. aegyptiacus.*

The other typical characteristic of *A.* (*M.*) *kervazoi* is the shortening of the bill, with a depth/length ratio larger than in the continental form *A. aegyptiacus.* Unfortunately, the bill is unknown in *A. sirabensis* (none in MNHN, see also Cowles, 1994) as well as in *A. mauritianus.* Such shortening is very conspicuous in the extinct genera from Hawaii, *Thambetochen* and *Chelychelynechen* (Olson and James, 1991). The similarity of morphology between the species from Réunion and Hawaii is undoubtedly a convergent adaptation to an insular environment.

Genus *Anas* Linnaeus

Anas theodori Newton and Gadow, 1893

Sauzier's Teal

FIGURE 7*q,r*

MATERIAL.—Marais de l'Ermitage: Sternum, anterior part, 1895; l. ulna, 1810; l. tibiotarsus, 1894.

REMARKS.—*Anas theodori* was described by Newton and Gadow (1893) from material including the anterior part of a sternum, two coracoids, eight humeri, and two tarsometatarsi from Mauritius. The material preserved in MNHN includes a cast of this sternum, a coracoid, four humeri, an incomplete juvenile carpometacarpus, a tibiotarsus, and two juvenile tarsometatarsi. The anterior part of the sternum from Réunion is poorly preserved and does not allow detailed comparison. The Réunion tibiotarsus (Figure 7*r*), however, is absolutely identical in shape and dimensions to that from Mauritius and therefore must belong to the same species.

Compared with living forms of *Anas* from Madagascar, *A. theodori* is larger than *A. bernieri* (Hartlaub) (Figure 5, Table 7) and smaller than *A. melleri* P.L. Sclater (Howard, 1964). We compared it in the USNM with various species of *Anas*. The one it resembles most is *Anas gibberifrons* Müller, which lives in the east and northeast of the Indian Ocean, from the Andaman Islands to Indonesia and Australia, and on islands in the western Pacific Ocean (Mayr and Cottrell, 1979). The common characteristics and the differences between *A. theodori* and *A. gibberifrons* are as follows. If the anterior part of the sternum illustrated by Newton and Gadow (1893, pl. 34: figs. 11, 12) is perfectly preserved, the carina projects further anteriorly and the ventral manubrial spine (spina externa of Newton and Gadow) is narrow and elongated in *A. gibberifrons* and is more elongated than in *A. theodori*. The coracoid of *A. theodori* looks very similar to that of *A. gibberifrons*. On the internal side of the posterior face, above the sternal facet, there is a small, proximally directed spike, followed by a small depression, which also is present in *A. gibberifrons*. On the anterior face, near the internal side of the acrocoracoid, an almost circular muscular scar occurs in *A. the-*

TABLE 7.—Dimensions (mm) of the main bones of the extinct *Anas theodori*, from Mauritius and Réunion, compared with modern *Anas gibberifrons* (USNM) and *Anas bernieri* (two specimens; Steve Goodman, pers. comm., 1995). For *Anas theodori* from Mauritius, the dimensions are from material at MNHN (prefix MAD), from Newton and Gadow (N. & G., 1893), or measured from their figures; Réunion dimensions are from material at MHNR (prefix FE-O). (a=width of front part of sternum, measured between the two lateral intermuscular lines; b=sternum-keel depth, from dorsal surface of sternum to ventral tip of keel; c=measured without cnemial crests; d=measured with cnemial crests; *n*=number of specimens.)

Measurement	*Anas theodori*				*Anas bernieri*	*Anas gibberifrons*	
	Réunion	Mauritius	Mauritius	Mauritius		mean (*n*=4)	range
Sternum		MAD-4057 (cast)					
width (a)		27.7				24.25	23.2–25.8
keel depth (b)		21.7				20.78	19.4–21.8
Coracoid		MAD-4993	N. & G., 1893				
internal length		41.1	42.5		~30.9, ~31.2	37.55	35.1–38.9
proximal width		~9	~8		–	8.03	7.4–8.4
proximal depth		8.3	–			7.20	6.8–7.6
sternal-facet length		–16	17.2		–	15.33	14.5–16.3
sternal-facet depth		3.6	–		–	2.98	2.7–3.2
minimum shaft width		4.3	4.1		–	3.80	3.7–4.0
depth at same level		3.5	–		–	2.98	2.6–3.2
Humerus		MAD-4988	MAD-4989	MAD-4991			
total length		73.0	69.6	73.1	64.5, 66.5	69.93	~68–71.4
proximal width		–16	15.5	16.1	13.3, 13.5	15.18	14.5–15.5
proximal depth		–	7.9	8.2	–	7.68	7.4–8.0
distal width		11.2	11.3	11.6	10.0, 10.3	10.75	9.9–11.2
distal depth		6.6	6.5	6.5	–	6.50	6.2–6.7
midshaft width		5.2	5.2	5.6	–	5.33	5.1–5.6
midshaft depth		4.5	4.2	4.6	–	4.50	4.2–4.8
Ulna	FE–O–1810						
total length	~63				58.0, 60.6	61.55	59.5–63.2
proximal width	7.5				7.4, 7.6	7.45	7.1–7.6
proximal depth	7.0				–	6.88	6.2–7.5
distal width	6.0				6.0, 6.1	5.98	5.7–6.1
depth external condyle	7.1				–	6.50	6.2–6.8
midshaft width	4.4				–	3.95	3.6–4.2
midshaft depth	3.9				–	4.00	3.6–4.4
Tibiotarsus	FE–O–1894	MAD-7161					
total length (c)	71.0	71.0			65.1, 67.6 (d)	64.38	59.5–67.4
proximal width (c)	8.5	8.6			6.7, 6.8	7.50	~7–7.9
proximal depth (c)	9.7	9.2			–	8.53	~8–9.3
distal width	8.0	8.0			6.7, 6.8	6.78	6.6–7.1
distal depth	–	9.0			–	7.58	7.0–8.0
minimum shaft width	3.8	3.7			–	3.08	3.0–3.1
depth at same level	3.0	3.2			–	2.68	2.5–2.8
Tarsometatarsus		MAD-4992*	N. & G., 1893				
total length		~42	42.0		38.7, 39.3	36.15	33.3–38.9
proximal width		–	9.2		7.0, 7.3	7.48	7.1–8.1
proximal depth		–	8.3		–	6.83	6.3–7.2
distal width		–	9.2		7.3, 7.5	7.70	7.1–8.3
distal depth		–	–		–	5.48	5.1–5.9
midshaft width		4.2	4.3		–	3.35	3.0–3.9
midshaft depth		3.6	–		–	2.93	2.7–3.1

*Specimen very juvenile.

odori as well as in *A. gibberifrons*. The humerus of *A. theodori* also looks very similar to that of *A. gibberifrons*. The humeral head forms a well-developed rim above the tricipital fossa, and the pectoral attachment is well developed and elongated. On the distal part, the brachialis anticus impression and the olecranal fossa are deep. The ulna of *A. theodori* (Figure 7*q*) is short and stout, exactly as in *A. gibberifrons*, and its size is the same as in a male of that species (USNM 610562). The humero-ulnar depression is pronounced proximally. Distally, the external condyle is extended by a narrow and well-defined lip, which rises proximad along the shaft, as in *A. gibberifrons*. The tibiotarsus and tarsometatarsus, compared with those of *A. gibberifrons*, are longer, more robust, and their proximal and distal parts are proportionally wider (Table 7).

The proportions of *A. theodori* are very close to those of *A. gibberifrons* (Figure 6), but the coracoid, tibiotarsus, and tar-

FIGURE 7 (opposite).—Fossils of ibis and waterfowl from Réunion Island. *Threskiornis solitarius: a,* left tibiotarsus, Marais de l'Ermitage, 1867, anterior view; *b,* same, posterior view; *c,* right tarsometatarsus, Marais de l'Ermitage, 1801, anterior view; *d,* same, posterior view; *e,* right tarsometatarsus, distal part, Grotte des Premiers Français, 1993-37, anterior view. *Alopochen* (*Mascarenachen*) *kervazoi: f,* cranium, Grotte de l'Autel, 330525, forsal view; *g,* rostrum, holotype, Grotte des Premiers Français, 1993-19, dorsal view; *h,* left coracoid, Grotte de l'Autel, 330519, posterior view; *i,* right humerus, Grotte de l'Autel, 330517, anconal view; *j,* right tarsometatarsus, Grotte de l'Autel, 330521, anterior view; *k,* right carpometacarpus, Grotte de l'Autel, 330522, internal view; *l,* right carpometacarpus, paratype, Grotte des Premiers Français, 1993-20, internal view; *m,* left femur, Grotte de l'Autel, 330526, posterior view; *n,* sternum, anterior part, Grotte de l'Autel, 330523, right lateral view. *Aythya* sp.: *o,* right carpometacarpus, Marais de l'Ermitage, 1924, internal view; *p,* left carpometacarpus, proximal part, Marais de l'Ermitage, 1925, internal view. *Anas theodori: q,* left ulna, Marais de l'Ermitage, 1810, internal view; *r,* left tibiotarsus, Marais de l'Ermitage, 1894, anterior view. All figures are natural size.

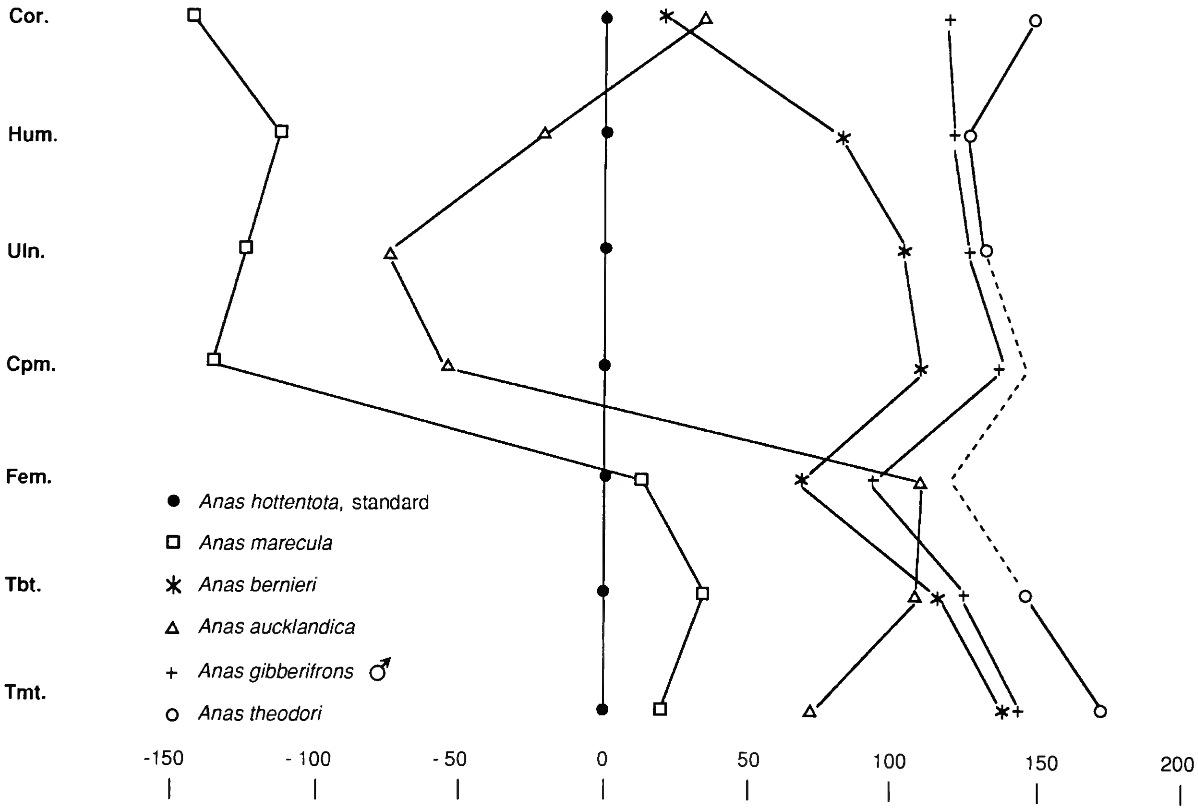


FIGURE 6.—Ratio-diagram of the mean dimensions of *Anas theodori* compared with *A. gibberifrons* (male, USNM 610562) and to the mean dimensions of two *Anas bernieri* (Steve Goodman, pers. comm., 1995). The standard is *Anas hottentota* (male, USNM 430832). For comparison, the dimensions of two flightless forms are indicated, *Anas aucklandica* (USNM 612796), and the extinct *Anas marecula,* after Martinez (1987). For *A. bernieri* the internal length of the coracoid has been estimated from its total length. Coracoid measurement is of internal length; for other bones, measurement is of total length. When measurements are not known, successive points are united by dashed lines. (Cor.=coracoid, Cpm.=carpometacarpus, Fem.=femur, Hum.=humerus, Tbt.=tibiotarsus, Tmt.=tarsometatarsus, Uln.=ulna.)


A
B
MHN·RUN·FE·O·1867
C
D
E
F
330525
G
H
I
330517
J
330521
K
L
M
330526
N
330523
O
P
Q
R

sometatarsus are proportionally longer. These proportions do not indicate a reduction in flying ability. They are very different from those of flightless teals, such as *A. aucklandica* (Gray) or the extinct form *Anas marecula* Olson and Jouventin (1996) from Amsterdam Island (Martinez, 1987; Olson and Jouventin, 1996). Thus it is possible that *A. theodori* had normal flying ability and could fly between Mauritius and Réunion, which explains how the same species could occur on both islands.

The only mention of small anatids on Réunion is by Dubois: "River ducks, smaller than European ones, feathered like teals. They are good [to eat])" (Barré and Barau, 1982:30, our translation).

ANATIDAE, cf. *Aythya* Boie

cf. *Aythya* sp.

FIGURE 7*o,p*

MATERIAL.—Marais de l'Ermitage: r. carpometacarpus, 1924; l. p. carpometacarpus, 1925.

REMARKS.—Two carpometacarpi from the Marais de l'Ermitage differ from the genus *Anas* in that the alular metacarpal does not project very far anteriorly, does not rise very much proximally, and, on the internal face, the posterior outline of the carpal trochlea is less rounded. Thus, they look more similar to the genus *Aythya*, but the pisiform process is broken, making the generic attribution uncertain.

In their dimensions (total length 46.8 mm), the carpometacarpi from Réunion correspond to the Northern Hemisphere species *A. marila* (Linnaeus) or *A. ferina* (Linnaeus). Around the Indian Ocean the genus *Aythya* is represented by three species, *A. baeri* (Radde) (Southeast Asia and China), *A. australis* (Eyton) (Australia), and *A. innotata* (Salvadori) (Madagascar). The length of the carpometacarpus is known for one individual of *A. innotata* (42.9 mm; Goodmann, pers. comm., 1995). Given the wide range of variation in this species (Hoyo et al., 1992), it is possible that the Réunion specimens belong to *A. innotata*.

Family FALCONIDAE

Genus *Falco* Linnaeus

Falco duboisi Cowles, 1994

Réunion Kestrel

FIGURE 13*a–e*

MATERIAL.—Grotte des Premiers Français. *Holotype:* l. tarsometatarsus, 1993-28. *Paratypes:* Mandible, left part and symphysis, 1993-34; furcula, 1993-32; l. coracoid, 1993-31; l. femur, 1993-29; l. tibiotarsus, large size, 1993-30; r. tibiotarsus, small size, 1993-33. *Additional Specimen:* r. ulna, 1993-53.

Grotte de l'Autel: r. coracoid, 330547; l. coracoid, 330548.

REMARKS.—This species was described by Cowles (1994) on the material from the Grotte des Premiers Français. An additional ulna was found later, and two additional coracoids were found in the Grotte de l'Autel. The species is characterized by a size generally comparable to that of *Falco tinnunculus* Linnaeus but with more robust leg bones. In the holotypical tarsometatarsus in particular, the proximal and distal ends are wider and deeper.

The two tibiotarsi (Figure 13*b,c*) are very different in size (57.9 mm compared with 66.8 mm). Cowles indicated that the smaller one is immature, but we disagree because the external aspect of the bone is that of an adult. The difference between the two bones is similar to the range of variation between extremes in *Falco punctatus* Temminck from Mauritius (Table 8). This size variation is due to sexual dimorphism, with the largest individuals being the females, as in other species of *Falco* (Jones, 1987).

As a whole, *Falco duboisi* is much larger than *F. araea* (Oberholser) (Seychelles) or *F. newtoni* (Gurney) (Madagascar and Aldabra) and is slightly larger than *F. punctatus*. Jones (1987:209) indicated that in *F. punctatus* the wings are short and rounded at their tip, which is an adaptation for forest-dwelling raptors and also is found in other insular forms of the genus *Falco*, such as *F. novaeseelandiae* Gmelin, from New Zealand, and *F. araea*. The shape of the wings is convergent with that of the hawks of the genus *Accipiter*, which also live in forests.

Compared with *Falco tinnunculus*, the coracoid (Figure 13*f*) and wing bones of *F. punctatus* are much shorter, the femur and tibiotarsus are slightly shorter, and the tarsometatarsus is almost the same size (Figure 8). In *F. duboisi* the humerus and carpometacarpus are unknown, but the coracoid and the ulna are not reduced compared with the femur and the tarsometatarsus. The coracoid, the femur, and the tarsometatarsus have the same relative proportions as in *F. tinnunculus*, whereas in *F. punctatus* the coracoid is very reduced compared with the leg bones. Thus, it can be concluded that the wings of *F. duboisi* were not as shortened as in *F. punctatus*.

In the historical accounts, Dubois noted three birds of prey. The first were the *papangues*, *Circus maillardi* Verreaux, which are still living. "The second ones are named yellow-feet, with the size and shape of falcons. They do harm to the fowls of the inhabitants and the game of the island. The third ones are émerillons, which, although small, do not fail to carry away chickens and eat them" (Barré and Barau, 1982:31, our translation). The word *émerillon* is the French name of *Falco columbarius*, the merlin, which is a small form, whereas *F. duboisi* was almost the same size as *F. tinnunculus*, the kestrel. We think that it is perhaps the term "yellow-feet" that corresponds to *F. duboisi*.

TABLE 8.—Dimensions (mm) of the main bones of the extinct *Falco duboisi* (Réunion) (MNHN, prefix LAC; UCB, prefix FSL) compared with modern *Falco punctatus* (Mauritius) and modern *Falco araea* (Seychelles). Dimensions of *F. punctatus* come from an incomplete skeleton in the Mauritius Institute, the measurements given by Cowles (1994) for material at BMNH, and fossil material from Mare aux Songes and Montagne du Pouce, Mauritius (MNHN). Dimensions of *F. araea* come from a trunk skeleton (female, USNM 488428) and from Cheke and Jones (1987:412) (tarsus length from study skins and living examples). (*n*=number of specimens.)

Measurement	*Falco duboisi*		*Falco punctatus*		*Falco araea*
			mean (*n*)	range	
Coracoid	LAC 1993-31 (paratype)	FSL 330547, FSL 330548			
internal length	29.6	30.2, 29.6	23.55 (4)	21.8–25.3	20.0
proximal width	7.5	–	–	–	4.7
proximal depth	6.5	6.6, 6.6	4.63 (4)	4.2–4.9	4.4
sternal-facet length	–	11.6, 12.5	10.0 (1)	–	8.5
sternal-facet depth	2.6	2.5, 2.6	2.0 (1)	–	1.3
midshaft width	3.0	3.3, 3.0	2.23 (4)	2.0–2.5	2.0
midshaft depth	3.4	3.3, 3.6	2.43 (4)	2.3–2.6	1.7
Humerus					
total length	–		44.33 (6)	42.0–46.6	–
Ulna	LAC 1993-53				
total length	62.7		46.40 (2)	45.3–47.5	–
proximal width	6.7		5.3 (1)	–	–
proximal depth	6.8		4.9 (1)	–	–
distal width	6.2		4.8 (1)	–	–
depth external condyle	5.2		3.8 (1)	–	–
midshaft width	3.8		2.8 (1)	–	–
midshaft depth	3.8		3.0	–	–
Carpometacarpus					
total length	–		28.23 (4)	25.3–29.6	–
Femur	LAC 1993-29 (paratype)				
total length	49.0		41.20 (2)	37.7–44.7	32.6
proximal width	9.0		7.1 (1)	–	5.9
proximal depth	6.7		4.8 (1)	–	4.4
distal width	9.2		7.0 (1)	–	5.8
distal depth	8.1		5.3 (1)	–	4.9
midshaft width	4.8		~3.0 (1)	–	2.7
midshaft depth	4.3		~3.1 (1)	–	2.7
Tibiotarsus	LAC 1993-30 (paratype)	LAC 1993-33 (paratype)			
total length	66.8	57.9	56.80 (4)	51.7–60.4	–
proximal width	7.8	–	–	–	~5.0
proximal depth	8.8	7.6	–	–	5.6
distal width	8.2	7.0	6.50 (4)	6.3–6.9	–
distal depth	6.4	5.4	4.77 (3)	4.6–5.1	–
midshaft width	4.2	3.6	2.97 (3)	2.8–3.1	–
midshaft depth	3.7	3.2	2.65 (2)	2.5–2.8	–
Tarsometatarsus	LAC 1993-28 (holotype)				(tarsus length)
total length	45.7		40.54 (5)	~38–42.6	27.7±3.3 (*n*=17)
proximal width	8.6		6.80 (5)	6.4–7.1	
proximal depth	7.2		5.60 (2)	5.4–5.8	
distal width	8.7		6.33 (6)	5.7–7.0	
distal depth	5.6		4.28 (4)	3.7–4.7	
midshaft width	4.4		3.25 (4)	2.9–3.5	
midshaft depth	3.7		2.33 (3)	2.2–2.5	

Family RALLIDAE

Genus *Dryolimnas* Sharpe

Dryolimnas augusti, new species

Réunion Rail

FIGURE 9

HOLOTYPES.—Right and left tarsometatarsi, MHNR (prefix MHN-RUN-CT) 13, 14, from the same individual.

TYPE LOCALITY.—Caverne de la Tortue, locality of Saint-Paul, Réunion Island, Indian Ocean.

HORIZON.—Holocene.

MEASUREMENTS.—See Table 9.

PARATYPES.—All at MHNR (prefix MHN-RUN-CT): Fragment of left mandible, CT 1; sacrum, CT 2; l. s. coracoid, CT 3; r. p. humerus, CT 4; l. d. humerus, CT 5; r. ulna, CT 6; l. p. femur, CT 7; l. d. femur, CT 8; 2 r. d. femur, CT 9, CT 10; r. p. tibiotarsus, CT 11; l. d. tibiotarsus, CT 12; pedal phalanx (p. p.) 1 of digit II, CT 15; 2 p. p. 2 of digit II, CT 16–17; p. p. 1 of digit III, CT 18; 2 p. p. 2 of digit III, CT 19–20; p. p. 3 of digit III, CT 21; p. p. 1 of digit IV, CT 22; 5 vertebrae, CT 23–27.

ETYMOLOGY.—This species is dedicated to Auguste de Villèle, whose interest for the history of his island and tireless

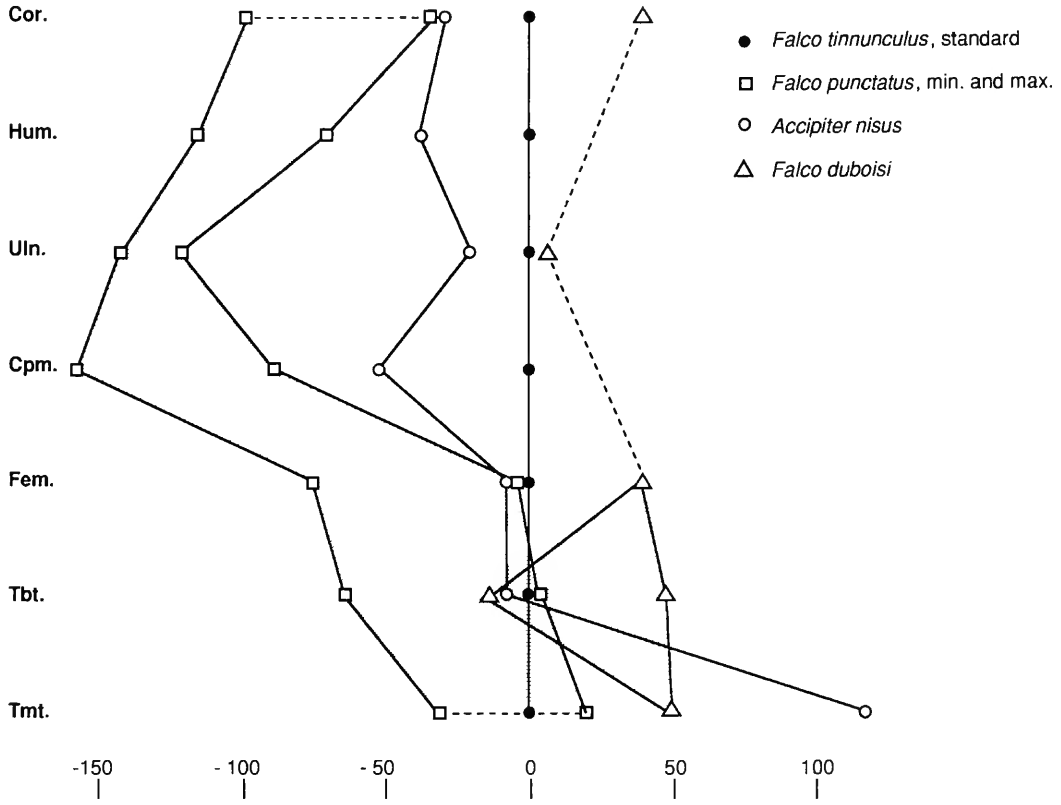


FIGURE 8.—Ratio-diagram of the dimensions of the bones of *Falco duboisi* compared with the minimum and maximum dimensions of *F. punctatus*. For *F. duboisi* the dimensions of the two known tibiotarsi have been indicated. The standard is *Falco tinnunculus* (UCB, Lyon 119-8). *Accipiter nisus* (male, UCB, Lyon 96-5) is included for comparison. Coracoid measurement is of internal length; for other bones, measurement is of total length. When measurements are not known, successive points are united by dashed lines. (Cor.=coracoid, Cpm.=carpometacarpus, Fem.=femur, Hum.=humerus, Tbt.=tibiotarsus, Tmt.=tarsometatarsus, Uln.=ulna.)

activity and hospitality made it possible for numerous naturalists to discover the caves of Réunion and, in particular, the Caverne de la Tortue.

DIAGNOSIS.—Species larger and with stouter tarsometatarsus than the recent species of the genus.

COMPARISONS WITH LIVING FORMS.—We tentatively place the extinct rail of Réunion in the genus *Dryolimnas,* which traditionally includes only the species *D. cuvieri* (Pucheran). This species is represented by two living subspecies, the flying *D. cuvieri cuvieri* from Madagascar and the flightless *D. cuvieri aldabranus* (Günther) from Aldabra, and by one extinct subspecies, *D. cuvieri abbotti* (Ridgway) from Assumption Island.

The two living forms show great differences in the proportions of their skeletons and in their morphological characteristics; the coracoid and wing bones are strongly reduced, and the sternal carina is lower and more posteriorly situated in the Aldabra subspecies.

The extinct Réunion Rail shows the following morphological similarities to *D. cuvieri.* On the coracoid, the coracoidal fenestra is situated along the middle axis of the shaft and there is a well-pronounced sternocoracoidal fossa; on the coracoid from Réunion, only the middle part of the shaft is preserved, but it is possible to see the top of this sternocoracoidal fossa (Figure 9*j*). On the humerus, the shaft is thin and sinuous, and there is an elongated, narrow depression on the anconal face, distally below the dorsal pillar of the internal tuberosity (crus dorsale fossae; Baumel, 1979) (Figure 9*c*). The ulna is relatively elongate (Figure 9*d,e*). The femur is very elongate and incurved. It has two curvatures in two different planes; the proximal and distal extremities are incurved both posteriorly and internally (Figure 9*f–h*).

The main differences between the Réunion Rail and *D. cuvieri* are in size, the former being larger, and in the shape of the tarsometatarsus (Figure 9*a,b*), which in the Réunion Rail is much more robust. The internal trochlea, however, is posteriorly displaced and is only slightly splayed internally, as in *D. cuvieri.* The ossified tendinal loop (retinaculum extensorium tarsometatarsi; Baumel, 1979) is broken on the two tarsometa-

FIGURE 9.—Fossils of the Réunion Rail, *Dryolimnas augusti*, new species, from Caverne de la Tortue: *a*, right tarsometatarsus, holotype, CT 13, anterior view; *b*, left tarsometatarsus, holotype, CT 14, posterior view; *c*, right humerus, proximal part, paratype, CT 4, anconal view; *d*, right ulna, paratype, CT 6, palmar view; *e*, same, internal view; *f*, proximal part and shaft of left femur, paratype, CT 7, posterior view; *g*, distal part and shaft of right femur, paratype, CT 9, posterior view; *h*, same, anterior view; *i*, right tibiotarsus, paratype, CT 11, proximal view; *j*, left coracoid, shaft, paratype, CT 3, posterior view. All figures × 1.5.

tarsi, but it was present, as in *D. cuvieri.* It also is present in *Gallirallus australis* (Sparrman), whereas it is absent in *Aphanapteryx* and *Erythromachus.* On the internal side of the hypotarsus there are three ridges and two open grooves, as in *Dryolimnas, Aphanapteryx,* and *Erythromachus,* whereas in *Gallinula* and *Fulica,* for example, the most internal groove is closed.

The accurate lengths of the pectoral and wing bones are unknown, but the proportions of the wing bones compared to those of the leg bones are similar to those of the subspecies *D. cuvieri aldabranus,* so it is likely that the Réunion Rail also was flightless. This hypothesis is corroborated by the robustness of the tarsometatarsus.

The modern species *Lewinia pectoralis* (Temminck) is considered by Olson (1973) to belong to the genus *Dryolimnas.* The Réunion form differs from it by its much larger size.

COMPARISON WITH FOSSIL FORMS.—For the extinct rail of Rodrigues, Milne-Edwards (1874) created the genus *Erythromachus* as distinct from the extinct genus *Aphanapteryx* of Mauritius. Günther and Newton (1879) transferred the Rodrigues species to *Aphanapteryx* and were followed by Olson (1977), who, however, indicated that these two species have numerous differences in their osteology as well as in their plumage, which is known from historical accounts. Piveteau (1945) had already mentioned strong differences in the cranial morphology.

The main osteological differences between *Aphanapteryx bonasia* (Sélys-Longchamps), from Mauritius, and *Erythromachus leguati* Milne-Edwards, from Rodrigues, are as follows. In *Aphanapteryx* the skull is narrower and longer, the temporal fossae are deeper, and the nostrils are shorter and higher (Olson, 1977). On the sternum, the sternal carina is much lower, and the gap between the coracoidal facets is much wider. The humerus is longer, its shaft is more incurved, and its bicipital surface is proportionally shorter, whereas in *Erythromachus* the humeral shaft is straighter. The carpometacarpus is unknown because the bone illustrated by Günther and Newton (1879, pl. 43: fig. G), and referred to *E. leguati,* does not belong to the Rallidae. The femur is elongated and anteroposteriorly incurved in *Aphanapteryx* but is shorter and stouter in *Erythromachus.* The tarsometatarsus is proportionally more robust, and its trochleae are less splayed in *Erythromachus,* whereas in *Aphanapteryx* the shaft of the tarsometatarsus is proportionally narrower, and the trochleae are more splayed, particularly the internal trochlea. For these reasons we consider the rails of Mauritius and Rodrigues to be two different genera.

The Réunion Rail differs from *Aphanapteryx* by the shape of the tarsometatarsus, which is stouter, with proportionally nar-

TABLE 9.—Dimensions (mm) of the bones of the Réunion Rail, *Dryolimnas augusti*, new species, compared with recent *Dryolimnas cuvieri cuvieri* from Madagascar (BMNH 1897.5.10.47), and *D. cuvieri aldabranus* from Aldabra (BMNH s/1989.38.5, BMNH s/1993.6.2). (*n*=number of specimens.)

Measurement	*Dryolimnas augusti*, n. sp. (*n*)	Dryolimnas cuvieri	
		cuvieri (*n*=1)	*aldabranus* (*n*=2)
Coracoid			
midshaft width	3.2 (1)	3.1	2.1, 2.2
midshaft depth	2.3 (1)	1.9	1.5, 1.5
Humerus			
total length	~48 (1)	47.9	37.7, 39.0
proximal width	10.0 (1)	9.7	8.1, 8.7
head width	3.0 (1)	2.8	2.2, 2.2
midshaft width	3.3 (2)	3.1	2.2, 2.3
midshaft depth	3.3 (2)	2.9	2.1, 2.2
Ulna			
total length	~40 (1)	41.2	31.0, 32.5
proximal width	4.8 (1)	4.7	3.8, 4.0
proximal depth	5.4 (1)	5.1	3.8, 4.0
midshaft width	2.7 (1)	2.3	1.6, 2.1
midshaft depth	3.0 (1)	2.6	2.1, 2.3
Femur			
total length	~61 (1)	50.5	42.8, 44.8
distal width	10.1–11.3 (3)	8.3	7.1, 7.5
distal depth	9.0–9.1 (2)	7.3	6.6, 6.6
midshaft width	4.5–4.9 (4)	3.6	2.9, 3.3
midshaft depth	4.4–5.0 (4)	3.6	3.1, 3.3
Tibiotarsus			
proximal width	9.7 (1)	7.4	6.3, 6.4
proximal depth	12.1 (1)	10.1	8.9, 9.4
distal width	~7.8 (1)	6.7	5.8, 5.9
distal depth	~8.0 (1)	7.0	6.0, 6.5
Tarsometatarsus			
total length	53.0–53.1 (2)	47.6	40.2, 44.2
proximal width	8.7–8.8 (2)	7.2	6.1, 6.5
proximal depth	9.2 (2)	7.1	6.3, 6.4
distal width	9.5 (1)	7.2	6.6, 6.6
distal depth	7.2 (1)	5.9	5.3, 5.4
midshaft width	4.3–4.4 (2)	3.0	2.7, 2.7
midshaft depth	3.8–3.9 (2)	2.6	2.2, 2.3

rower proximal and distal parts. In *Aphanapteryx* the hypotarsus projects more posteriorly and the external calcaneal ridge is situated closer to the external side; in the Réunion Rail this ridge is situated more medially. The Réunion Rail differs from *Erythromachus* by the characteristics of the humerus (shaft thin and incurved), femur (more elongated and incurved), and tarsometatarsus (trochleae less splayed).

In the ratio distal width × 100: total length, the Réunion Rail occupies an intermediate position between *Dryolimnas cuvieri*, which has less splayed trochleae, and more terrestrial rails, such as *Erythromachus*, *Aphanapteryx*, and *Gallirallus*, which have more splayed trochleae. This ratio varies between 14.9 and 16.4 in *D. cuvieri*, is 17.9 in *D. augusti*, varies between 19.2 and 21.2 in *E. leguati* (after the measurements given by Günther and Newton, 1879), varies between 20.6 and 20.9 in *A. bonasia* (MNHN), and reaches 20.2 and 22.8 in two specimens of *Gallirallus australis* (MNHN).

REMARKS.—The Réunion Rail is likely to correspond to a bird that was mentioned only by Dubois (1674) as *Râle des Bois*. It cannot correspond to the *Oiseau Bleu*, which must have been larger, being the same size as a solitaire, according to Dubois, or the size of a large capon, according to Feuilley (Cheke, 1987). The Réunion Rail was smaller, approximately the size of a Common Moorhen (*Gallinula chloropus* (Linnaeus)), with reduced wings.

A fossil rail from Mauritius was recently identified as *Dryolimnas cuvieri* by Cowles (1987).

Genus *Fulica* Linnaeus

Palaeolimnas Forbes, 1893:544 [type by monotypy, *Fulica newtonii* Milne-Edwards, 1867].

Paludiphilus Hachisuka, 1953:154 [type by monotypy, *Fulica newtonii* Milne-Edwards, 1867].

Fulica newtonii Milne-Edwards, 1867

Newton's Coot

FIGURE 13*i–m*

Fulica newtonii Milne-Edwards, 1867:203, pl. 10.
Fulica newtoni.—Anonymous [=A. Newton], 1868:482.
Palaeolimnas newtoni.—Forbes, 1893.
Paludiphilus newtoni.—Hachisuka, 1953.

MATERIAL.—Grotte des Premiers Français: Rostrum, anterior part, 1993-44; sternum, 1993-39; incomplete pelvis, 1993-38; 2 vertebrae, 1993-46; r. tibiotarsus, 1993-40; r. tibiotarsus, 1993-41; fibula, 1993-43; r. tarsometatarsus, 1993-42; 5 pedal phalanges, 1993-45.

Grotte de l'Autel: Pedal phalanx 1 of digit III, 330528; pedal phalanx 2 of digit III, 330531.

Marais de l'Ermitage: Fragments of pelvis, 1819; r. coracoid, 1814; r. p. coracoid, 1922; l. d. ulna, 1815; l. carpometacarpus, 1921; r. d. tibiotarsus, 1816; 2 tarsometatarsi, r. and l., from same individual?, 1811, 1812; r. tarsometatarsus, 1920; r. p. tarsometatarsus, 1813; pedal phalanx 1 of digit II, 1817; pedal phalanx 1 of digit II, 1818; 2 pedal phalanges, 1896, 1923.

REMARKS.—Remains of *Fulica newtonii* in MNHN from the Mare aux Songes, Mauritius, were compared with those from Réunion and were found to be identical, so both populations must have belonged to a single species. The tarsometatarsi show a great range of variation (Table 10), which probably relates to sexual dimorphism, with the males being larger than the females.

Newton and Gadow (1893:292) wrote: "The sternum of *F. newtoni* resembles in several points that of *Aphanapteryx*, *Erythromachus*, and *Ocydromus*, and differs from *Tribonyx*, *Fulica* proper, and *Porphyrio*, first in the configuration of the whole anterior margin of the sternum, especially in the double or basally divided spina externa, which is moreover broad and flat, while in the other genera this spine is single and furnished with a ventral longitudinal sharp ridge; secondly, by the receding and broad anterior margin of the keel, which, however, is well developed, although less than in *Tribonyx* and *Fulica atra*, but the tendency towards a reduction of the keel is apparent." The sternum of *Fulica newtonii* from Réunion (Figure 13*i*) is

TABLE 10.—Dimensions (mm) of the main bones of the extinct *Fulica newtonii* from Mauritius (MNHN) and Réunion. (a=maximum length in median plane, b=width between sterno-coracoidal processes, c=width between ventral labial prominences, d=measured with cnemial crests, e=measured without cnemial crests; *n*=number of specimens.)

Measurement	Mean (*n*)	Range
Sternum (Réunion)		
length (a)	66.7 (1)	
width (b)	36.6 (1)	
width (c)	27.7 (1)	
keel depth	20.7 (1)	
Coracoid (Réunion)		
internal length	39.4 (1)	
proximal width	10.60 (2)	
proximal depth	6.70 (2)	10.4–10.8
midshaft width	5.1 (1)	6.5–6.9
midshaft depth	3.8 (1)	
Humerus (Mauritius)		
total length	85.40	83.5–87.3
proximal width	17.15 (2)	16.7–17.6
proximal depth	9.6 (1)	
distal width	12.15 (2)	11.7–12.6
distal depth	7.10 (2)	6.9–7.3
midshaft width	5.50 (2)	5.3–5.7
midshaft depth	4.70 (2)	4.5–4.9
Ulna (Réunion)		
distal width	7.2 (1)	
external condyle depth	7.3 (1)	
midshaft width	4.6 (1)	
midshaft depth	5.1 (1)	
Carpometacarpus (Réunion)		
total length	49.1 (1)	
proximal width	4.6 (1)	
proximal depth	9.3 (1)	
distal width	3.5 (1)	
distal depth	4.8 (1)	
width metacarpale majus	3.9 (1)	
depth metacarpale majus	3.2 (1)	
Tibiotarsus (Mauritius+Réunion)		
total length (d)	129.24 (5)	126.8–131.3
total length (e)	122.54 (5)	120.2–124.6
proximal width	12.56 (5)	12.1–13.0
proximal depth	18.60 (5)	17.7–19.4
distal width	12.06 (9)	11.2–12.8
distal depth	11.67 (3)	11.5–11.8
midshaft width	6.75 (8)	6.2–7.0
midshaft depth	5.14 (8)	4.6–5.7
Tarsometatarsus (Mauritius+Réunion)		
total length	84.15 (6)	76.7–89.3
proximal width	13.53 (7)	~12.5–14.2
proximal depth	12.35 (2)	11.4–13.3
distal width	13.95 (6)	12.4–14.8
distal depth	10.80 (6)	9.7–11.7
midshaft width	6.51 (7)	6.0–6.8
midshaft depth	5.09 (7)	4.7–5.3
Phalanx 1 digit II (Réunion)		
total length	37.25 (2)	36.2–38.3
proximal width	5.27 (3)	5.1–5.5
Phalanx 1 digit III (Mauritius+ Réunion)		
total length	34.30 (2)	34.3–34.3
proximal width	7.20 (2)	~7–7.4
Phalanx 2 digit III (Réunion)		
total length	27.3 (1)	
proximal width	6.5 (1)	

identical to that from Mauritius illustrated by Newton and Gadow (1893, pl. 35: figs. 5–7). It presents a ventral manubrial spine (spina externa) that is wide, with two small lateral points separated by a shallow notch. This characteristic cannot be considered as different from *Fulica,* however, for in numerous living species of that genus the ventral manubrial spine is very variable among individuals. Some individuals have a narrow, short point prolonged by a median ventral ridge, others have a short, wide point, and others have two points separated by a notch, as in *F. newtonii.* We have observed that the shape of the ventral manubrial spine is very variable in *F. cristata* Gmelin (7 individuals), *F. americana* Gmelin (20), *F. caribaea* Ridgway (3), and *F. leucoptera* Vieillot (7) from the USNM. In *F. ardesiaca* Tschudi (1) and *F. rufifrons* Philippi and Landbeck (3), the ventral manubrial spine is wide and short. Three of seven individuals of *F. cristata* and two of seven individuals of *F. leucoptera* have two points separated by a notch, rather than a single point.

In *Fulica newtonii* the anterior carinal margin is more posteriorly displaced than in *F. cristata,* but the carina is still well developed. The shape of this carina is very different from that of the flightless species *Tribonyx mortierii* Du Bus, in which the carina is low and the anterior carinal margin is wide and is formed by two ridges separated by a median groove. It is still more different from that of *Aphanapteryx bonasia,* in which the anterior carinal margin is very wide, with two ridges separated by a wide groove, and the carina itself is strongly displaced posteriorly and is very low (Newton and Gadow, 1893, pl. 35: figs. 14–16). In conclusion, the characteristics of the sternum indicate only a slight reduction in flying ability.

Milne-Edwards (1867, 1867–1871) wrote that the shape of the posterior iliac crests of the pelvis of *F. newtonii* was more similar to that of *F. atra* Linnaeus than to that of *F. cristata.* Although the two pelves from Réunion are not complete enough to see if this characteristic is constant in *F. newtonii,* we think that by the marked widening of the pelvis at the level of the acetabula and by the strong projection of the antitrochanters externally, *F. newtonii* is more similar to *F. cristata* than to *F. atra* (see Milne-Edwards, 1867–1871, pl. 99: figs. 1–5, pl. 107: figs. 1–4).

In *Fulica newtonii* the bones of the scapular girdle and the wing (coracoid, humerus, carpometacarpus) are the same size as in a large male of *F. cristata,* the tibiotarsus and the phalanx of pedal digit II are slightly larger, and the femur and the tarsometatarsus are much larger (Figure 10). Compared to *F. cristata, F. newtonii* was a poorer flier as indicated by the reduction of the coracoid and wing bones. For comparison we present the curves of *Tribonyx mortierii,* the flightless Tasmanian Native-Hen, and of *Aphanapteryx bonasia,* the extinct, flightless Mauritius Red Rail. In these two species, the cora-

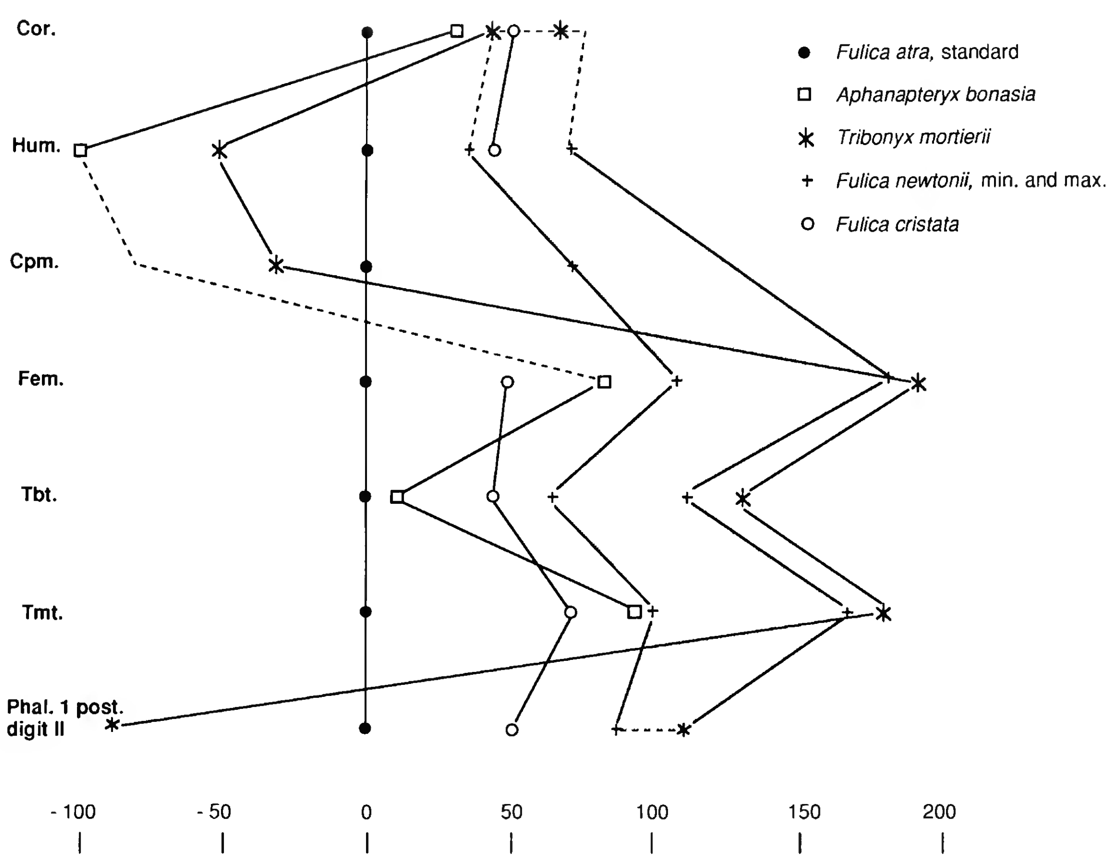


FIGURE 10.—Ratio-diagram of long bones of *Fulica newtonii* compared to those of *F. cristata* (male, USNM 430843), *Tribonyx mortierii* (UCB, Lyon 1975-1), and *Aphanapteryx bonasia*. The standard is *Fulica atra* (UCB, Lyon 147-2). For *Fulica newtonii* the minimum and maximum dimensions of the fossil material from Mauritius and Réunion are indicated and include measurements given by Newton and Gadow (1893). For the extinct *Aphanapteryx bonasia*, the dimensions are from the fossil material at MNHN (MAD 6501, 6502, 6561, 6565, 6566, 6579, 6580, 6818, 6937, 6967) and from Newton and Gadow (1893). Coracoid measurement is of internal length; for other bones, measurement is of total length. When measurements are not known, successive points are united by dashed lines. (Cor.=coracoid, Cpm.=carpometacarpus, Fem.=femur, Hum.=humerus, Phal.= phalanges, post.=posterior, Tbt.=tibiotarsus, Tmt.=tarsometatarsus.)

coids are the same size as in *F. newtonii*, and the proportions of the leg bones are very similar to those of *F. newtonii*, but the reduction of the wing is much more advanced. The pedal phalanges are much shorter in *T. mortierii*. So it can be concluded that *F. newtonii* had some reduction in flying ability but was still able to fly, which explains how the same species could be present on both Mauritius and Réunion.

Several early authors have mentioned the presence of "moorhens" on Réunion, but the most detailed description was given by Dubois: "Moorhens, which are as big as hens. They are completely black and have a big white crest on the head" (Barré and Barau, 1982:30, our translation). On these grounds, Milne-Edwards (1867–1871) said that *F. newtonii* must have been very different from *F. cristata*, the forehead shield of which is dark red; actually, the forehead shield in *F. cristata* is white, sometimes tinged with pink, and is topped by two more or less developed red tubercles in the adult (Langrand, 1990). Keith (in Urban et al., 1986:129) wrote that the Red-knobbed Coot is "not easy to tell from the Eurasian Coot, *F. atra*. At close range red knobs at top of shield distinguish it, but during non-breeding season they are small and very hard to see."

In conclusion we think that *F. newtonii* was probably derived from *F. cristata*, which lives mainly in southern and East Africa and on Madagascar. It is not possible, however, to exclude the possibility that it could be derived from *F. atra*, for this species is widely distributed in the Palearctic region as well as in India, Indonesia, Australia, Tasmania, and New Zealand (Cramp and Simmons, 1979).

Family SCOLOPACIDAE

Genus *Numenius* Brisson

Numenius phaeopus (Linnaeus, 1758)

Whimbrel

MATERIAL.—Grotte des Premiers Français: 1. tarsometatarsus, 1993-52.

REMARKS.—The Whimbrel is a palearctic migrant that still occurs regularly, between September and March, on the mud flats and beaches of the west coast of Réunion. It was known to the early explorers, who mentioned it using its old French name of *corbigeau* (Barré and Barau, 1982).

Family COLUMBIDAE

Two species of pigeons are known from Mauritius, *Alectroenas nitidissima,* the extinct Blue Pigeon, or *Pigeon hollandais,* and *Nesoenas mayeri* (Prévost), the Pink Pigeon, which still survives (Jones, 1987). Milne-Edwards (1874) described a very special sternum from Rodrigues, which did not correspond to any living genus, under the new name of "*Columba*" *rodericana,* and he attributed a tarsometatarsus to the living species *Streptopelia picturata* (Temminck), of Madagascar. Günther and Newton (1879) said there was no reason to put these two elements into two different species and listed them both under *Columba rodericana.* Shelley (1883:258) wrote: "*Columba rodericana* Milne-Edwards, is only known by a few bones. It was a native of Rodriguez, and probably belonged to the genus *Alectroenas.*" Later, Rothschild (1907) referred to it as *Alectroenas* (?) *rodericana,* and Hachisuka (1953) referred to it as *Alectroenas rodericana,* without a question mark. Although Cowles (1987:97) also placed *C. rodericana* in the genus *Alectroenas,* he recognized that the sternum was "quite unlike that of any living genus known today."

The sternum described and illustrated by Milne-Edwards (1874, pl. 12: figs. 1, 1a–c) is quite different from that of the genus *Alectroenas.* Among the living genera of Columbidae that we have been able to examine, it is most similar to that of the genus *Gallicolumba,* the present distribution of which extends from the Philippines, New Guinea, and Celebes and adjacent islands to Polynesia (Peters, 1937; Steadman, 1992). The tarsometatarsus (Milne-Edwards, 1874, pl. 12: fig. 2f) appears inseparable from *Streptopelia picturata.* There is no fossil evidence that the genus *Alectroenas* was present on Rodrigues. Rather, the island probably was occupied by an extinct genus, including "*Columba*" *rodericana,* and by *Streptopelia picturata,* the Madagascar Turtledove.

On Réunion, Bontekoe indicated "*ramiers* of the species with blue wings" (Barré and Barau, 1982:26), and Dubois mentioned two kinds of wild pigeons, in addition to *ramiers* and turtledoves, thus apparently indicating four species of columbids. Dubois described the wild pigeons as "some with slaty-coloured feathering, the others russet-red. They are a little larger than the European pigeons, and have a stronger bill, red at the end close to the head, the eyes bordered by the colour of fire, like the pheasants" (Barré and Barau, 1982:30, our translation). The slaty or blue-winged birds are generally considered to belong to the genus *Alectroenas,* and the russet-red birds are considered a form related to *Nesoenas mayeri* from Mauritius (Cheke, 1987). On the basis of Dubois' description, Rothschild (1907) named the red form *Nesoenas duboisi,* citing for this species only the characteristics of the bill and of the border of the eyes, which in Dubois' account apply not only to the red form but also to the blue one. Because one of the fossil species found on Réunion belongs to the genus *Nesoenas,* the name created by Rothschild must be used for it, as in the case of *Nycticorax duboisi.*

Genus *Nesoenas* Salvadori

Nesoenas duboisi Rothschild, 1907

Réunion Pink Pigeon

FIGURE 13*g,h*

MATERIAL.—Grotte des Premiers Français: r. d. humerus, 1993-55.

Grotte de l'Autel: r. humerus, 330546.

REMARKS.—The humerus from Grotte de l'Autel (Figure 13*g,h*) is similar to that of *Nesoenas mayeri,* the Pink Pigeon of Mauritius. It differs from the genus *Alectroenas* by the following characteristics. On the anconal face, in *Nesoenas* as in *Columba,* there is a slightly indicated tubercle situated distally compared with the humeral head, more or less on the median axis of the bone, at the place where the capital groove ends on its medial side. This tubercle does not exist in *Alectroenas.* The humeral head is more proximodistally elevated in *Alectroenas* and is more flattened in *Nesoenas.* The bicipital surface is more internally projecting in *Nesoenas.* The pectoral attachment is narrow and elongated, only slightly protruding, and oriented along the axis of the bone in *Alectroenas,* whereas it is more protruding, with a more triangular shape, and obliquely oriented in *Nesoenas.* The distal part is more mediolaterally elongated in *Alectroenas.* On the palmar face, the impression of M. brachialis anticus is much wider and more diffuse in *Alectroenas,* whereas it is smaller and with a more discrete outline in *Nesoenas.* The internal condyle, more globular in *Alectroenas,* is more elongate in *Nesoenas.* The attachment of the anterior ligament is more protruding in *Nesoenas.*

We have compared humeri of *Nesoenas* from Réunion with three humeri of captive *N. mayeri* from the USNM collection and with a series of 39 fossil humeri from the caves of Le Pouce Mountain, Mauritius (MNHN). Most of the dimensions of the Réunion humeri fall within the range of variation of *N. mayeri* except for the total length, which is a little larger (Table 11). Because we have a good sample of comparative material, we think that the Réunion *Nesoenas* belongs to a different species, characterized by slightly larger size than the Mauritian one. With the hope of finding more fossil material, we refer it for now to *Nesoenas duboisi* Rothschild.

TABLE 11.—Dimensions (mm) of the humerus of *Nesoenas mayeri*, modern and fossil, from Mauritius, and *N. duboisi*, extinct, from Réunion. The modern skeletons of *N. mayeri* are from USNM, and the fossil humeri are from the caves of Montagne du Pouce, Mauritius (MNHN). (a=from external tuberosity to bicipital crest, without deltoid crest; b=from internal tuberosity to bicipital surface, without deltoid crest; *n*=number of specimens; *s*=standard deviation.)

Measurement	*Nesoenas mayeri*			*Nesoenas duboisi*
	mean (*n*)	*s*	range	
Humerus				
total length	45.58 (34)	1.64	42.5–49.2	50.4
proximal width (a)	13.63 (29)	0.54	12.7–14.4	14.2
proximal depth (b)	8.38 (27)	0.37	7.7–9.1	–
distal width	10.54 (35)	0.46	9.3–11.4	10.4, 11.1
distal depth	6.54 (31)	0.18	6.2–6.9	6.6, 6.6
midshaft width	4.95 (39)	0.20	4.6–5.3	5.1
midshaft depth	3.88 (39)	0.24	3.4–4.4	4.0
midshaft width×10/total length	1.09 (33)	0.05	1.01–1.20	1.01

Genus *Streptopelia* Bonaparte

Streptopelia picturata (Temminck, 1813)

Madagascar Turtledove

FIGURE 13*n*

MATERIAL.—Grotte "au sable": r. p. humerus, 330738; l. d. ulna, 330739.

REMARKS.—Both remains correspond to the living *Streptopelia picturata* (one skeleton in MNHN). They are similar to fossil remains from the caves of Le Pouce Mountain, Mauritius. The Madagascar Turtledove lives now in Madagascar and on other islands of the western Indian Ocean (Glorioso, Anjouan in the Comoros, Aldabra, Assumption, the Amirantes, some of the Seychelles, and Diego Garcia; Peters, 1937). Although assumed to have been introduced to Réunion, Mauritius, and Rodrigues, its presence as a fossil indicates that it was living on these three islands before humans arrived, disappeared, and was then reintroduced (Cheke, 1987).

Dubois spoke of *ramiers* and turtledoves in Réunion, and according to Cheke (1982), the name *Pigeon ramier* is still used in Mauritius and Réunion to designate *S. picturata*.

Family PSITTACIDAE

Genus *Mascarinus* Lesson

Mascarinus mascarinus (Linnaeus, 1771)

Mascarene Parrot

FIGURE 13*o–x*

MATERIAL.—Grotte des Premiers Français: r. d. coracoid, 1993-56.

Grotte de l'Autel (bones probably from one individual): l. coracoid, 330545; r. and l. humeri, 330539, 330540, respectively; l. ulna, 330541; l. carpometacarpus, 330544; l. femur, 330543; l. tibiotarsus, 330542.

Grotte "au sable": l. scapula, 330810; 2 l. coracoids, 330741, 330742; r. p. coracoid, 330743; r. s. carpometacarpus, 330740; r. d. tarsometatarsus, 330744.

REMARKS.—We think the few remains of a large parrot are from *Mascarinus mascarinus*, a genus and species endemic to Réunion that became extinct between 1750 and 1800 (Barré and Barau, 1982). Unfortunately, no skeleton has been preserved for this species, which is known from two mounted specimens, one in MNHN (Paris, 1998-1725) and the other in the Natural History Museum of Vienna (Austria, 50.688). X-radiographs made it possible to take the measurements of some bones, which show that the fossil remains are intermediate between those of the two modern specimens (Table 12).

We have compared the fossil remains from Réunion with the species *Coracopsis nigra* (Linnaeus), the Lesser Vasa Parrot, which lives on Madagascar, the Comoros, and on Praslin in the Seychelles. *Coracopsis nigra* was introduced to Réunion very early, circa 1780 (Cheke, 1987), and is about the same size as *M. mascarinus;* in both species the total length is 35 cm (Langrand, 1990; Forshaw, 1973). The lengths of the coracoid, femur, and tibiotarsus of the Réunion parrot fall within the range of variation of *C. nigra,* whereas the humerus, ulna, and carpometacarpus are somewhat smaller (Table 12). The parrot of Réunion also shows morphological differences compared with *C. nigra.* The distal part of the humerus is more laterally compressed in the Réunion form, and the olecranal fossa is narrower, whereas in *Coracopsis nigra,* as well as in *C. vasa* (Shaw), the distal part of the humerus is mediolaterally wider (Figure 11). The ratio distal depth×100:distal width is 65.6 in the Réunion parrot, whereas it ranges from 57.3 to 63.0 in six modern *C. nigra* and from 57.8 to 59.7 in two modern *C. vasa.* On the distal part of the tibiotarsus from Réunion (Figure 13*x*), on the anterior face, the internal condyle is narrow, not flattened, and is proximodistally oriented, whereas in *C. nigra* it is wide, flattened, and oriented proximointernally. In five of the six *C. nigra* examined, the tendinal groove is situated almost in the median plane of the bone; in the Réunion form, it is situated almost on the internal side. On the Réunion tibiotarsus there is a depression on the anterior face, above the external condyle, but this depression does not exist in *C. nigra.* Other differences probably occur in the proximal part of the tarsometatarsus, but this is unknown in the Réunion form. At the distal end, on the posterior face, the accessory trochlea is less anteroposteriorly developed in the Réunion parrot than in *C. nigra.*

TABLE 12.—Dimensions (mm) of the main long bones of *M. mascarinus* fossil (UCB, prefix FSL) and mounted specimens, compared with modern *Coracopsis nigra* (USNM, AMNH, MNHN).

Measurement	*Mascarinus mascarinus*				*Coracopsis nigra*	
	Grotte de l'Autel	Grotte "au sable"	mounted specimens			
			Paris	Vienna	mean (*n*)	range
Coracoid	FSL-330545	FSL-330741–743				
internal length	29.2	28.9			30.05 (8)	28.7–30.9
proximal width	7.2	7.6–7.2			8.08 (6)	7.7–8.3
proximal depth	4.3	~4.4–4.3			4.88 (6)	4.6–5.4
sternal-facet length	–	~8.2			8.83 (6)	7.4–10.1
sternal-facet depth	–	2.0–2.0			2.48 (6)	2.2–2.7
midshaft width	2.9	3.2–3.2			3.50 (6)	3.1–3.8
midshaft depth	2.5	2.4–2.4			2.43 (3)	
Humerus	FSL-330539–40					
total length	48.8–48.8				51.88 (6)	50.2–53.6
proximal width	13.0				13.27 (6)	12.5–14.2
proximal depth	7.6				7.67 (6)	7.3–8.1
distal width	9.3–9.3				10.43 (6)	10.0–11.0
distal depth	6.1–6.1				6.23 (6)	5.9–6.4
midshaft width	4.7–4.7				4.85 (6)	4.5–5.4
midshaft depth	3.9–3.9				3.97 (6)	3.8–4.1
Ulna	FSL-330541					
total length	57.8		60.5		61.98 (5)	59.3–64.4
proximal width	7.6		–		7.52 (5)	7.5–7.6
proximal depth	6.0		–		6.32 (5)	6.2–6.6
distal width	6.0		–		6.20 (5)	6.0–6.5
external condyle depth	5.4		–		5.62 (5)	5.5–6.0
midshaft width	3.5		3.8		3.72 (6)	3.5–4.0
midshaft depth	3.6		–		3.80 (3)	3.6–4.0
Carpometacarpus	FSL-330544	FSL-330740				
total length	35.9	–	37.2	35.0	38.22 (6)	36.7–40.0
proximal width	4.0	–	–	–	4.06 (5)	3.8–4.3
proximal depth	9.0	–	9.0	–	9.34 (5)	9.0–10.0
distal width	3.8	3.9	–	–	4.06 (5)	3.8–4.2
distal depth	5.6	–	–	–	6.02 (5)	5.8–6.3
width metacarpale majus	3.0	3.1	–	2.7	3.10 (3)	3.0–3.2
depth metacarpale majus	2.6	2.6	2.7	2.5	2.87 (6)	2.6–3.1
Femur	FSL-330543					
total length	39.7				38.43 (7)	37.0–40.1
proximal width	7.5				7.46 (7)	6.9–8.2
proximal depth	4.4				4.81 (7)	4.6–5.0
distal width	7.6				7.60 (7)	7.1–8.3
distal depth	6.2				5.99 (7)	5.6–6.4
midshaft width	3.1				3.08 (7)	2.9–3.4
midshaft depth	2.9				2.93 (3)	2.8–3.0
Tibiotarsus	FSL-330542					
total length	57.8				56.84 (7)	54.6–59.5
proximal width	6.0				6.40 (6)	5.9–7.0
proximal depth	7.2				7.18 (6)	6.9–7.9
midshaft width	3.0				2.89 (7)	2.4–3.4
midshaft depth	2.7				2.63 (3)	2.4–3.0
Tarsometatarsus		FSL-330744				
total length		–		18.5	22.30 (7)	21.1–23.8
midshaft width		–		2.7	3.32 (6)	3.0–3.8
width middle trochlea		3.6		–	3.50 (6)	3.2–3.9
depth middle trochlea		2.8		–	3.03 (6)	2.9–3.3
depth external trochlea		4.0		–	4.47 (6)	4.2–4.7

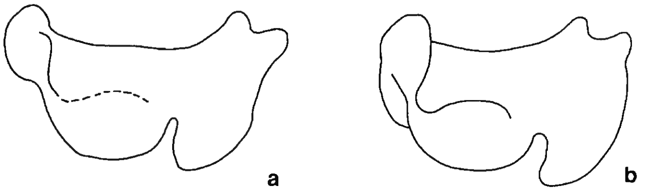


FIGURE 11.—Drawing of the distal part of the right humerus in the genus *Coracopsis* (*a*) (*Coracopis nigra*, MNHN LAC 1883-507), compared with a humerus from Réunion referred to *Mascarinus mascarinus* (*b*) (FSL 330539).

In conclusion, the parrot remains of Réunion present some differences in their dimensions and morphological characteristics compared with *C. nigra*, and because their dimensions are compatible with those available for *M. mascarinus*, we think that they can be referred to that species. Compared to modern *C. nigra*, *M. mascarinus* had the femur and tibiotarsus of the same size, but the wing bones and tarsometatarsus were shorter (Figure 12). The main difference is the length of the tarsometatarsus from Vienna, which is much smaller than the tarsometatarsus of *C. nigra* from Madagascar, although the

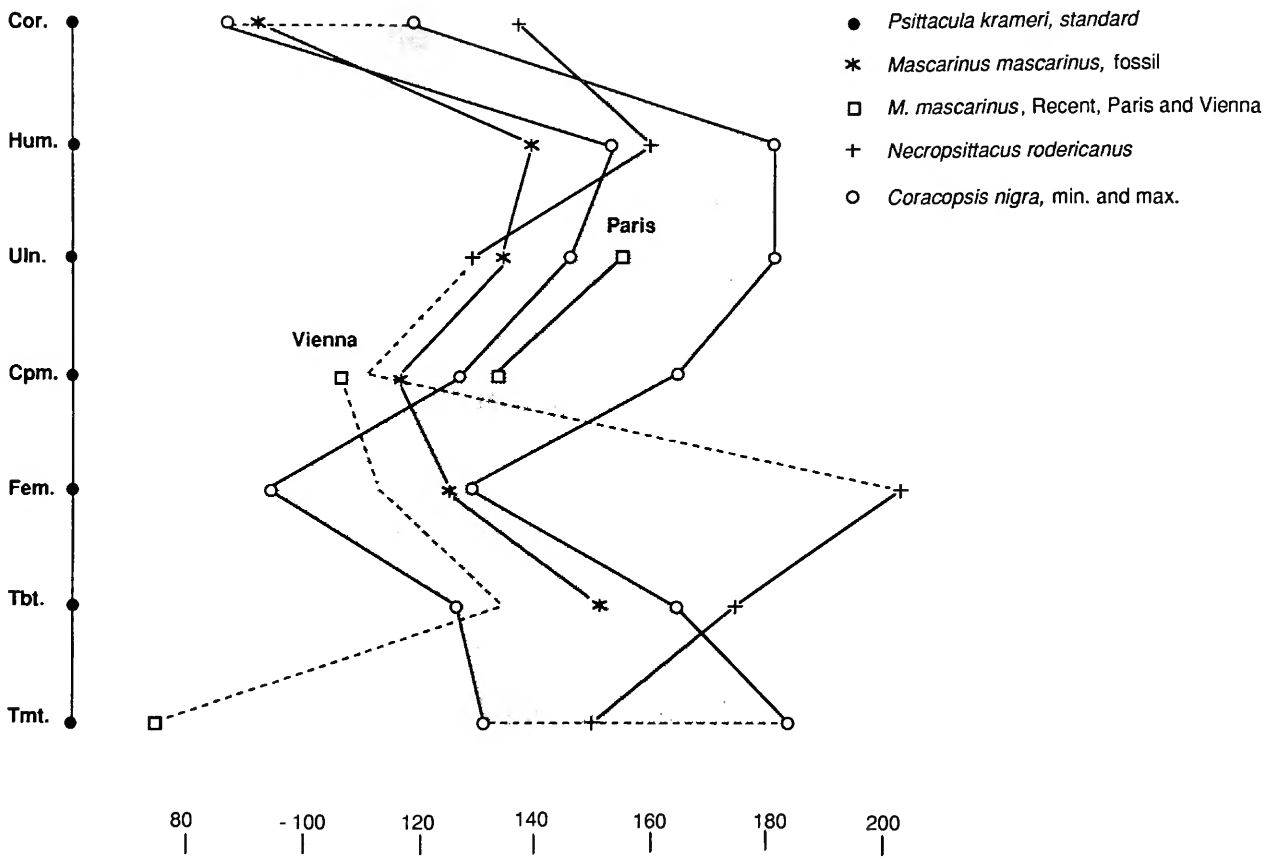
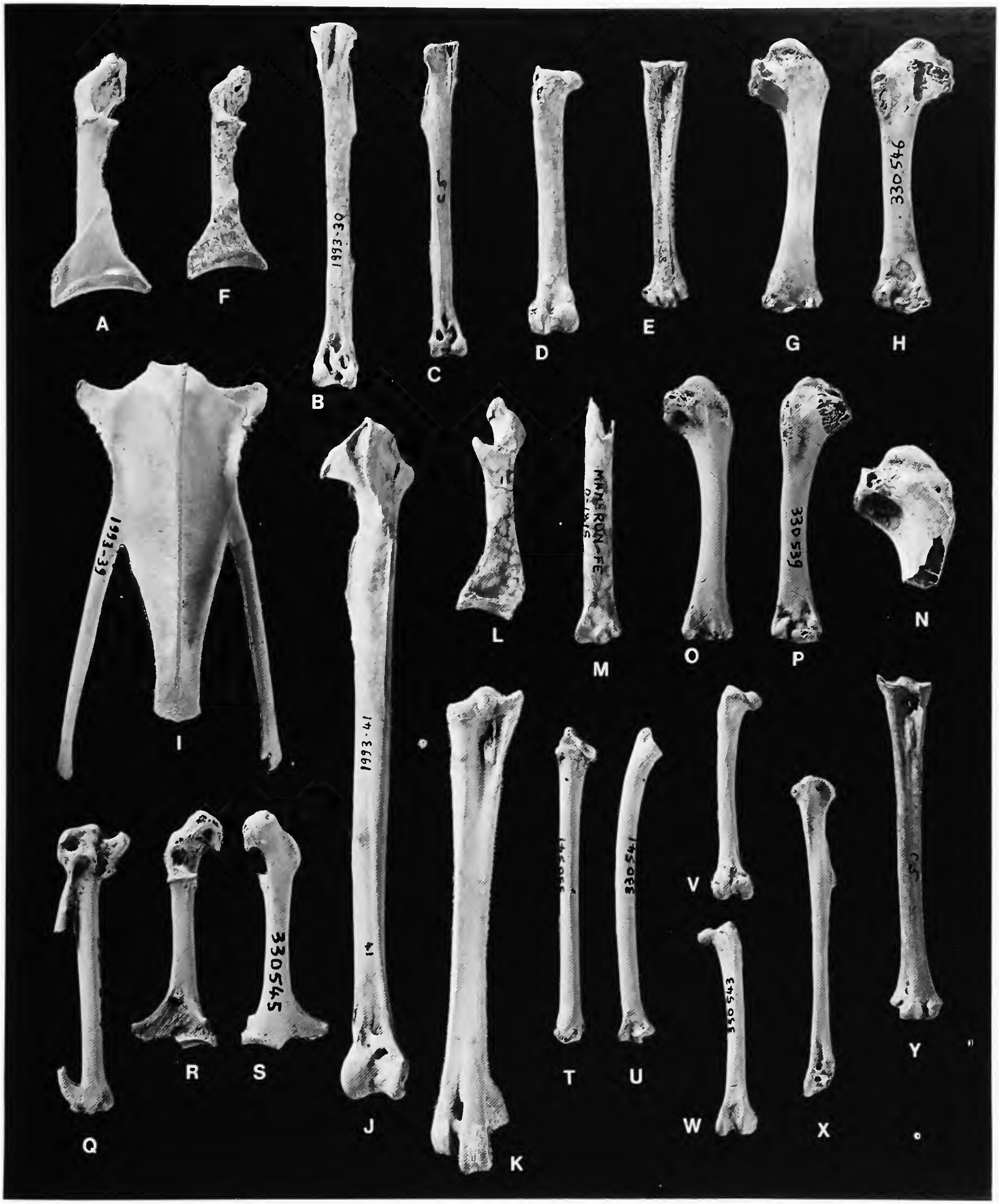


FIGURE 12.—Ratio-diagram of the dimensions of bones of fossil *Mascarinus mascarinus* from Réunion, compared with those taken from x-radiographs of the two mounted specimens (MNHN, Natural History Museum of Vienna) and with *Coracopsis nigra*. The standard is *Psittacula krameri* (Pierce Brodkorb 27712). For *C. nigra* the dimensions are the minimum and maximum of the specimens at AMNH (3571, 4399), MNHN (LAC 1883-507–1883-509), and USNM (224810, 292917, 432236). Coracoid measurement is of internal length; for other bones, measurement is of total length. When measurements are not known, successive points are united by dashed lines. (Cor.=coracoid, Cpm.=carpometacarpus, Fem.=femur, Hum.=humerus, Tbt.=tibiotarsus, Tmt.=tarsometatarsus, Uln.=ulna.)

subspecies from the Comoros and Praslin are smaller (Forshaw, 1973).

According to the accounts of the early explorers, there were at least four species of parrots on Réunion. The description given by Dubois of "parrots a little bigger than pigeons, the feathering of the color of *petit-gris*, a black hood on the head, the beak very strong and the color of fire" is considered to apply to *M. mascarinus* (Barré and Barau, 1982:31, our translation). *Petit-gris* is the name given to the fur of the Eurasian Red Squirrel (*Sciurus vulgaris* Linnaeus) in its dark phase. Two other species were a grey parrot, which according to Feuilley was smaller than *M. mascarinus*, and a green parakeet with a black ring, the Réunion Ring-necked Parakeet, *Psittacula eques* (Boddaert), which probably was conspecific with the still-living Mauritian Echo Parakeet (Cheke, 1987). A fourth species, which was the same size as *P. eques*, was described by Dubois as a "green parrot with head, upper parts of wings, and tail color of fire" (Barré and Barau, 1982:31, our translation).

FIGURE 13 (opposite).—Fossils of falcons, coots, pigeons, and parrots from the Mascarenes. *Falco duboisi: a*, left coracoid, Grotte de l'Autel, 330548, posterior view, ×1.5; *b*, left tibiotarsus, paratype, Grotte des Premiers Français, 1993-30, anterior view; *c*, right tibiotarsus, paratype, Grotte des Premiers Français, 1993-33, anterior view; *d*, left femur, paratype, Grotte des Premiers Français, 1993-29, posterior view; *e*, left tarsometatarsus, holotype, Grotte des Premiers Français, 1993-28, anterior view. *Falco punctatus: f*, left coracoid, Montagne du Pouce caves, Mauritius, MNHN, not numbered, posterior view, ×1.5. *Nesoenas duboisi: g*, right humerus, Grotte de l'Autel, 330546, anconal view; *h*, same, palmar view. *Fulica newtonii: i*, sternum, Grotte des Premiers Français, 1993-39, ventral view; *j*, right tibiotarsus, Grotte des Premiers Français, 1993-41, anterior view; *k*, right tarsometatarsus, Marais de l'Ermitage, 1811, anterior view; *l*, right coracoid, Marais de l'Ermitage, 1814, posterior view; *m*, left ulna, distal part, Marais de l'Ermitage, 1815, internal view. *Streptopelia picturata: n*, right humerus, proximal part, Grotte "au sable," 330738, anconal view, ×1.5. *Mascarinus mascarinus: o*, right humerus, Grotte de l'Autel, 330539, anconal view; *p*, same, palmar view; *q*, left carpometacarpus, Grotte de l'Autel, 330544, internal view, ×1.5; *r*, left coracoid, Grotte de l'Autel, 330545, posterior view, ×1.5; *s*, same, anterior view, ×1.5; *t*, left ulna, Grotte de l'Autel, 330541, palmar view; *u*, same, internal view; *v*, left femur, Grotte de l'Autel, 330543, posterior view; *w*, same, anterior view; *x*, left tibiotarsus, Grotte de l'Autel, 330542, anterior view. *Mascarenotus grucheti: y*, right tarsometatarsus, holotype, Grotte des Premiers Français, 1993-49, anterior view. (*a*, *f*, *n*, *q*, *r*, *s* ×1.5; others natural size.)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Without any justification, Rothschild (1907) placed this form in the genus *Necropsittacus* of Rodrigues and described it as *N. borbonicus.*

Family STRIGIDAE

Genus *Mascarenotus* Mourer-Chauviré, Bour, Moutou, and Ribes

Mascarenotus grucheti Mourer-Chauviré, Bour, Moutou, and Ribes, 1994

Gruchet's Mascarene Owl

FIGURE 13*y*

MATERIAL.—Grotte des Premiers Français. *Holotype:* r. tarsometatarsus, 1993-49. *Paratypes:* l. humerus, 1993-50; r. p. tibiotarsus, 1993-48; r. d. tibiotarsus, 1993-47.

Grotte de l'Autel: r. tarsometatarsus, 330537; r. d. tarsometatarsus, 330538.

Grotte "au sable": l. quadrate, 330809; l. p. femur, 330737.

Marais de l'Ermitage: r. tarsometatarsus, 1800.

REMARKS.—We have not found any additional remains other than those used in the original description of *Mascarenotus grucheti* (Mourer-Chauviré et al., 1994). We have placed all the Mascarene strigiforms in the extinct genus *Mascarenotus,* which resembles the genus *Otus* but presents some distinctive morphological characteristics. This genus includes one species on Mauritius, *Mascarenotus sauzieri,* based on *Strix sauzieri* Newton and Gadow, 1893 (synonyms, *Otus commersoni* Oustalet (1896), *Strix newtoni* Rothschild (1907)), one species on Rodrigues, *Mascarenotus murivorus* based on *Strix* (*Athene*) *murivora* Milne-Edwards (1874) (synonym, *Bubo* (?) *leguati* Rothschild (1907)), and one species on Réunion, *Mascarenotus grucheti* Mourer-Chauviré et al., 1994.

The tarsometatarsi of *M. grucheti* are very close in size to those of *M. sauzieri,* although the only humerus known from Réunion is clearly smaller than those of *M. sauzieri,* for which we have a good sample of comparative material (12 specimens). The ratio of element lengths (Mourer-Chauviré et al., 1994, fig. 1) shows *M. sauzieri* to be strikingly parallel to modern insular species of the genus *Otus,* such as *Otus lawrencii* (Sclater and Salvin), or *O. nudipes* (Daudin), from the West Indies, in which the legs are much more elongated than in continental forms. The same adaptation is found in the four extinct insular species of the genus *Grallistrix,* from Hawaii, which is derived from the genus *Strix* (Olson and James, 1991). In the Strigiformes, as well as in the genus *Accipiter,* this lengthening of the legs corresponds to an adaptation for catching birds on islands lacking terrestrial mammals.

This species must have had a very secretive life in the forests or remote areas, because the early explorers of Réunion never spoke of nocturnal raptors, although eared owls were noted historically on the other Mascarene Islands.

Family STURNIDAE

Genus *Fregilupus* Lesson

Fregilupus varius (Boddaert, 1783)

Réunion Starling

MATERIAL.—Grotte des Premiers Français: l. d. femur, 1993-57.

REMARKS.—This passerine femur agrees in size and morphological characteristics with what is known of the Réunion Starling. On the posterior face, the proximal edge of the internal condyle ends internally with a point that projects proximad. On the internal face, the internal condyle is anteroposteriorly compressed. This characteristic accentuates the shape of the external condyle, which looks very protruding, and the rotular groove on the anterior face is deep, as was indicated by Murie (1874), who described the only known skeleton of this species. The distal width (7.2 mm) and the distal depth (5.8 mm) agree with a femur the total length of which ranges from 31.6 mm (Berger, 1957) to 35.6 mm (Murie, 1874) or 37 mm (Günther and Newton, 1879).

The Réunion Starling became extinct between 1838 and 1858 (Barré and Barau, 1982).

Relationships, Origin, and Fate of the Réunion Avifauna

The avifauna found as fossils on Réunion differs from that of the other two Mascarenes (Table 13) in that, with the exception of *Dryolimnas augusti,* none of the species had lost their ability to fly.

Lacking on Réunion are the most distinctive Mascarene birds, namely, the dodo and solitaire (*Raphus, Pezophaps*), the large flightless rails (*Aphanapteryx, Erythromachus*), and the large parrots with enormous bills and atrophied wings (*Lophopsittacus mauritianus, Necropsittacus rodericanus*) (Newton and Newton, 1876; Günther and Newton, 1879). Among the forms that perhaps had lost the ability to fly is the *Oiseau bleu,* placed by Olson (1977) in the genus *Porphyrio,* and which was either an extinct species of that genus or a population of the modern species *Porphyrio porphyrio* (Linnaeus). Dubois (1674) said that it could not fly, but in 1724 Father Brown said that it was able to fly, but rarely and just above the ground (Barré and Barau, 1982, our translation). The authenticity of Father Brown's report has been questioned (Lougnon, 1970, 1992), but Cheke (1987) thinks that his report comes from an unidentified but authentic source. Remains referable to *Oiseau bleu* are yet to be found, so we know nothing more about it.

The other genera represented on Mauritius and Rodrigues by species with reduced flying ability are represented on Réunion by species with normal flying ability. This is the case for *Nycticorax,* with the flying species *N. duboisi,* and for *Falco duboisi,* the coracoid and ulna of which are not reduced, unlike that of *F. punctatus,* of Mauritius. The other extinct species, namely

TABLE 13.—Native resident land birds of the Mascarene Islands. L=species still living on the island today, E=species completely extinct, X=species now extinct but known by modem specimens, F=species known from fossils found on the specified island, H=species known by historical accounts (when not known from fossils). (*Egretta dimorpha* on Mauritius is after Milne-Edwards (1874, pl. 33: fig. 3). There is no indication that "*Necropsittacus*" *borbonicus* belongs to the same genus as *N. rodericanus*. *Hypsipetes* (species undescribed) and Timaliinae (genus and species undescribed) on Rodrigues from Cowles (1987). A supposed grebe from Mauritius was based on a fossil of the migratory Whimbrel, *Numenius phaeopus* (Cowles, 1987).)

Family	Réunion	Mauritius	Rodrigues
PHALACROCORACIDAE	*Phalacrocorax africanus?* (as "Cormoran"), H	*Phalacrocorax africanus*, F	–
ARDEIDAE	*Nycticorax duboisi*, E,F	*Nycticorax mauritianus*, E,F	*Nycticorax megacephalus*, E,F
	Egretta dimorpha? (as "Aigrette blanche et grise"), H	*Egretta dimorpha*, F	–
THRESKIORNITHIDAE	*Threskiornis solitarius*, E,F	–	–
PHOENICOPTERIDAE	*Phoenicopterus ruber*, F	*Phoenicopterus ruber*, F	possibly historical "géant," H
ANATIDAE	*Alopochen* (*M.*) *kervazoi*, E,F	*Alopochen mauritianus*, E,F	–
	Anas theodori, E,F	*Anas theodori*, E,F	–
	Aythya sp., F	–	–
ACCIPITRIDAE	*Circus maillardi*, L	*Circus alphonsi*, E,F	–
FALCONIDAE	*Falco duboisi* (as "Pieds jaunes"), E,F	*Falco punctatus*, L,F	–
	"Emerillons," E,H"	–	–
TURNICIDAE	*Turnix nigricollis* (as "Petites perdrix"), L,H	–	–
RALLIDAE	*Dryolimnas augusti*, n. sp. E,F	*Dryolimnas cuvieri*, X,F	–
	–	*Aphanapteryx bonasia*, E,F	*Erythromachus leguati*, E,F
	Porphyrio caerulescens (as "Oiseau bleu"), E,H	–	–
	Fulica newtonii, E,F	*Fulica newtonii*, E,F	–
RAPHIDAE	–	*Raphus cucullatus*, E,X,F	*Pezophaps solitaria*, E,F
COLUMBIDAE	*Alectroenas* sp.? (as "Pigeon couleur d'Ardoise"), E,H	*Alectroenas nitidissima*, E,X,F	–
	Nesoenas duboisi, E,F	*Nesoenas mayeri*, L,F	–
	–	–	"*Columba*" *rodericana*, E,F
	Streptopelia picturata, L,F	*Streptopelia picturata*, L,F,H	*Streptopelia picturata*, L,F
PSITTACIDAE	–	*Lophopsittacus mauritianus*, E,F	–
	"Perroquet gris," E,H	"*Lophopsittacus*" *bensoni*, E,F	–
	"*Necropsittacus*" *borbonicus* (as "Perroquet vert à tête, dessus des ailes et queue couleur de feu"), E,H	–	*Necropsittacus rodericanus*, E,F
	Mascarinus mascarinus, E,X,F	–	–
	Psittacula eques/echo? (as "Perroquet vert à collier noir"), H	*Psittacula eques/echo*, L,F	*Psittacula exsul*, E,X,H
STRIGIDAE	*Mascarenotus grucheti*, E,F	*Mascarenotus sauzieri*, E,F	*Mascarenotus murivorus*, E,F
APODIDAE	*Collocalia francica*, L	*Collocalia francica*, L	–
HIRUNDINIDAE	*Phedina borbonica*, L	*Phedina borbonica*, L	–
CAMPEPHAGIDAE	*Coracina newtoni*, L	*Coracina typica*, L	–
PYCNONOTIDAE	*Hypsipetes borbonicus*, L	*Hypsipetes olivaceus*, L	*Hypsipetes*, sp. undescribed, E,F
MUSCICAPIDAE	*Terpsiphone bourbonnensis*, L	*Terpsiphone bourbonnensis*, L	–
TURDIDAE	*Saxicola tectes*, L	–	–
TIMALIIDAE	–	–	TIMALIINAE, genus and sp. undescribed, E,F
SYLVIIDAE	–	–	*Acrocephalus rodericanus*, L
ZOSTEROPIDAE	*Zosterops borbonicus*, L	*Zosterops borbonicus*, L	–
	Zosterops olivaceus, L	*Zosterops chloronothos*, L	–
PLOCEIDAE	*Foudia* sp. (as "Moineaux"), E,H	*Foudia rubra*, L	*Foudia flavicans*, L
STURNIDAE	*Fregilupus varius*, E,X,F	–	*Necropsar rodericanus* E,F

Threskiornis solitarius, *Alopochen* (*M.*) *kervazoi*, *Anas theodori*, *Nesoenas duboisi*, and *Mascarinus mascarinus*, do not show reduction in the scapular girdle or wing bones. *Alopochen* (*M.*) *kervazoi* shows a very slight reduction compared with the recent African forms, but this also exists in the extinct form from Madagascar. We suggest that this reduction had already occurred in the Malagasy forms before they colonized Réunion. *Fulica newtonii* shows a reduction of the coracoid and wing bones, but it is the same species as in Mauritius, and it probably colonized Réunion from that island. *Mascarenotus grucheti* has a more reduced humerus than does *M. sauzieri*, but it is the only exception.

Réunion Island dates back 3 Ma (Molnar and Stock, 1987), a length of time amply sufficient for birds to lose their flying ability in such a way that it can be perceived in the skeleton. For example, the flightless ibises from Hawaii are known only from islands dating to less than 1.8 Ma (Olson and James, 1982). Thus it is necessary to find a cause for this absence of flightless forms. We have good reason to believe that this cause may be found in the volcanic past of the island.

Réunion is situated on a hotspot that gave rise to the Deccan traps during the Cretaceous, then the Chagos-Laccadive Ridge, the Mascarene Plateau, and Mauritius (Bonneville, 1990). It is made up of two volcanoes: the oldest is Piton des Neiges, in the northwest, the volcanic activity of which now consists only of thermal springs, whereas the more recent Piton de la Fournaise, in the southeast, is still active.

Piton des Neiges is a strato-volcano, made up of hundreds of lava flows spread out on gentle slopes. Built up on a 4000 m deep seafloor, it emerged about three million years ago (m.y.a.), but the oldest dated rocks are 2.1 Ma in age. Its construction includes two main phases, one with tholeiitic and transitional basalts, dating back 2.1 to 0.43 Ma, and one with differentiated alkaline lavas, dating from 0.35 Ma to less than 30,000 years ago (Kieffer, 1990; Deniel et al., 1992; Kieffer et al., 1993). The alkaline products appeared in the course of very explosive eruptions that resulted in several calderas.

Piton de la Fournaise appeared above the ocean about one m.y.a. but collapsed several times on its eastern side. After each collapse a new cone appeared farther westward. The first collapse is marked by the caldera of Rivière des Remparts, which is very close to the massif of Piton des Neiges.

The second phase of Piton des Neiges, with differentiated alkaline lavas, shows three major explosive episodes. The first one, before 230,000 years ago, emitted pyroclastites that fell down on the whole western flank and probably also on the northern flank. The Quenched Bombs Formation, which belongs to this episode, is found from the Dos d'Ane, in the northwest, to Saint-Pierre, in the south of the Piton des Neiges massif. Thus at this time, the massif must have been almost entirely covered by pyroclastites. The second one, known as the *dalle soudée* (welded slab) episode, dates back to 230,000 years. It was produced by huge lava fountains that shot up several km into the air and came down while still fluid, welding after falling. After this explosive event, the center of the volcano collapsed, resulting in a caldera, the diameter of which was eight to 10 km. The third explosive episode, dated back to 188,000 years, produced ignimbrites that flowed down mainly on the eastern flank. Other explosive phenomena occurred subsequently, but the material emitted remained mainly inside the caldera. Thus, during these explosive volcanic eruptions, almost all the massif of Piton des Neiges was covered by incandescent products. In the meantime, the Piton de la Fournaise, which had no explosive episodes, collapsed several times into the ocean.

It may be supposed that Réunion Island was colonized by the same birds that colonized Mauritius and Rodrigues, that is, a pigeon ancestor of the Dodo and Solitaire, a rail ancestor of the genera *Aphanapteryx* and *Erythromachus,* and a parrot ancestor of the genera *Lophopsittacus* and *Necropsittacus,* and that they evolved on Réunion as on the other islands, progressively losing their ability to fly. These flightless or almost flightless forms disappeared during the explosive episodes of the second phase of activity of Piton des Neiges, between 300,000 and 180,000 years ago. Either they disappeared instantaneously or their environment was so depleted that they were not able to survive. The island was colonized again by forms from Africa or Madagascar, such as the ibis, *Alopochen,* falcon, and night heron, or by forms from Mauritius, such as *Anas theodori* and *Fulica newtonii,* and none of these forms had enough time to become flightless.

Two genera, however, *Mascarinus* and *Fregilupus,* are endemic to Réunion. It is probable that if they had arrived on Réunion after 180,000 years ago, they would not have had enough time to become generically distinct. One may propose the hypothesis that the ancestral forms of these genera arrived on Réunion at a more ancient period and survived the holocaust.

The presence of a flightless rail of the genus *Dryolimnas* is compatible with this hypothesis because we have the example of *D. cuvieri aldabranus,* which has become flightless, whereas the Madagascan subspecies, *D. cuvieri cuvieri,* is still able to fly. Aldabra Island has undergone several cycles of emergence and submergence, and its most recent emergence occurred about 80,000 years BP (Braithwaite et al., 1973). The Aldabra White-throated Rail must have arrived on the island after the last emersion, so 80,000 years or less were enough for its skeleton to be considerably modified.

The study of bats and of the Réunion land tortoise, *Cylindraspis borbonica,* does not refute the foregoing hypothesis. The bats include two extinct species, *Pteropus niger* (Kerr) and *Pteropus subniger* (Kerr), another that is probably extinct, *Scotophilus borbonicus* (E. Geoffroy) (=*S. leucogaster*), and two species that are still present, *Mormopterus acetabulosus* (Hermann) and *Taphozous mauritianus* E. Geoffroy. All but *Scotophilus* once lived, or are still living, on Mauritius (Cheke and Dahl, 1981; Moutou, 1982). *Scotophilus borbonicus* also occurs in Africa and Madagascar and probably colonized Réunion in recent times (Cheke, 1987).

The genus *Cylindraspis,* endemic to the Mascarenes and now extinct, is represented on Réunion by a single species, whereas two species are known on Mauritius, and another two are known on Rodrigues. The two Mauritian species, *Cylindraspis neraudii* (Gray) (=*C. inepta;* =?*C. indica*) and *Cylindraspis triserrata* (Günther) (=?*C. graii*), can be distinguished from each other by their skeleton and particularly by their skull, the latter showing a specialization of the triturating surfaces (supplementary ridges). These two sympatric and synchronous species indicate either a long in situ evolution, with speciation, or two successive colonizations from a common ancestral stock. On Rodrigues the two species *Cylindraspis rodericensis* (Günther) (=?*C. vosmaeri*) and *C. peltastes* (Duméril and Bibron) (the smallest form in the genus) exhibit a striking synapomorphy (predominance of the palatine arterial circulation over the stapedio-temporal circulation; Bour, 1985), which indicates that their common ancestor evolved independently from the Mauritian populations before it was subjected to the environmental constraints that led to the present-day situation. On the other hand, the Réunion land-tortoise, although immediately identifiable by its extremely robust dentary and maxillary alveolar surfaces, remained close to one of the Mauritian species (*C. neraudii*) and did not show advanced specializations as in the other three species. Therefore it could have colonized Réunion in a relatively recent period from an ancestor related to that Mauritian species. Its distribution on the island, restricted as far as we know to the leeward regions (the western part), reinforces the hypothesis of a recent immigration. It is not possible to know, however, if it reached the island before or after the explosive phenomena of the Piton des Neiges, or if Réunion housed in far-off days a previous population of tortoises that was exterminated together with other representatives of the original fauna. We must remember that the first vestiges of the Bourbon tortoise, their whereabouts unfortunately unknown, were found by L. Maillard in 1854, at Cap La Houssaye, under four meters of lava (Bour, 1980b). Were they the representatives of an ancient population, wiped out a long time ago by a cataclysm, or were they the ancestors of the recently extinct form?

As a result of the above considerations, we propose the hypothesis that most of the birds that were present on Réunion colonized the island only after the explosive episodes of Piton des Neiges.

At the time when the Europeans were colonizing the island, the Réunion avifauna included about 33 species of resident land birds (Table 13). Of these 33 species, 14 have been found as fossils. Among those that were certainly present but have not been found as fossils are members of the genera *Circus, Alectroenas, Psittacula, Collocalia,* and all the small passerines, *Phedina, Coracina, Hypsipetes, Terpsiphone, Saxicola, Zosterops,* and *Foudia.* We think that the small passerines were not present in the fossiliferous sites that we have exploited. Among these 33 species, 17 (52%) are extinct, four or five are no longer present on Réunion, and 11 are still present there. Among the 11 surviving species, eight are very small birds (Apodiformes and Passeriformes), and one species, *Coracina newtoni* (Pollen), is very endangered.

The extinctions took place very rapidly, over a period of two centuries from 1646. A first group of species, reported by the early visitors and by Dubois (1674), in 1671–1672, became extinct almost immediately because they are not mentioned afterwards. Species that disappeared at that time are *Nycticorax duboisi, Alopochen (M.) kervazoi, Anas theodori, Falco duboisi,* a smaller falcon known as *Émerillon, Dryolimnas augusti, Fulica newtonii,* a parrot known as *perroquet vert à tête ... couleur de feu,* and *Foudia* sp. In Dubois' time the island had only 314 human inhabitants (Bour, 1980a). Rats were absent in 1671, as indicated in the log of *Le Breton* and by Dubois (1674) in 1671–1672, but they invaded the island in 1675 (Cheke, 1987). This first wave of extinction mainly included aquatic forms that were living in the ponds and marshes of the west coast, the area that was first settled. There was no other refuge possible for these species. They were still able to fly but they had become flightless in their behavior. Numerous writers emphasize how tame they were and how easily they allowed themselves to be killed without fleeing. Moreover, anseriforms are very vulnerable during their period of molt. The two falcons were perhaps adapted for capturing prey living in the dry west coast palm savanna and the western lowland dry forest, environments that were completely cleared for cultivation. According to Cheke (1987), *Foudia* was exterminated by rats.

The second wave included species mentioned by Feuilley in 1704 (Barré and Barau, 1982) but not recorded thereafter. Species that disappeared at that time are a cormorant (probably *Phalacrocorax africanus* (Gmelin)), an egret (probably *Egretta dimorpha* Hartert), *Phoenicopterus ruber, Threskiornis solitarius,* and four species of pigeons, *Alectroenas* sp., *Nesoenas duboisi, Streptopelia picturata,* and another dove. Flamingos were known to be breeding on the island, and they are vulnerable during their colonial nesting. The Réunion Ibis, known as "Solitaire," survived for a short time, taking refuge in the mountains, but it was decreasing and was not reported after 1708. Cats were introduced into the island in 1703 to fight rats and must have played a large part in the destruction of birds because in 1704 Feuilley wrote: "*Ramiers* have not been seen for some time, either they have deserted the island, or they have been destroyed by the cats," and, concerning the *huppes* (*Fregilupus*) and the *merles* (*Hypsipetes*): "*Marron* cats destroy many of them. These birds let the cats get very close and they are caught without getting out of their places" (Barré and Barau, 1982:38, our translation).

Then, between 1734 and 1740, *Oiseau bleu,* a grey parrot, and a parakeet, *Psittacula eques/echo,* disappeared, followed about 1780 by *Mascarinus mascarinus,* and lastly, between 1838 and 1858, by *Fregilupus varius.* According to Cheke (1987:24) the Solitaire and *Oiseau bleu* "were probably victims of feral cats but the parrots may have been dependent on the lowland habitats."

It is difficult to evaluate accurately the role played by different factors in the extinction of these birds. But these factors—excessive hunting by humans, the action of introduced predators (e.g, pigs, rats, cats), and habitat destruction—cannot account for the disappearance of the Réunion Starling, for which the introduction of a disease or parasite has been invoked (Cheke, 1987).

The example of Réunion shows that, in an insular environment, flying birds disappear almost as quickly as flightless ones. The relief of Réunion is very rugged, much more than that of Mauritius or Rodrigues. It has many places that are difficult to reach and where birds may have been protected, but this rugged topography did not prevent the tame, naive birds of Réunion from disappearing.

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The Fossil Avifauna of Amsterdam Island, Indian Ocean

Trevor H. Worthy and Pierre Jouventin

ABSTRACT

The fossil avifauna of Amsterdam Island is described from 23,562 identifiable bones representing 2060 individuals from 30 sites. Twenty species of seabirds and one land bird are represented by the fossils. This may underestimate the prehuman species richness because two of the 10 indigenous species that now breed on the island are not represented among the fossils. Lengths of bones for all common species on Amsterdam are compared with those of populations elsewhere. On Amsterdam, Great-winged Petrel (*Pterodroma macroptera* (Smith)) and Grey Petrel (*Procellaria cinerea* Gmelin) populations were composed of individuals of relatively small mean size. The Macgillivray's Prion (*Pachyptila macgillivrayi* (Mathews)) is shown to be specifically distinct from the Broad-billed Prion (*P. vittata* (Forster)) and Salvin's Prion (*P. salvini* (Mathews)), based on osteological measurements.

Introduction

Amsterdam (37°50′S, 77°31′E) and St. Paul islands lie 80 km apart in the middle of the Indian Ocean, more than 3,000 km from any continent (Figure 1); both islands are of volcanic origin. Amsterdam is roughly circular, 9.2 km long and 7.4 km wide, and rises to 881 m above sea level (a.s.l.). The western coastal cliffs are spectacularly high (400–700 m), but cliffs are 20–80 m high over most of the remaining coastline. Average air temperature varies between 11.2° C in August and 17° C in February. The climate is windy and humidity is high, with rainfall (annual mean 1114 mm) usually falling as a light drizzle on 239 days of the year (Jouventin, 1994). This high humidity and frequent rain has promoted peat development over much of the island.

Prior to human disturbance, lowland areas less than 250 m that were above the coastal cliffs, and where the soil was wet and deep, were covered by a thick, six- to seven-meter-high forest of the tree *Phylica nitida* (Rhamnacae). In the highlands, and on the central plateau, peatlands were dominated by an association of clubmoss (*Lycopodium trichiatum*) and a fern (*Gleichenia polypodioides*), with some grasses, sedges, and forbs (*Uncinia brevicaulis, Poa fuegiana, Trisetum insulare, Acaena seurguisarbae,* and *Scirpus aucklandicus*) (Jouventin, 1994; Micol and Jouventin, 1995).

HISTORY OF EXPLORATION.—The island was discovered on 18 March 1522, but the first landing was not until 1696. Drawings made then showed that 27% of the island was forested, but by 1875 forest cover was reduced to 5%, and by 1990 only 12 ha, or 0.2%, remained (Jouventin, 1994). Deforestation was caused by ships stopping en route from South Africa to Australia to collect wood, and by repeated fires.

Fur seals (*Arctocephalus tropicalis* (Gray)) were harvested in great numbers from about 1790, but they disappeared by 1893. A small colony was found in 1905 and is making a good recovery (Jouventin, 1994). Other human visitors to the island killed penguins, albatrosses, and petrels for food or for bait for lobster pots. Many animals were introduced. The dog (*Canis familiaris* Linnaeus), pig (*Sus scrofa* Linnaeus), and goat (*Capra hircus* Linnaeus) died out, whereas the house mouse (*Mus musculus* Linnaeus), Norway rat (*Rattus norvegicus* (Berkenhout)), cat (*Felis catus* Linnaeus), and cow (*Bos taurus* Linnaeus) remain (Jouventin, 1994; Micol and Jouventin, 1995).

Habitat degradation caused by repeated fires and cattle grazing, plus predation by other mammals and active hunting by people, combined to decimate the avifauna, which consisted mainly of seabirds. The breeding fauna on Amsterdam at first human contact has been estimated to include at least 20 species (Jouventin, 1994), of which only the following 10 species remain (Micol and Jouventin, 1995) (nomenclature for modern avifauna discussed herein follows Marchant and Higgins, 1990). The Northern Rockhopper Penguin (*Eudyptes chrysocome*) and the Yellow-nosed Albatross (*Diomedea chlororhynchos*) are common. The Sooty Albatross (*Phoebetria fusca*) is rare, with about 240 pairs, and only about 20 breeding pairs of the endemic Amsterdam Albatross (*Diomedea amsterdamen-*

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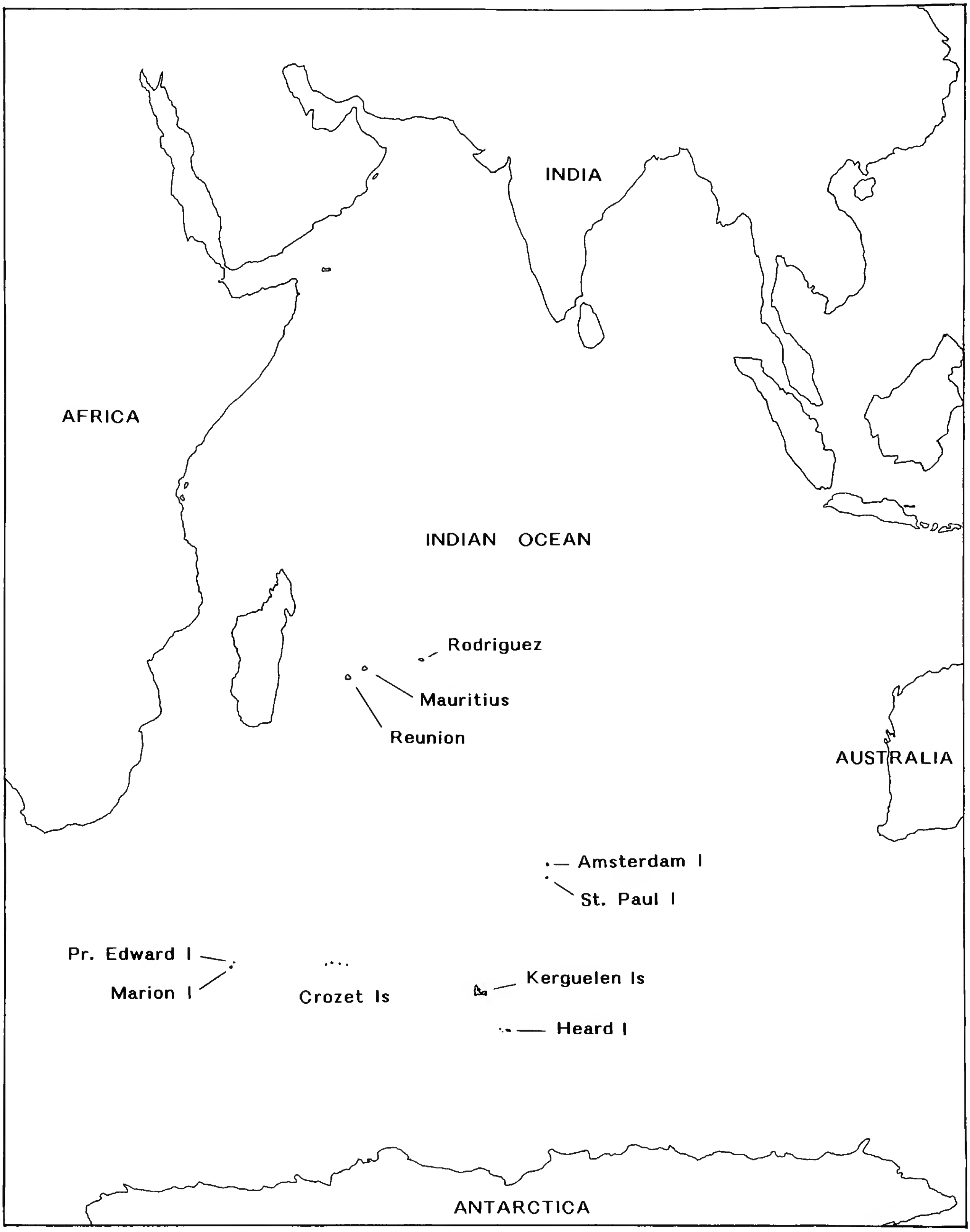

FIGURE 1.—Location of Amsterdam Island and St. Paul Island in the Indian Ocean.

sis) survive. Both the Soft-plumaged Petrel (*Pterodroma mollis*) and the Grey Petrel (*Procellaria cinerea*) are now very rare and are believed to be breeding on cliffs away from cattle trampling. Macgillivray's Prion, listed as *Pachyptila salvini macgillivrayi* by Micol and Jouventin (1995), is rare and endangered with 100–200 pairs, and the Diving Petrel (*Pelecanoides* sp.) is very rare, with only one record of a breeding pair. The Antarctic Tern (*Sterna vittata tristanensis*) breeds on coastal cliffs, and a few Brown Skua (*Catharacta skua hamiltoni*) nest inland (Jouventin, 1994; Micol, 1995).

Fortunately, St. Paul has a small rock stack, Roche Quille, just offshore, that has remained predator free, allowing the precarious survival of the following species of procellariiforms that no longer breed on Amsterdam or on St. Paul: Fairy Prion (*Pachyptila turtur,* 10–20 pairs), Great-winged Petrel (*Pterodroma macroptera,* 40–60 pairs), and Little Shearwater (*Puffinus assimilis,* 25 pairs) (Micol, 1995). The Flesh-footed Shearwater (*Puffinus carneipes*), previously reported from Roche Quille (Tollu, 1984; Jouventin, 1994), is absent there now, but it is present on St. Paul, where Micol (1995) reported 532 pairs. The White-bellied Storm-petrel (*Fregetta grallaria*) survives on both Roche Quille and St. Paul in small numbers, and Wilson's Storm-petrel (*Oceanites oceanicus*) has been found breeding in small numbers on St. Paul (Micol, 1995). Roche Quille has the only other known population of Macgillivray's Prion (100–200 pairs) apart from that on Amsterdam.

The survival of several species on Roche Quille and not on St. Paul or Amsterdam suggests that several species of storm petrels, prions, shearwaters, and petrels have disappeared from Amsterdam. Of the remaining 10 breeding species, eight are now rare. Apart from the loss of several procellariiforms from Amsterdam, the only known native terrestrial species, a minute, endemic, flightless duck, *Anas marecula* (Bourne et al. 1983; Martinez, 1987; Olson and Jouventin, 1996), is extinct.

PREVIOUS INVESTIGATIONS OF THE FOSSIL FAUNA.—The volcanic origin of Amsterdam Island has resulted in the formation of many lava caves, the collapsed roofs of which have in many places formed pitfall traps into which birds have fallen. Fossil bones have been found to be abundant in these sites. The first fossils were collected in 1955 by Jouanin and Paulian (1960), who identified several bones from one individual as a Wandering Albatross (*Diomedea exulans*). They noted two sizes of *Pterodroma* (listed as *Bulweria*): they identified the larger one as *P. neglecta,* primarily on the basis of size, and the smaller one as *P. mollis.* Other species identified included *Puffinus assimilis, Pachyptila vittata, Pelagodroma marina, Pelecanoides urinatrix,* and *Anas* sp. Lastly, they reported a mummified rail that "crumbled to dust," which they tentatively referred to *Crex crex* (Linnaeus).

Bourne et al. (1983) examined the duck bones reported by Jouanin and Paulian (1960) and suggested that they had some similarity to those of a Garganey (*Anas querquedula*). Martinez (1987) briefly described the collection of fossils that he made in 1983 and 1984. He listed 17 species: one albatross, two *Procellaria,* three *Pterodroma,* two *Puffinus,* two *Pachyptila,* a *Pelecanoides,* three storm petrels, a *Eudyptes,* a *Catharacta,* and a flightless duck whose bones he described and compared to other ducks, but which he did not name. This collection is the subject of this paper.

The fossil sites are all lava caves (Figure 2) that vary in length from a few meters to about 200 m (Figures 3, 4). No radiocarbon dates for the fossils are available, and without dating each site these would not establish the relative ages of all sites. In their absence, however, we make the observation that all bones were found on the surface, and many had organic remains, including dried tissue and feathers on them, suggesting that most are between a few hundred and a few thousand years old.

The material was collected without retention of skeletal associations, and, later, Martinez made a preliminary sort of it into species by element. After most *Anas* and *Diomedea* bones were removed for independent analysis, the collection was shipped to the Museum of New Zealand Te Papa Tongarewa (MNZ) (formerly National Museum of New Zealand) for analysis.

We describe herein the fossil fauna from Amsterdam Island, detailing the species represented, their relative abundance, and their size (using bone lengths) relative to that of modern populations. Extensive comparative descriptions and mensural comparisons were necessary to justify our specific determinations.

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METHODS

The Martinez collection is cataloged under numbers MNZ S34560–S35079 in the Museum of New Zealand Te Papa Tongarewa. One of us (THW) examined it in 1994 and 1995 and is responsible for all identifications, measurements, and comparisons. Material that remained in France, including the majority of the albatross and duck bones, was not included in the analysis. The duck bones are now at the National Museum of Natural History, Smithsonian Institution (USNM, housing the col-

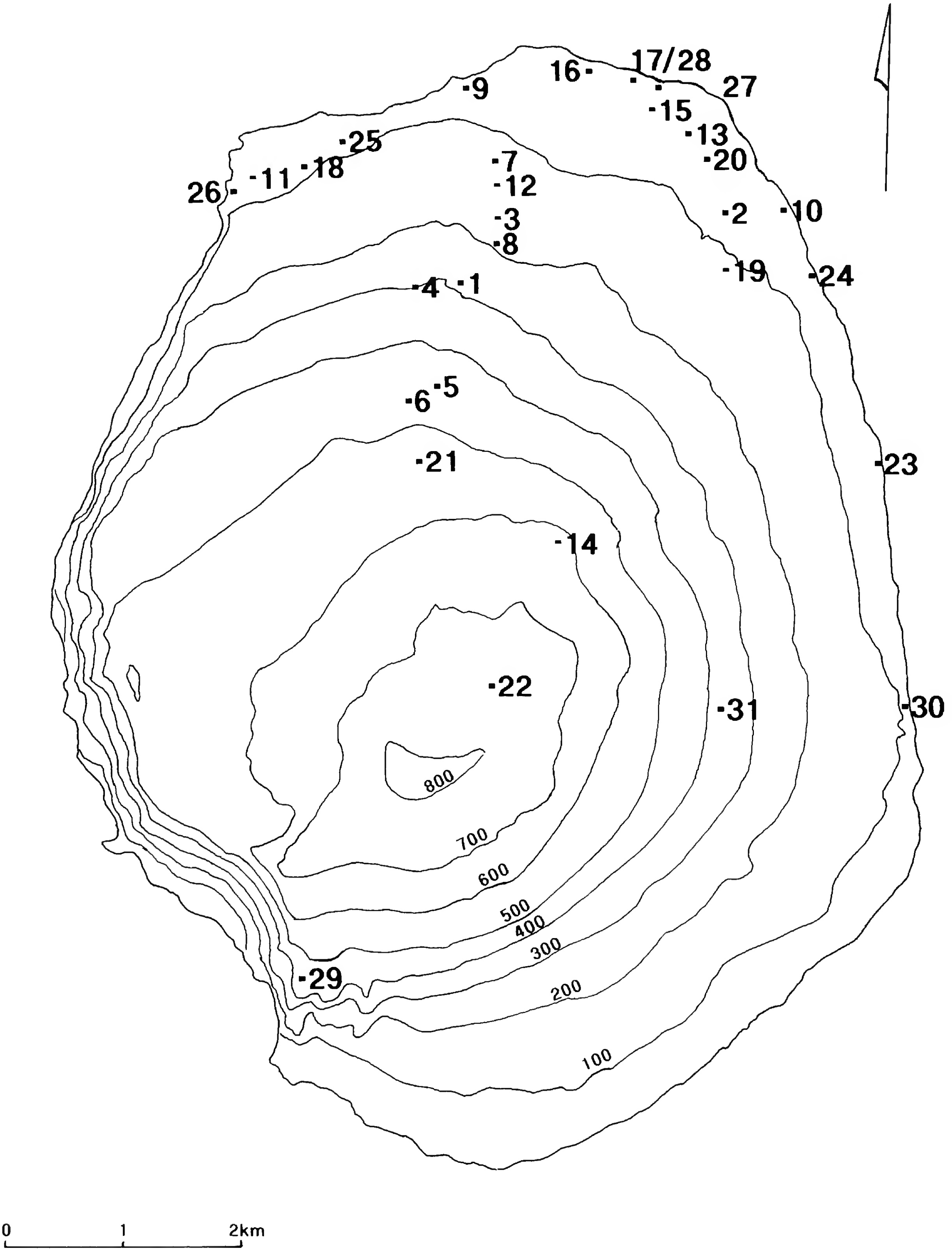

FIGURE 2.—Distribution of fossil sites on Amsterdam Island; numbers indicate locations of lava caves (see Figures 3, 4).

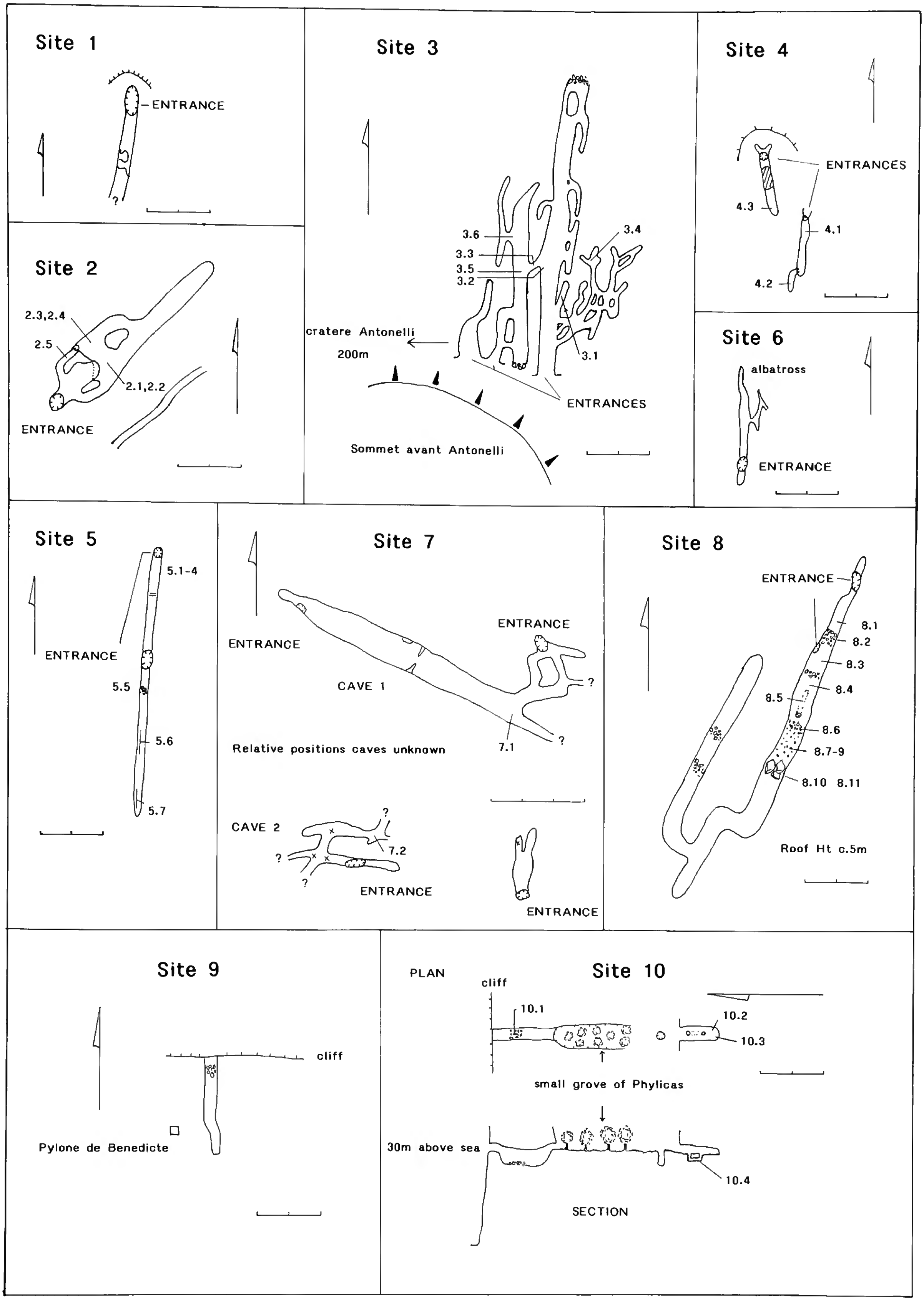

FIGURE 3.—Sketch maps of the caves in which the fossil sites were located. Scale bars=10 m.

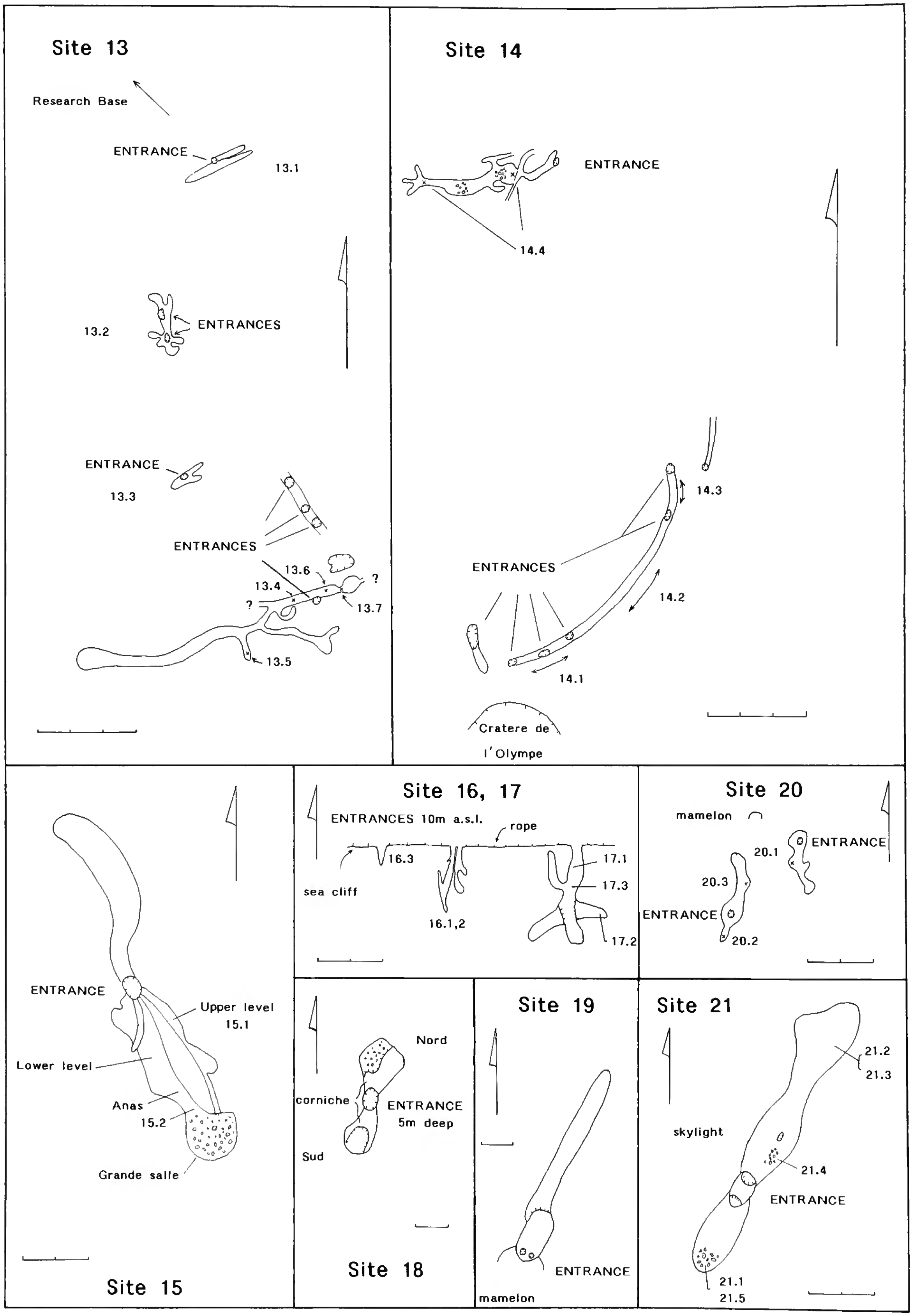

FIGURE 4.—Sketch maps of the caves in which the fossil sites were located. Scale bars=10 m.

lections of the former United States National Museum) (Olson and Jouventin, 1996). Fossils were compared with the extensive collections of modern material held in the MNZ. Notes justifying specific identifications are given below. The geographic ranges of species are taken from data in Marchant and Higgins (1990) unless otherwise stated.

The following measurements were taken: total skull length (Skull TL) from tip of premaxilla to cerebellar prominence; basicranial skull length (BCL) from occipital condyle to premaxilla articulation; skull width at lacrimals (Lac W), but where lacrimals are not fused in adults, for example, *Procellaria* and *Puffinus*, the width was measured between the articular surfaces of the lacrimals (Preorb W); maximum skull width across the postorbital processes (PO W); width across the zygomatic processes (ZP W); length of the premaxilla from the tip to the nasofrontal hinge (Pmx L); maximum width of premaxillae (Pmx W); total length for femora (Fem L), tibiotarsi (Tib TL), tarsometatarsi (Tmt L), humeri (Hum L), ulnae (Ulna L), and carpometacarpi (Cmc L); and tarsometatarsus-shaft width (Tmt SW). The cranial cnemial crests of procellariid tibiotarsi are so elongate they are easily broken, so tibiotarsi also were measured from the proximal articular surface to the distal end (Tib AL). Coracoid length (Cor L) was measured from the medial sternal angle because this is robust, and length could still be measured when the lateral process was broken, which it often was.

Summary statistics of measurements are given in Appendices 1–8. Because no individual associations of skeletal elements were preserved by the collectors (the collection was sorted by element), statistical comparisons are limited to univariate statistics. The significance of the difference in mean lengths of similar species was compared using two sample *t*-tests assuming unequal variances.

COMPARATIVE MATERIAL EXAMINED.—Unless otherwise stated, specimens are from the New Zealand area. Specimens listed in the appendices are not repeated below.

Eudyptes chrysocome filholi (Eastern Rockhopper Penguin): MNZ 624, 9147, 11221, 11236, 14087/1, 23674.

E. chrysolophus (Macaroni Penguin): MNZ 12840, 12841 (South Sandwich Id.).

E. pachyrhynchus (Fiordland Penguin): MNZ 17176, 19309, 22934, 23160.

E. robustus (Snares Penguin): MNZ 23735, 23736, 23737.

E. sclateri (Erect-crested Penguin): MNZ 668S, 24429, 24704.

Diomedea chlororhynchos (Yellow-nosed Albatross): MNZ 22417.

Pterodroma macroptera gouldi (Great-winged or Grey-faced Petrel): MNZ 541-S, 11426, 13597, 13598, 13605, 15903, 21101, 21103, 21419, 23714, 24073, 24076, 24248, 24369.

P. solandri (Providence Petrel): CSIRO Pros 389 (Lord Howe Id.); CSIRO Pros 724 (Lord Howe Id.), MNZ 23504.

P. neglecta (Kermadec Petrel): MNZ 23720.

P. incerta (Atlantic or Schlegel's Petrel): MNZ 22421, 22422, 22426 (all Gough Id.).

P. externa (Juan Fernandez Petrel): MNZ 24356.

P. rostrata (Tahiti Petrel): MNZ 23900.

P. arminjoniana (Herald Petrel): MNZ 22140 (Trindade Id.); MNZ 24691 (Henderson Id.).

P. baraui (Barau's Petrel): MNZ 23831 (Réunion Id.); Museum d'Histoire Naturelle de Paris, no. 772 (at sea off Réunion Id.); Museum d'Histoire Naturelle de Paris, no. 2601, female, Rivierre St. Etienne; Museum d'Histoire Naturelle de Paris, no. 2603, (Réunion Id.).

Pachyptila vittata (Broad-billed Prion): MNZ 559S, 751S, 753S, 754S, 755S, 919S, 11405, 11406, 12481, 12482, 12667, 12668, 13617, 15021, 15268, 15269.

P. salvini (Salvin's Prion): MNZ 590S, 591S, 12056, 12057, 12665, 13710, 15020, 15506, 15918, 24221.

P. turtur (Fairy Prion): MNZ 13628, 13629, 13630, 13631, 13632, 13634, 13635, 13713, 15270, 15271, 15272, 15920, 18317, 18362, 19808, 21461.

Procellaria cinerea (Grey Petrel): MNZ 602S, 607S, 791S, 792S, 918S, 12035, 12248, 12474, 12475, 12510, 16486, 17183, 18136, 21862, 24089, 24153, 24215, 24432, 24511, 24512, 24614, 24659, 24662, 24663, 24664.

P. parkinsoni (Black Petrel): MNZ 793-S, 17258, 18905–18907, 18968, 18969, 19282, 19283, 19298, 19781, 24236, 24247.

P. westlandica (Westland Petrel): MNZ 838-S, 11511, 13566, 13594, 15900, 19281, 19299, 19311, 21091–21094, 21099, 21106, 21422–21424, 21499, 22084, 22085, 22668, 22937, 22968.

P. aequinoctialis (White-chinned Petrel): MNZ 22077.

Puffinus assimilis assimilis (Little Shearwater): MNZ 519S, 520S (Norfolk Id.).

P. assimilis elegans (Little Shearwater): MNZ 21861, 21865, 22079, 22080–22083 (all from Antipodes Id.).

P. assimilis haurakiensis (Little Shearwater): MNZ 18321 (Waipu Beach); MNZ 20985 (Poor Knights Id.).

P. assimilis kermadecensis (Little Shearwater): MNZ 15911, 15912, 23895, 23972, 23986, 24229, 24230, 24279, 24381, 24382 (all Kermadec Id.).

P. assimilis subspecies indeterminate: MNZ 906S, 13569–13574, 15022, 15286, 15926, 18321, 19784, 22786 (all New Zealand beach-cast).

Pelagodroma marina (White-faced Storm-petrel): MNZ 803S–805S, 810S, 15027, 15028, 15507, 15612, 15613, 17262, 18360, 24237, 24591, 24680.

Oceanites nereis (Grey-backed Storm-petrel): MNZ 13609, 15031, 18911, 23740.

O. oceanicus (Wilson's Storm-petrel): MNZ 12824, 24783, 24784, 24823 (Heard Id.); MNZ 22153 (New Jersey, U.S.).

Pelecanoides urinatrix chathamensis: MNZ 807S, 18097, 18098, 18267, 18315, 18316, 18341 (Southeast Id., Chatham Ids.).

P. urinatrix exsul (Common Diving-petrel): MNZ 908S, 17623–17625, 18096 (Auckland Id.); MNZ 24785, 24786 (Heard Id.).

P urinatrix urinatrix: MNZ 546S, 547S, 13610, 13613, 13614, 16601, 17198, 17202 (Wellington-area beaches, New Zealand).

P. georgicus (South Georgian Diving-petrel): MNZ 24790, 24816–24822 (Heard Id.).

Catharacta skua lonnbergi (Subantarctic (Brown or Southern Great) Skua): MNZ 13568, 18332 (Auckland Id.); MNZ 18900 (Southeast Id., Chatham Ids.); MNZ 23702 (Campbell Id.); MNZ 24698, 24699 (Snares Id.).

C. maccormicki (South Polar or Antarctic Skua): MNZ 13320 (Franklin Id.); MNZ 22955, 22956 (Cape Evans); MNZ 22935, 22947, 23035, 23158 (Scott Base).

Systematics and Comparative Osteology

Table 1 lists the species determined in the Martinez collection, the number of bones identified as belonging to each species, and the minimum number of individuals (MNI) per species. The fossils described herein provide evidence for the previous fauna having at least 20 species of seabird and one duck. To this total can be added the records of a presumably vagrant rail, *Crex crex*, and a domestic fowl, *Gallus gallus* (Linnaeus), the latter found in a site used by sailors for shelter.

Eudyptes chrysocome

All penguin bones are referred to *Eudyptes*. They are the same size as bones of the Fiordland Penguin (*E. pachyrhynchus*), Snares Penguin (*E. robustus*), and Eastern Rockhopper Penguin (*E. chrysocome filholi*). Bones of the Macaroni Penguin (*E. chrysolophus*) and the Erect-crested Penguin (*E. sclateri*) are much larger. Because the Northern Rockhopper Penguin (*E. chrysocome moseleyi*) breeds on Amsterdam in large numbers (Jouventin, 1994), the bones are referred to that species.

Diomedea chlororhynchos

Most albatross bones were removed from the collection before THW examined them. A mandible from site 26, and eight bones of one individual from site 2.1, however, are all indistinguishable from the Yellow-nosed Albatross (*Diomedea chlororhynchos*) and are referred to that species. Large numbers of these albatrosses currently breed on Amsterdam (Jouventin et al., 1984).

Diomedea amsterdamensis

The Martinez collection contained numerous remains of *Diomedea amsterdamensis* that were removed prior to THW's examination of the collection. These were reported on by Jouventin et al. (1989), who recorded bones representing 81 individuals of *D. amsterdamensis* from several unspecified sites distributed between 80 m and 700 m a.s.l., including 52 individuals from a single site at 332 m, which is probably site 4. About 80 bones of a large species of albatross remained in the collection, however, and are referred to *D. amsterdamensis* because they do not match any other species. *Diomedea amsterdamensis* is restricted to breeding sites above 400 m (Jouventin et al., 1989).

TABLE 1.—List of species, number of bones, and minimum number of individuals (MNI) calculated as the sum of MNI in individual sites, as defined by the collectors, represented in the fossils from Amsterdam Island.

Species	Number of bones	MNI
Eudyptes chrysocome	281	21
Diomedea sp.	42	3
Diomedea amsterdamensis	80	9(81)*
Diomedea chlororhynchos	9	2
Procellaria cinerea	980	117
Pterodroma macroptera	3711	282
Pterodroma mollis	4766	375
Pterodroma baraui	263	31
Pterodroma baraui/arminjoniana	11	3
Pterodroma arminjoniana	6	4
Pterodroma sp. *?aterrima*	2	2
Pachyptila macgillivrayi	9235	731
Pachyptila cf. *turtur*	57	12
Pachyptila cf. *desolata*	1	1
Pachyptila sp. chicks	7	2
Pelecanoides urinatrix	106	29
Puffinus assimilis	1882	152
Puffinus carneipes	21	1
Puffinus cf. *griseus*	2	1
Pelagodroma marina	1780	206
Fregetta grallaria	72	25
Oceanites sp.	17	4
Hydrobatidae sp. indet.	5	2
Catharacta skua hamiltoni	179	19
Anas marecula	44	24(33)*
Gallus gallus	3	1
Total	23562	2059

*Jouventin et al. (1989) recorded 81 individuals of *D. amsterdamensis,* and Olson and Jouventin (1996) reported a minimum of 33 individuals of *Anas marecula,* and there is probably overlap between those samples and what we examined in the study.

Pterodroma

FIGURES 5–8

A preliminary examination of the *Pterodroma* bones in the collection revealed the predominance of two different species that differed mainly in size. In order to characterize these better, a large sample was measured, revealing that both species have apparently normal distributions for all bones (Figures 7, 8; Appendices 1, 2).

Species in the size range of the larger taxon include the Great-winged or Grey-faced Petrel (*Pterodroma macroptera*), Juan Fernandez Petrel (*P. externa*), Providence Petrel (*P. solandri*), Magenta Petrel (*P. magentae*), and White-necked

FIGURE 5.—Photographs of *Pterodroma mollis* skulls in dorsal (left) and lateral (right) views. A,D, modern specimen MNZ 22424, Gough Island; B,C, fossil specimen from site 18.7. Scale bar=5 cm.

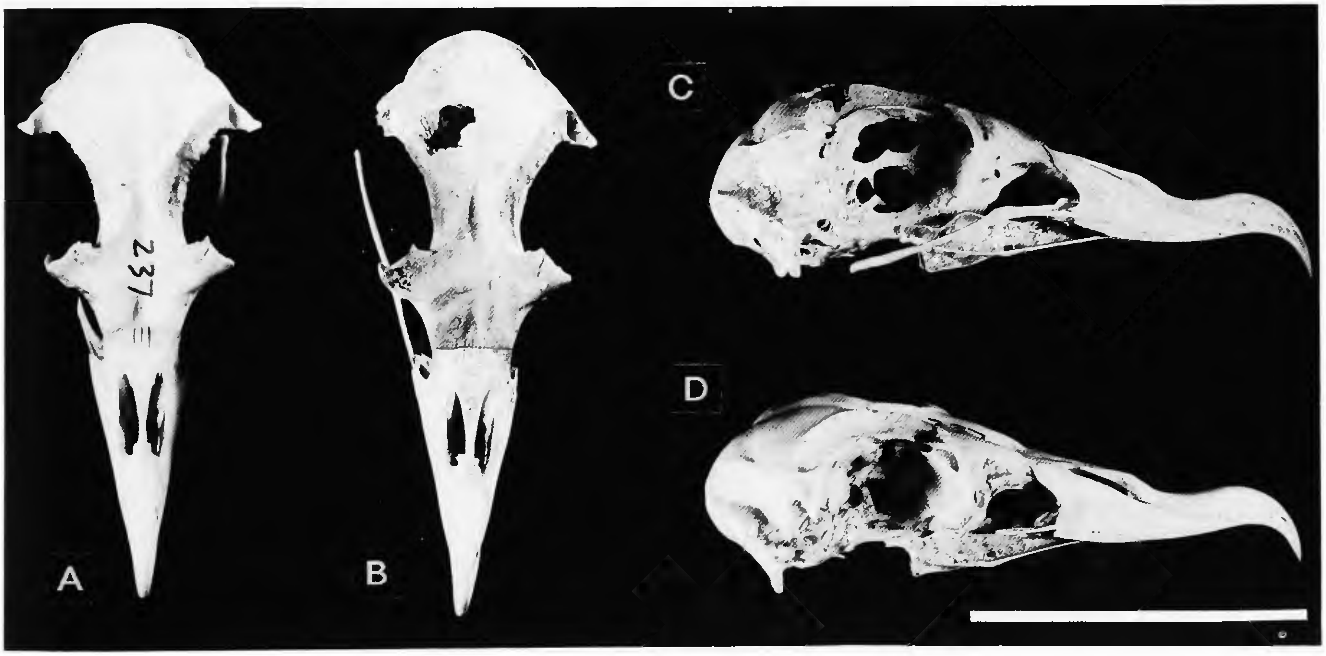

FIGURE 6.—Photographs of *Pterodroma macroptera* skulls in dorsal (left) and lateral (right) views. A,D, modern specimen CSIRO PROS237, Eclipse Island, Western Australia; B,C, specimen from fossil site 18.3. Scale bar=5 cm.

Petrel (*P. cervicalis*). The smaller taxon is about the size of a Soft-plumaged Petrel (*P. mollis*), Mottled Petrel (*P. inexpectata*), Black-winged Petrel (*P. nigripennis*), or Kerguelen Petrel (*P. brevirostris*). Bones of the Atlantic Petrel (*P. incerta*), White-headed Petrel (*P. lessoni*), and Tahiti Petrel (*P. rostrata*) are larger than those of any *Pterodroma* from Amsterdam, and the last has unusually slender wing bones and an extra-stout bill. The small species in the *Cookilaria* group, Chatham Petrel (*P. axillaris*), Cook's Petrel (*P. cookii*), and Pycroft's Petrel (*P. pycrofti*), are smaller than the small taxon and are biogeographically improbable. Similarly, Stejneger's Petrel (*P. longirostris*) and Gould's Petrel (*P. leucoptera*) are subtropical or tropical Pacific species and thus are unlikely candidates for the small Amsterdam species.

Pterodroma macroptera

All *Pterodroma* long bones within the larger size range indicated above are referred to *P. macroptera* for the following reasons. Among similar-sized species, *P. cervicalis* is a tropical Pacific species, so it was discounted, and *P. externa* from the eastern Pacific has a much stouter bill and a different cranial shape. *Pterodroma magentae* is smaller and breeds on the Chatham Islands, and limited evidence suggests that it ranges across the eastern Pacific. Its crania differ from those of *P. macroptera*, particularly in the form of the os lacrimale, as follows: the nasal process is deeper; the exterior surface of the ventral processes are subparallel rather than convergent on each other; the lacrimal foramen is markedly bigger; and the ventral border of the os ectethmoidale has a marked lump in it rather than being straight. The fossils from Amsterdam were the same size as those of *P. solandri* and those of the nominate race of *P. macroptera* from Eclipse Island, Western Australia, but are significantly smaller than those of *P. macroptera gouldi* from the New Zealand region. The fossils are the same shape as bones of *P. macroptera,* however, and they differ from those of *P. solandri* in that (1) the cranium is less inflated posterior to the orbit so that in dorsal view the crista temporalis is nearly straight (posterolaterally curved in *P. solandri*), (2) the extension of the crista temporalis on the processus postorbitalis is more laterally directed (more anteriorly directed in *P. solandri*), (3) the prominentia cerebellaris is compressed (rounded in *P. solandri*), (4) the os palatium in *P. macroptera* is flat ventrally (curved ventrally in *P. solandri*), (5) the foramen bound by the lacrimal, jugal, and premaxilla is relatively shorter in *P. macroptera* than in *P. solandri,* (6) the width between the temporal fossae is narrower in *P. macroptera,* (7) the lacrimals at the point of maximum width are more angled in *P. macroptera* (more rounded in *P. solandri*), and (8) the premaxilla has a steep, straight posterior end in *P. macroptera,* but the posterior end is shallower and notched in the relatively narrower premaxilla of *P. solandri. Pterodroma solandri* is a winter breeder on Lord Howe Island in the Tasman Sea and migrates to the North Pacific in the southern summer, making it further unlikely to be the Amsterdam petrel. *Pterodroma macroptera* is regularly seen offshore around Amsterdam (Roux and Martinez, 1987) and as already noted, it is the only large *Pterodroma* still nesting in the Amsterdam/St. Paul area.

Pterodroma mollis

Bones of the smaller species of *Pterodroma* are identical to those of *P. mollis,* which has a remnant population still surviving on Amsterdam Island (Roux and Martinez, 1987; Micol, 1995). Other similar-sized species of *Pterodroma* can be discounted: *P. brevirostris* has an unmistakably shorter, stouter bill; *P. nigripennis* is a tropical to subtropical Pacific species; and *P. inexpectata,* although ranging to the Antarctic, migrates to the North Pacific in the nonbreeding season. The size range of the Amsterdam population is shown by the upper and lower points of the apparently normally distributed length data (Figure 8). The smallest individuals from Amsterdam are considerably smaller than the few available recent specimens from Gough Island and New Zealand beaches, and they probably represent the lower end of the size variation in a population that is only slightly smaller than the nominate race of *P. mollis* from Gough Island. Birds from the Antipodes in the New Zealand region are most similar to the nominate race. Although the Indian Ocean birds have been referred to a distinct subspecies, *P. mollis dubia,* on the basis of color, there is much variation in coloration, which also alters with wear (see discussion in Marchant and Higgins, 1990).

Pterodroma arminjoniana

A few *Pterodroma* bones are intermediate in size between those referred herein to *P. mollis* or to *P. macroptera* and are similar in size to those of the Kermadec Petrel (*P. neglecta*), Phoenix Petrel (*P. alba*), Barau's Petrel (*P. baraui*), and Herald Petrel (*P. arminjoniana*). *Pterodroma alba* and *P. neglecta* are primarily subtropical to tropical Pacific species (Marchant and Higgins, 1990) and so are considered unlikely candidates; however, *P neglecta* has been found recently at Round Island, Mauritius (A. Tennyson, Museum of New Zealand, pers. comm., May 1996). Both *P. baraui* and *P. arminjoniana* breed in the Indian Ocean. A premaxilla in this size range from site 18, where wing bones of the intermediate-sized *Pterodroma* also were found, is 33.3 mm long, 15 mm wide, and 8.1 mm high at mid-nares, so it is much shorter and wider than either *P. neglecta* or *P baraui* but is very similar to *P. arminjoniana* (MNZ 22140) from Trindade Island in the South Atlantic. Thus, this premaxilla and the intermediate-sized *Pterodroma* wing bones from site 18 are referred to *P. arminjoniana.*

Pterodroma baraui

Intermediate-sized bones of *Pterodroma* included crania at sites 8.3 and 8.11, two premaxillae at site 8.4 and one at site 8.6, and a fragmentary premaxilla at site 8.8. These premaxillae are narrower and are not as deep as those of *P. macroptera* from Amsterdam Island. They are narrower and more elongate than those of *P. arminjoniana* but are similar to *P. baraui.* The two fossil crania also are identified as *P. baraui* because although they are of similar size to crania of *P. arminjoniana* as

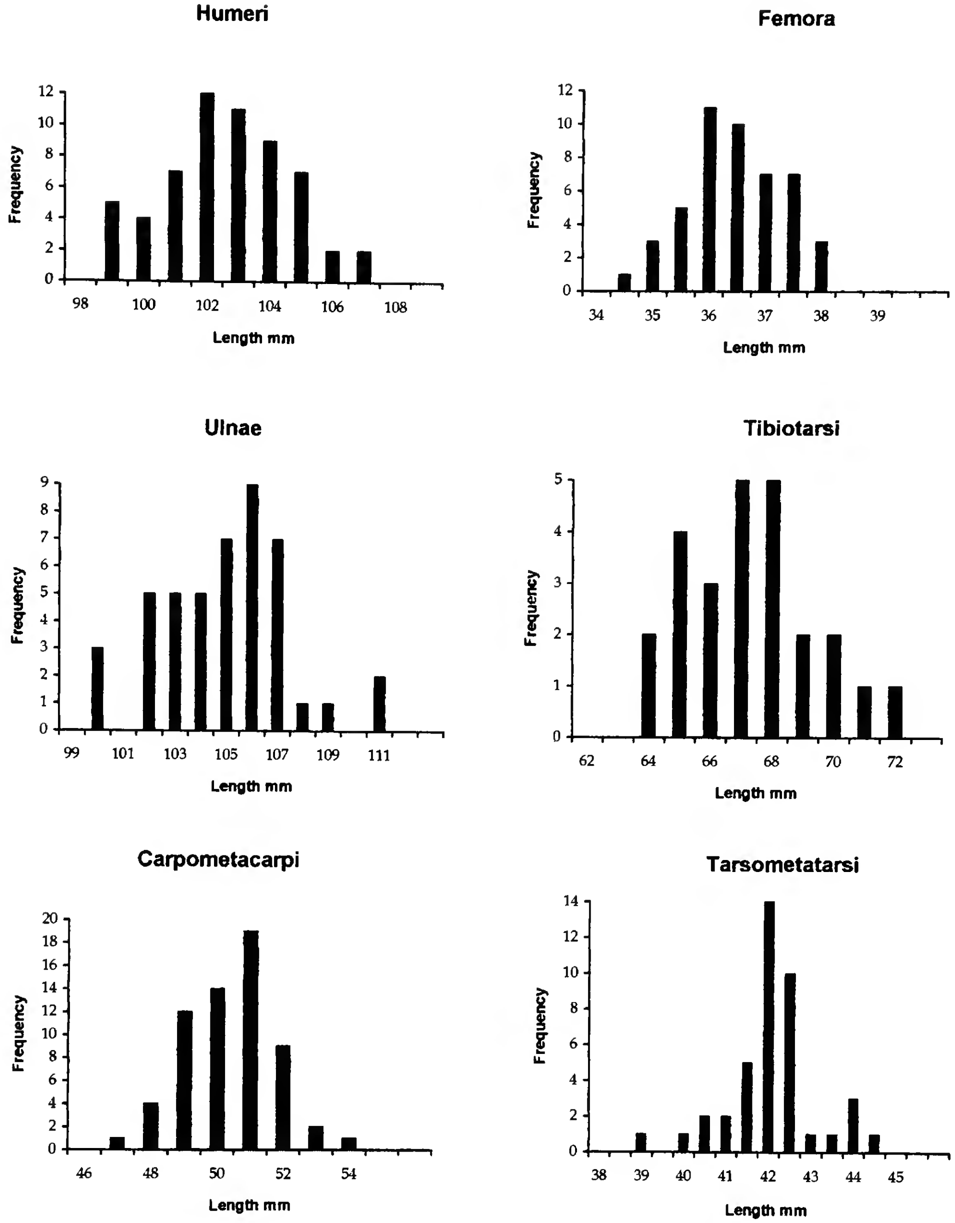

FIGURE 7.—Histograms of lengths of *Pterodroma macroptera* bones from Amsterdam Island.

measured across the lacrimals, crania of these two species differ as follows. The temporal fossae in *P. baraui* are anteroposteriorly much broader than those of *P. arminjoniana* (9.0–9.4 mm (n=3) vs. 6.8 mm), and the width across the zygomatic processes in *P. baraui* (Table 2) is greater (28.2–29.7 mm vs. 26.8 mm). In both *P. baraui* and *P. arminjoniana* the os lacrimale has a robust ventral portion with a facet that is longer than high, articulating with the quadratojugal. This facet is much

TABLE 2.—Measurements (mm) of modern specimens of *Pterodroma baraui.* Abbreviations are defined in the text.

Catalog number	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Lac W	PO W	ZP W	Pmx L	Pmx W
MNZ 23831	33.4	58.4	38.3	96.5	99.7	49.2	26.9	83.6	25.8	32.9	29.7	43	17.4
Paris, number 2603	34.93	63.3	39.8	98.51	102.96	50.27	28.08	–	–	–	–	–	–
Paris, number 2601	33	59.17	37.34	97.4	98.75	48.08	26.86	82	25.7	31.24	28.5	41.2	17.3
Paris, number 772	32.88	59.44	36.82	92.04	96.18	47.72	27.7	80.2	24.6	31.08	28.26	40.5	16.94

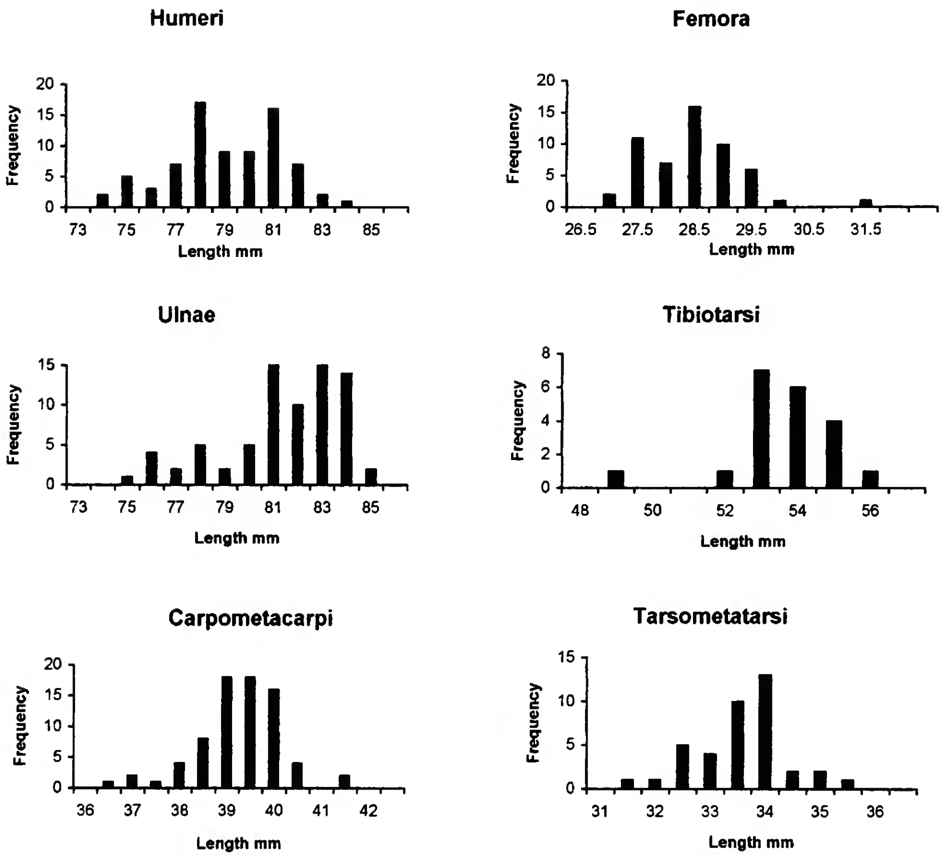

FIGURE 8.—Histograms of lengths of *Pterodroma mollis* bones from Amsterdam Island.

more robust than in the similar-sized *P. neglecta. Pterodroma baraui* differs from *P. arminjoniana* in that the ventral process of the os lacrimale, where it descends from the os ectethmoidale, is much shorter, with a different shape of the articular facet. The lower fonticulus orbitocranale is more elongate in *P baraui* (*n*=3, 5.8 mm high × 9.1 mm long, 6.0 × 8.6 mm, 6.0 × 8.8 mm, vs. 6.5 × 7.7 mm in *P. arminjoniana*). The fossil cranium from site 8.11 has a basicranial length of 37 mm but is too broken to measure further; however, the extensive temporal fossae, lacrimal shape, and shape of the fonticulus orbitocraniale clearly identify it as *P baraui.* The posterior portion of the cranium from site 8.3 (width at zygomatic processes 25.5 mm) has wide temporal fossae like *P. baraui* and is referred to that species. The postcranial bones in *P. baraui* and *P. arminjoniana* are very similar, and subtle differences, if present, between them would not be of use in identifying fossil material that is worn, weathered, or broken. Because all cranial material from site 8 is referred to *P. baraui,* all the postcranial bones of mid-sized *Pterodroma* from this site also are referred to that species (Table 3). This is further supported by the tarsometatarsi from site 8, which are similar to those of *P. baraui* (Table 4) and are shorter and stouter than those of *P. macroptera.*

TABLE 3.—Summary statistics for bones attributed to fossil *Pterodroma baraui* and measurements (mm) of intermediate-sized fossil *Pterodroma* species, Amsterdam Island.

Species	Fem L	Tmt L	Hum L	Ulna L	Cmc L	Cor L
P. baraui						
mean	32.87	38.14	91.82	97.42	47.62	26.07
standard deviation	0.05	0.06	1.82	1.99	1.36	0.42
minimum	32.83	38.1	90.4	95	46	25.6
maximum	32.9	38.18	94.32	102.5	50.1	26.43
sample size	2	2	4	13	9	3
P. arminjoniana/ baraui						
site 18.1	–	–	–	96.8	–	–
site 18.27	–	–	95.4	–	–	–
site 18.26	–	–	95.8	–	–	–
P. arminjoniana						
site 18.2	–	–	–	97.3	–	–
site 18.8	–	–	89.7	–	–	–
site 18.11	–	–	91.5	–	–	–

Pterodroma sp.

Two premaxillae (MNZ S34852, MNZ S34859) are very short and stout and are not referable to any of the above species. Bourne (1968) gave measurements for a premaxilla of the

TABLE 4.—Measurements (mm) of fossil tarsometatarsi of *Pterodroma baraui* compared with modern specimens.

Catalog number	Length	Proximal width	Shaft width	Distal width
Fossil				
site 8.8	38.2	6.3	2.8	6.1
site 8.5	38.1	–	3.2	6.6
Modern				
MNZ 23831	38.2	6.8	2.8	6.7
Paris, number 772	36.8	6.3	2.8	5.8
Paris, number 2601	37.3	6.9	3.2	6.3
Paris, number 2603	39.8	6.4	2.8	6.2

Mascarene Petrel (*Pterodroma aterrima*) that compare well with those of the more complete specimen (MNZ S34852, measurements given second): length from nostrils 20 mm vs. ~22 mm; length of nostril 10 mm vs. 12 mm; length to angle gape 34 mm vs. 35 mm; depth at proximal end of nostril 11 mm vs. 10 mm. The width of MNZ S34852 at the angle gape is 16.5 mm.

Pachyptila macgillivrayi

FIGURES 9, 10

One species of prion that now breeds on Amsterdam Island is currently referred to *Pachyptila salvini macgillivrayi* (Roux et al., 1986; Jouventin, 1994; Micol and Jouventin, 1995), although previously it was referred to as a subspecies of the Broad-billed Prion (*P. vittata*) (e.g., Jouanin, 1953; Paulian, 1960; Roux and Martinez, 1987), presumably because of its similarly broad bill. It was allied with Salvin's Prion (*P. salvini*) on account of its similar size, its breeding cycle (which is more aligned with that of *P. salvini*), and its blue bill, as opposed to the "steel-grey bills" of *P. vittata* (Roux and Martinez, 1987).

Prion bones are very numerous in most sites. Their measurements exhibit an apparently normal, unimodal size distribution (Figure 10, Appendix 3), so we refer the bones in this size range to a single taxon with which we associate the numerous cranial remains characterized by very broad bills that are found in the same sites. The bones of this Amsterdam prion cannot be referred to either *P. vittata* or *P. salvini* for the following rea-

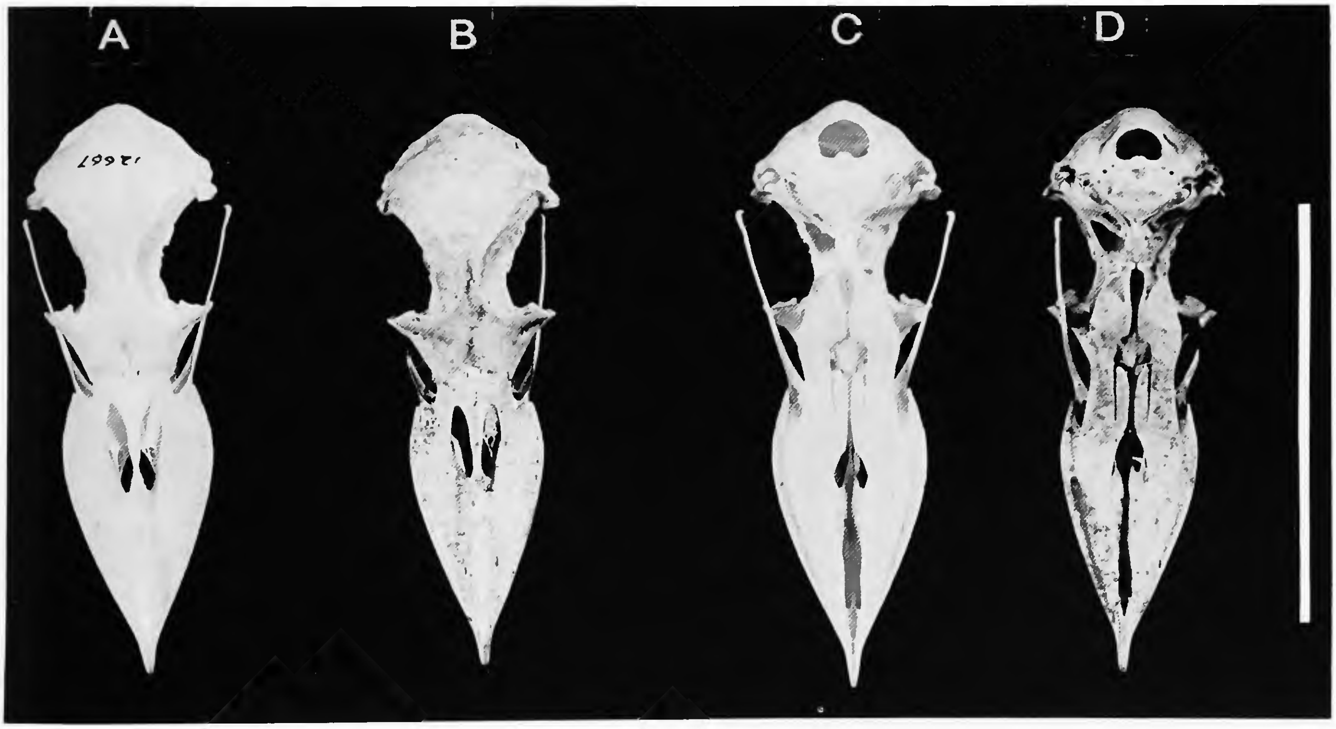

FIGURE 9.—Photographs of *Pachyptila* skulls in dorsal (left) and ventral (right) views. A,C, modern *P. vittata*, MNZ 12667, New Zealand; B,D, fossil *P. macgillivrayi* from site 18.7. Scale bar=5 cm.

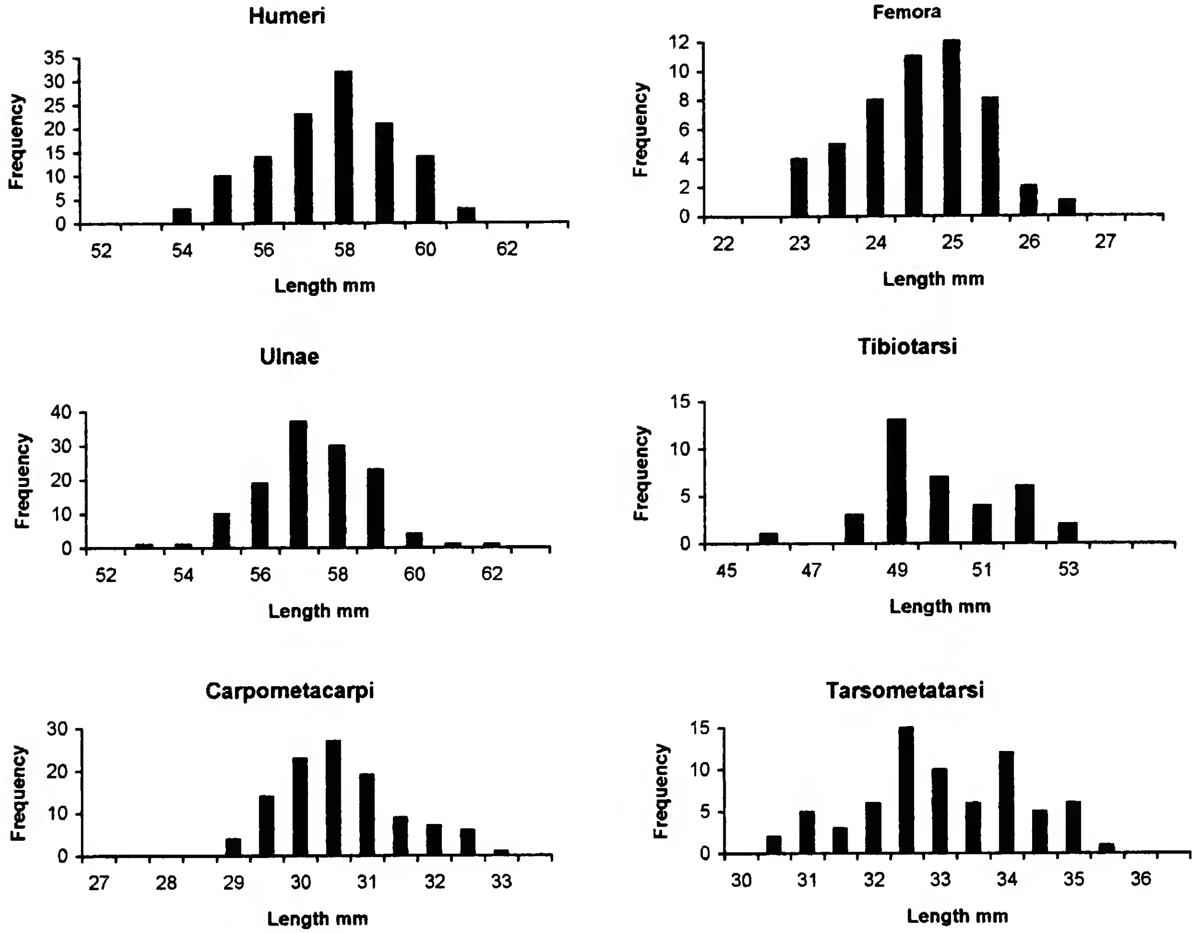

FIGURE 10.—Histograms of lengths of *Pachyptila macgillivrayi* bones from Amsterdam Island.

sons. Adult cranial and long bones of the Amsterdam prion were compared with those of the Broad-billed Prion (*Pachyptila vittata*) and Salvin's Prion (*P. salvini*) from the New Zealand region (Table 5; Appendix 3). The Amsterdam species is significantly smaller than *P. vittata* (*t* test, $P<0.001$) in all measurements. With the exception of lacrimal width, which is narrower ($P<0.001$), there is no significant difference in size between the Amsterdam prion and *P. salvini,* based on the postcranial and cranial measurements; however, although the length of premaxillae of *P. salvini* and the Amsterdam prion are not significantly different, those of Salvin's Prion are narrower ($P<0.001$), and the premaxillae width/length ratio is significantly different ($P<0.001$). In contrast, although premaxillae of *P. vittata* are longer and wider ($P<0.001$), the width/length ratio is not significantly different from that of the Amsterdam prion. Therefore, whereas the Amsterdam prion is of a size similar to the Salvin's Prion, it has a significantly narrower lacrimal width, and its bill is absolutely and relatively much wider than that of *P. salvini.* The Amsterdam prion's bill is relatively as wide as that of *P. vittata.* Because of these differences we think that the Amsterdam prion should be removed from *P. salvini* and reinstated as a distinct species, Macgillivray's Prion (*P. macgillivrayi*).

Pachyptila desolata

A single premaxilla identical to that of the Antarctic Prion (*P. desolata*) is present, but unfortunately it has no site data with it. *Pachyptila desolata* has not previously been recorded from Amsterdam Island or St. Paul Island, but it breeds on Crozet, Heard, and Kerguelen islands (Jouventin et al., 1984; Marchant and Higgins, 1990).

Pachyptila turtur

A few postcranial elements below the size range of *P. macgillivrayi* are present in some sites. These are referred to the Fairy Prion (*P. turtur*), which breeds on Roche Quille (<10 pairs) (Roux and Martinez, 1987; Micol, 1995).

TABLE 5.—A comparison of the significance of the difference between means of various measurements for the Amsterdam Island prion and for *Pachyptila vittata* and *P. salvini* by *t*-tests (Microsoft Excel, ver. 5), assuming unequal variances. Shown are *t*-statistic, degrees of freedom, and significance level (P>0.05=NS, P<0.001=***).

Measurement	Amsterdam prion vs. *P. vittata*	Amsterdam prion vs. *P. salvini*
Femur length	-11.381, 29, ***	-1.36, 11, NS
Tibiotarsus length	-7.956, 38, ***	-0.97, 11, NS
Tarsometatarsus length	-8.678, 30, ***	-0.38, 11, NS
Coracoid length	-8.163, 21, ***	-1.21, 11, NS
Humerus length	-14.727, 24, ***	-1.56, 10, NS
Ulna length	-15.331, 21, ***	0.22, 9, NS
Carpometacarpus length	-12.015, 21, ***	-0.49, 10, NS
Premaxilla length	-10.446, 27, ***	0.527, 9, NS
Premaxilla width	-6.060, 17, ***	4.987, 8, ***
Premaxilla width/length	-1.210, 20, NS	8.773, 18, ***

Procellaria cinerea

FIGURES 11, 12

Grey Petrels (*Procellaria cinerea*) are regularly seen offshore around Amsterdam and breed in small numbers on the main island (Roux and Martinez, 1987; Jouventin, 1994; Micol, 1995). White-chinned Petrels (*P. aequinoctialis*) are regular visitors offshore but are not known to breed on Amsterdam (Roux and Martinez, 1987).

The *Procellaria* crania indicate a single species that is identical in form to *P. cinerea* from New Zealand but is generally smaller (Figure 12; Appendix 4), except for a female (MNZ 24432) that is very similar in size. No specimens of *P. cinerea* from the Indian Ocean were available for comparison.

Bones of *P. cinerea* from the New Zealand region are similar in size to those of the Black Petrel (*P parkinsoni*) and are smaller than those of *P. aequinoctialis* or the Westland Petrel (*P. westlandica*) (Worthy and Holdaway, 1993). Because the Amsterdam *Procellaria* is even smaller than *P. cinerea* from New Zealand it is not referable to *P. westlandica* or *P. aequinoctialis.* Humeri of *P. parkinsoni* are much more gracile than those of *P. cinerea.* Skulls of *P. cinerea* differ from those of *P. parkinsoni* as follows: the premaxilla is about 5–6 mm longer in the region anterior to the nares in *P. cinerea,* although both have the same depth and width at the anterior end of the nares; the gap between the temporal fossae is narrower in *P. cinerea* than in *P. parkinsoni;* and the dorsal margins of the fossae are subparallel, in contrast to widely diverging in *P. parkinsoni;* on the posterior margin of the temporal fossae above the tympanic cavity there is a fossa that is small in *P. cinerea* (1–2 mm) but relatively large in *P. parkinsoni* (2–4 mm); the lateral process of the os ectethmoidale that abuts the os lacrimale is much more squared in *P. cinerea,* in contrast to rounded in *P. parkinsoni;* and the orbitocranial fonticulus is longer and narrower (dorsoventrally) in *P. cinerea* than in *P. parkinsoni.* The fossil crania of *Procellaria* are like *P. cinerea* in all these respects.

Puffinus assimilis

FIGURE 13

The majority of the bones attributable to *Puffinus* are readily identifiable as Little Shearwaters (*P. assimilis*) because of their small size (Appendix 5). This species breeds in small numbers on Roche Quille (Tollu, 1984; Roux and Martinez, 1987; Micol, 1995).

Puffinus carneipes

Twenty-one subadult bones of an individual much larger than *Puffinus assimilis* were in sites 15.4 and 15.5. The size of the bones, the shape of the skull and premaxilla, and the unusual features (for *Puffinus*) of having a humerus with a rounded shaft with a deep fossa M. brachialis and a femur with little dorsoventral curvature, allowed ready identification of these bones as those of a Flesh-footed Shearwater (*Puffinus carneipes*). This species breeds on St. Paul (Micol, 1995).

Puffinus griseus

A sacrum from site 18.11 and an imperfect right femur from site 18.7 were identified by their size and shape as a Sooty Shearwater (*Puffinus griseus*), matching the comparative series well. This species has been seen regularly around Amsterdam (Roux and Martinez, 1987).

Pelagodroma marina

At least three species of storm-petrels are represented. The bulk of the leg bones are readily identifiable as those of White-faced Storm-petrels (*Pelagodroma marina*).

Fregetta grallaria

Several very stout tarsometatarsi are immediately referable to *Fregetta.* White-bellied Storm-petrels (*F. grallaria*) have been seen, rarely, off Amsterdam, and they breed in low numbers on Roche Quille and St. Paul (Micol, 1995). Although Black-bellied Storm-petrels (*F. tropica*) do not breed in the area, they have been seen at sea nearby (Roux and Martinez, 1987).

Compared to *Pelagodroma marina,* tarsometatarsi of *Fregetta* spp. are relatively wide for their length, are absolutely shorter, with the distal ends twisted medially (vs. not twisted), and have a convex posterior distal surface (vs. bounded by ridges and concave). Tarsometatarsi of *F. tropica* are relatively narrower than in *F. grallaria* (Appendix 6). The Amsterdam bones are most similar to *F. grallaria,* and so we refer them to that species. Because other skeletal elements of *P. marina* and *F. grallaria* are of similar size, the following distinguishing characters are listed. Femora of *F. grallaria* are longer, are not as dorsoventrally curved, and have a deeper fossa poplitea than in *P. marina. Fregetta grallaria* and *F. tropica* have ulnae with a prominent ridge descending from under the facies articularis

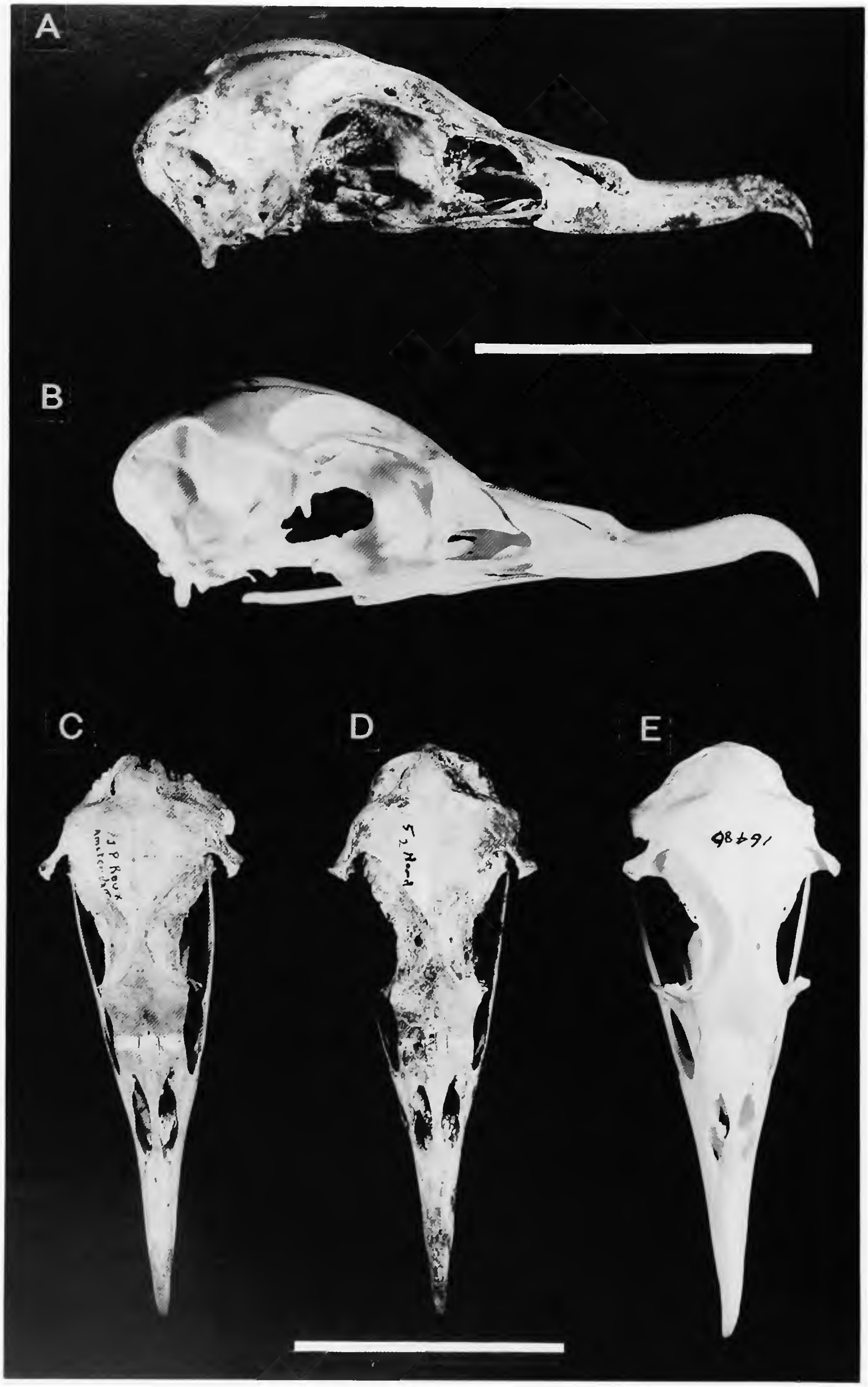

FIGURE 11.—Photographs of *Procellaria cinerea* skulls in lateral (top) and dorsal (lower) views. A,D, fossil specimen from site 5.2; C, fossil specimen from unrecorded site; B,E, modern specimen MNZ 16486, New Zealand region. Scale bar=5 cm.

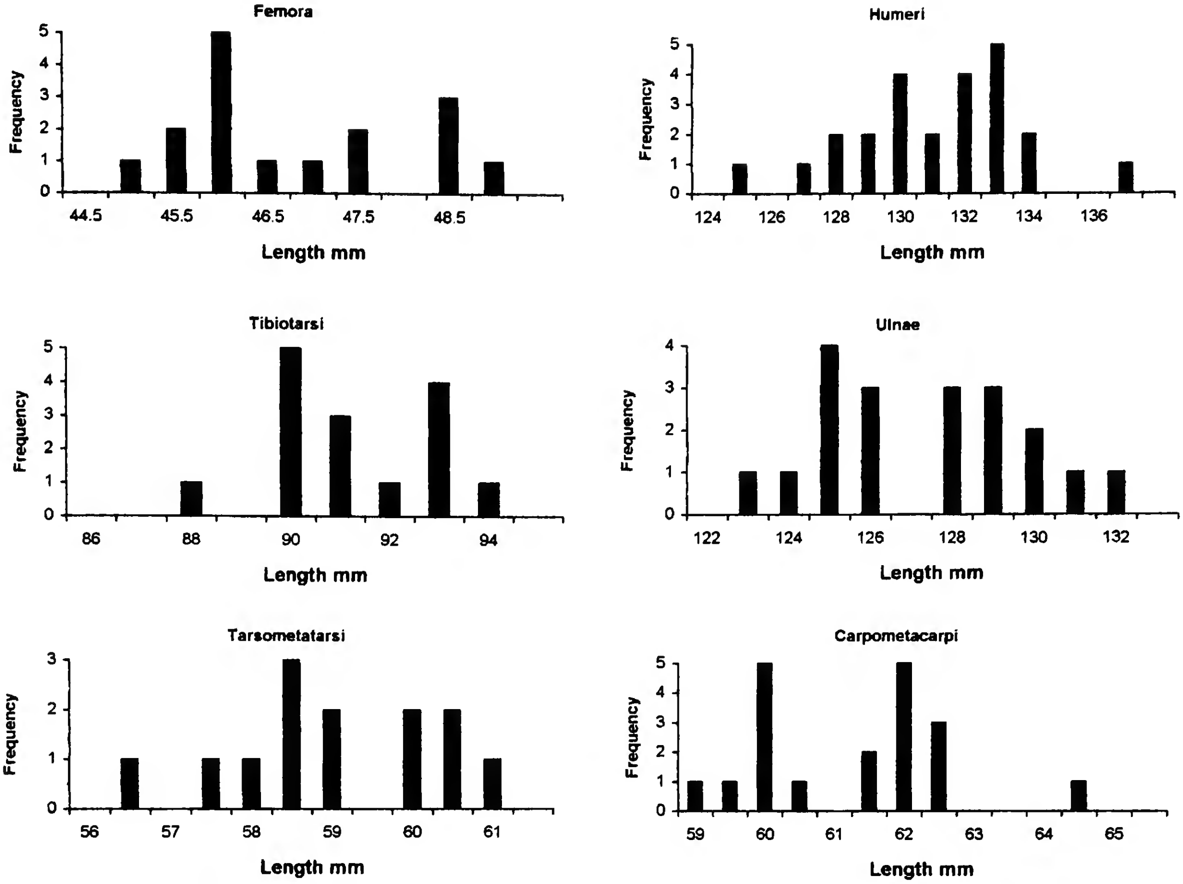

FIGURE 12.—Histograms of lengths of *Procellaria cinerea* bones from Amsterdam Island.

FIGURE 13.—Photographs of *Puffinus assimilis* skulls in dorsal (left) and lateral (right) views. A,D, modern specimen of *P. a. elegans*, MNZ 21865, Antipodes Island; B,C, fossil specimen from site 18.2. Scale bar=5 cm.

radiocarpalis (not so in *Pelagodroma*). Humeri of *F. grallaria* are longer, and the tuberculum dorsale is broader, not as raised above the margo caudalis, and not as elongate distally as those of *P. marina.* In *F. grallaria* the tuberculum ventrale is as high as wide rather than higher than wide as in *P. marina.* On the cranial surface, the sulcus at the base of the crista deltopectoralis is shallower than in *P. marina.* The sulcus ligamentis transversus ends ventrally beside a shallow sulcus on the ventral margin of the crista bicipitalis in *F. grallaria,* but not in *P. marina,* where there is no shallow sulcus.

Oceanites sp.

A few bones of a very small storm-petrel are smaller than those found in any genus except *Oceanites.* Comparisons were made with Grey-backed Storm-petrels (*Oceanites nereis*) and Wilson's Storm-petrels (*O. oceanicus*). The few measurements available suggest *O. nereis* is smaller, but although lengths of the tarsometatarsi overlap (*O. nereis,* mean=33.47 mm, range=31.1–34.6 mm, *n*=4; *O. oceanicus,* mean=35.21 mm, range=33.0–37.2 mm, *n*=5), those of the ulnae do not (*O. nereis,* mean=17.67 mm, range=16.7–18.4 mm, *n*=4; *O. oceanicus,* mean=19.73 mm, range=19.1–20.4 mm, *n*=5). Ulnae of two of the fossil specimens are 18.1 mm and 18.7 mm long, suggesting that they may belong to the smaller taxon. *Oceanites oceanicus* is regularly seen offshore, and a specimen of *O. o. parvus* was collected ashore on Amsterdam (Roux and Martinez, 1987). In 1995 a small colony of *O. oceanicus* was found breeding on St. Paul (Micol, 1995). Because the specimens of *O. oceanicus* measured were mainly from Heard Island, they may be bigger than birds breeding on more northern islands (see discussion in Marchant and Higgins, 1990), so it is possible that *O. oceanicus* from the Amsterdam group could be similar in size to *O. nereis.* The fossils are referred only to *Oceanites* sp.

Pelecanoides urinatrix

Bones of a diving-petrel are present in many sites. At present, two diving-petrels are found in the Indian Ocean. The smaller South Georgian Diving-petrel (*Pelecanoides georgicus*) breeds on subantarctic islands, and the larger Common Diving-petrel (*P. urinatrix*) has a more widespread distribution, between 35°S and 55°S (Marchant and Higgins, 1990). Both exhibit size variation that is to some extent clinal, with southern populations being larger (Marchant and Higgins, 1990), but this is not the case in New Zealand (Appendix 7).

The fossils, particularly the ulnae and carpometacarpi, are larger than bones of *P georgicus* from Heard Island, smaller than bones of *P. urinatrix exsul* from both Auckland and Heard islands, and smaller than bones of *P. u. urinatrix* from beaches around Cook Strait in New Zealand (Appendix 7). They are, however, similar in size to *P. u. chathamensis* from Southeast Island in the Chatham Group, and so they are referred to *P. urinatrix.* There are two records of *P. urinatrix* from Amsterdam (Roux and Martinez, 1987; Micol and Jouventin, 1995).

Catharacta skua

Skua bones were recovered from several sites, but most were in poor condition. They are much smaller than those of the Subantarctic (Brown or Southern Great) Skua (*Catharacta skua lonnbergi*) from the New Zealand subantarctic islands and are bigger than than those of the Antarctic Skua (*C. maccormicki*) (Appendix 8). The carpometacarpus is longer than the tarsometatarsus in *C. maccormicki,* in contrast to *C. skua lonnbergi,* in which the opposite is true. Unfortunately, none of the fossils were complete enough to use this feature. The Tristan Skua (*C. skua hamiltoni*), however, for which no comparative material was available, is smaller than *C. skua lonnbergi* and breeds on Gough Island and in small numbers on Amsterdam (Micol, 1995). Because the fossils are markedly smaller than bones of *C. skua lonnbergi* but are bigger than bones of *C. maccormicki,* it seems probable that the Amsterdam skua fossils are referable to *C. skua hamiltoni.*

Anas marecula

The bones of a small duck found in the collection were obviously missed when duck material was extracted for the study that resulted in the description of a new species, *Anas marecula,* by Olson and Jouvenin (1996) (see Table 1). The series they analyzed, now in the USNM, was composed of at least 33 individuals. Those listed herein are almost certainly parts of the same individuals.

Discussion

COMPOSITION OF THE FOSSIL FAUNA

We consider some records based on fossils from Amsterdam Island to be of questionable validity; these are as follows:

1. Wandering Albatross (*Diomedea exulans*). The record of this species is of bones of a single individual identified by Jouanin and Paulian (1960) before *D. amsterdamensis* was described, and which Jouventin et al. (1989) reported to be of similar size to the bones they referred to *D. amsterdamensis.*
2. Kermadec Petrel (*Pterodroma neglecta*). Jouanin and Paulian (1960) identified this species from a few bones that were smaller than those herein described of *Pterodroma macroptera* and bigger than those of *P. mollis.* The given lengths for the bones are in the size range of *P. baraui* and *P. arminjoniana. Pterodroma baraui* was only described in 1964, and neither of these two species was compared to the fossils. Pending reexamination of the bones, the record of *P. neglecta* from Amsterdam is suspect.
3. Broad-billed Prion (*Pachyptila vittata*). Jouanin and Paulian (1960) identified the prion bones they had as this species and thought it probable that they were of the subspecies *P.*

vittata macgillivrayi. Data herein show that *P. vittata* is distinct from *P. macgillivrayi,* and both are distinct from *P. salvini,* so the Amsterdam prion should not be listed as *Pachyptila vittata.*

The 20 species of seabird recorded herein as fossils from Amsterdam Island underestimate the total because the Sooty Albatross (*Phoebetria fusca*) and the Antarctic Tern (*Sterna vittata*) presently breed on Amsterdam (Jouventin et al.,1984) but are not represented among the fossils. Micol and Jouventin (1995) noted that at least one *Phoebetria fusca* had been identified in fossil material, but no material was seen by THW to substantiate this.

Jouventin (1994) and Micol and Jouventin (1995) reported the supposed presence of two extinct species of *Pterodroma* and two extinct storm-petrels. This study finds no evidence for any extinct procellarid having previously existed on Amsterdam Island. *Procellaria cinerea, Pterodroma macroptera,* and *P. mollis* are common as fossils and undoubtedly bred there. The large number of *P. baraui* bones from site 8 suggests this species also was breeding on Amsterdam; in contrast, the few bones of *P. arminjoniana* could be from nonbreeding visitors, or possibly from skua kills.

SIZE RANGES OF SPECIES

Pterodroma macroptera: Several species of seabirds represented in the fossil fauna of Amsterdam Island are smaller than conspecific populations in the New Zealand region. Data in Appendix 1 show that *P. macroptera* from Amsterdam are smaller than Australasian and South Atlantic specimens. The specimens available from Eclipse Island in Western Australia are of similar size to the Amsterdam specimens, but the one specimen from Coffin Island is larger than any Amsterdam specimen and is within the size range for *P. macroptera gouldi.* Measurements given in Marchant and Higgins (1990) show that *P. m. macroptera* is a little smaller than *P. m. gouldi.* They also show that males are slightly larger than females in most measurements, but there is no detectable dimorphism in the fossil sample, which has apparently normal, unimodal, size distributions.

Pterodroma mollis: The limited evidence suggests that *P. mollis* from Amsterdam is smaller than Australasian and Atlantic birds. Measurements in Marchant and Higgins (1990), however, indicate no geographical or sexual size variation. The fossil samples have mainly unimodal size distributions (Figure 8) except for humeri, where the distribution is bimodal, suggesting that there may be some sexual dimorphism.

Procellaria cinerea: The Amsterdam *Procellaria cinerea* have bone lengths 4%–6% smaller than birds from the New Zealand region. Measurements of birds from the Crozet and Kerguelen islands and from New Zealand (Marchant and Higgins, 1990) also indicate that Indian Ocean birds are smaller than New Zealand ones. Some sexual dimorphism is apparent in external measurements in Marchant and Higgins (1990), although their two data sets are contradictory: in one the males are larger and in the other the females are larger. Measurements of sexed skeletons in our comparative series (3 males, 7 females) suggest that females are smaller, although the small sample size precludes meaningful statistical comparison. The fossil bones have a length distribution (Figure 12) that trends in most cases toward bimodality, compared to the unimodal (apparently normal) distributions of *Pterodroma macroptera* and *Pachyptila macgillivrayi* (Figures 7, 10). If the modern sample is representative, then the larger bones probably represent males.

Pachyptila macgillivrayi: The differences detailed above show that the Amsterdam prion is a distinct species, *P. macgillivrayi,* that is endemic to the Amsterdam–St. Paul group. The very large samples of long bones are apparently normally distributed and unimodal, suggesting there is no sexual size dimorphism. Sexual dimorphism in prions is generally slight, although Genevois and Bretagnolle (1995) found male Thin-billed Prions (*P. belcheri*) to be larger overall and to have larger bills than do females.

Puffinus assimilis: There are several subspecies of *P. assimilis* in the southern oceans region. The nominate race from Norfolk Island (*P. assimilis assimilis*) is the smallest (Appendix 5). The two New Zealand subspecies, *P. a. haurakiensis* and *P. a. kermadecensis*, are of similar size and are larger than *P. a. assimilis* but are smaller than *P. a. elegans,* from farther south in the Antipodes (Appendix 5). None of the beach-cast specimens from New Zealand west-coast beaches are large enough to be *P. a. elegans,* and they are considered to be *P. a. kermadecensis* (J.A. Bartle, pers. comm., 18 June 1995; verified in many cases by the species of lice present). Size variation therefore appears to be clinal, with larger birds in the south.

Puffinus assimilis bones from Amsterdam are on average slightly smaller than those of *P. a. elegans* from the Antipodes but are much larger than those of the other subspecies considered above, and so they are probably referable to *P. assimilis elegans.* This subspecies ranges from the Antipodes and Chatham islands in the New Zealand region to Tristan da Cunha and Gough Island (Marchant and Higgins, 1990).

Pelecanoides urinatrix: As discussed above, there is considerable variation in mean size of individuals between populations in this species. Although some of the variation may be clinal, with more southern populations comprising larger individuals, this is not the case in New Zealand, where populations in Cook Strait and farther north are distinctly larger than those around Stewart Island and on the Chatham Islands. The limited data presented herein suggest that the Amsterdam birds are smaller than those from Heard Island, significantly smaller than those from the lower latitude populations in the Cook Strait–Wellington region of New Zealand, and similar to those from slightly higher latitudes on Southeast Island, in the Chatham Group. Size variation in *Pelecanoides* is thus not well explained by clinal factors.

COMPARISONS WITH OTHER ISLANDS

The 20 species of seabirds recorded as fossils from Amsterdam Island do not include *Phoebetria fusca* or *Sterna vittata,* which currently breed there, suggesting that up to 22 species had breeding populations. Species that are very rare in the fossil record, however, such as *Pachyptila desolata, Puffinus carneipes,* and *P. griseus* (each with one individual), are likely to have been nonbreeding vagrants or the result of skua kills, so a more realistic estimate is that no more than 19 species of seabirds bred on Amsterdam Island in the recent past.

Amsterdam Island is similar to the Crozet and Kerguelen islands in that most breeding species are seabirds; however, with at least 34 and 30 breeding species of seabirds, respectively, these subantarctic island groups have far richer communities than Amsterdam did (Jouventin et al., 1984). Although the fossil faunas of these islands have not been studied, it is likely that neither island group has suffered species extinctions as happened on Amsterdam because some islands in each group have remained free of predators (Jouventin et al., 1984).

The Mascarene islands Mauritius and Rodriguez are well known for their extinct, endemic land birds (Newton, 1888; Hachisuka, 1953; Gill, 1967), but the fossil seabirds have largely been ignored (Bourne, 1968). These islands are much farther north than Amsterdam, and various terns and boobies dominate the fauna, with a few species of petrel present. Bourne (1968) reported Wedge-tailed Shearwaters (*Puffinus pacificus*), a larger shearwater (possibly *P. carneipes*), and the Mascarene Petrel (*Pterodroma aterrima*) in addition to numerous remains of the White-tailed Tropic Bird (*Phaethon lepturus*) in a small collection of fossils from Rodriguez. The discovery of bones of Barau's Petrel (*Pterodroma baraui*) on Amsterdam extends the range of this species, previously known only from Réunion, and provides a faunal link with the Mascarene Islands. *Pterodroma aterrima,* also known only from Réunion Island, probably bred on Rodriguez (Bourne, 1968), and it may also have reached Amsterdam occasionally.

Studies of the fossil avifauna of St. Helena Island in the Atlantic Ocean (16°S) have revealed remains of 21 species, among which the greatest loss of species and individuals was five of the six resident petrels, three of which were endemic (Olson, 1975). Farther north in the Atlantic, the fossil avifauna of the eastern Canary Islands, which lie off the African coast between about 28°N and 29°N, is dominated by remains of two extinct species of *Puffinus* (Alcover and McMinn, 1995).

In the tropical Pacific Ocean the fossil faunas of numerous islands have been studied, and all are rich in terrestrial species: seabirds are dominated by procellariids, but toward the equator, the species diversity of terns, boobies, tropicbirds, and frigatebirds often equals or exceeds that of procellariids (Olson and James, 1991; Steadman, 1995). On every island studied, several species of land birds and populations of seabirds were exterminated following the arrival of humans in the last few thousand years (Steadman, 1989, 1995; Olson and James, 1991). Often losses, particularly of land birds, have exceeded 50% of the original species diversity, and, among seabirds, some of the greatest losses have been petrels and shearwaters, especially in eastern Polynesia (Steadman, 1989).

In the South Pacific the fossil faunas of the North and South islands of New Zealand have been studied extensively: Millener (1990) listed 34 species that became extinct in the late Holocene following the arrival of humans, to which Scarlett's Shearwater (*Puffinus spelaeus*), South Island Adzebill (*Aptornis defossor*), Bush Wren (*Xenicus longipes*), and Long-billed Wren (*Dendroscansor decurvirostris*) should be added, for a total of 38 species. In the New Zealand region, seabirds have not suffered the same degree of loss as elsewhere because, although numerous populations of seabirds have been extirpated from the main islands, colonies on offshore islands have ensured their species survival, with the exception of *Puffinus spelaeus* (Holdaway and Worthy, 1994). The fossil faunas of the New Zealand subantarctic islands have not been studied.

Conclusions

Like most islands where numerous extinctions followed the arrival of humans and commensal mammals, Amsterdam Island had a naive avifauna (Milberg and Tyrberg, 1993) unable to cope with predation by people and rats. Its location far from other landmasses was no doubt responsible for the paucity of land-bird species, and its relatively southern position resulted in a seabird fauna composed mainly of petrels. Studies of fossil faunas from islands throughout the world, reviewed above, show that petrels are particularly susceptible to the effects of humans and to predation by introduced commensal mammals. Amsterdam Island conforms to this generality in that only 10 of at least 19 species that formerly bred there survive; in other words, 47% of the original species have been extirpated. Five of these 10 surviving species, however, are critically endangered on Amsterdam. Only three species are endemic to Amsterdam and St. Paul, and of these the land bird *Anas marecula* is extinct, whereas *Diomedea amsterdamensis* and *Pachyptila macgillivrayi* survive.

Appendix 1

Summary statistics for *Pterodroma macroptera*

(Measurements are in mm. Abbreviations are defined in "Methods.")

Fossil *Pterodroma macroptera* specimen from Amsterdam Island.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Lac W	PO W	ZP W	Pmx L	Pmx W	BCL	Pmx W/L
Mean	36.20	66.67	41.83	102.21	104.52	50.01	26.82	83.29	26.68	33.08	27.53	37.78	15.52	39.33	0.40
Standard deviation	0.86	2.08	1.08	2.01	2.53	1.35	0.75	2.47	0.98	0.90	0.81	2.49	0.77	0.53	0.04
Minimum	34.20	63.03	38.63	98.20	99.10	47.00	24.90	80.0	25.4	31.38	26.05	35.5	14.4	38.0	0.35
Maximum	37.83	71.17	44.26	106.80	110.40	53.10	28.13	86.35	29.1	34.7	29.1	44.3	16.84	40.1	0.45
Sample size	47	25	41	59	45	62	43	10	16	13	22	11	11	16	7
Coefficient of variation	2.37	3.12	2.58	1.97	2.42	2.70	2.80	2.96	3.67	2.72	2.94	6.59	4.96	1.35	10.0

Modern *Pterodroma m. macroptera* specimens from the Indian and Atlantic oceans (WA=Western Australia).

Catalog number	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Lac W	PO W	ZP W	Pmx L	Pmx W	Pmx W/L	Loc
CSIRO PROS 240	36.18	67.98	–	102.7	–	–	27.52	82.95	27.6	34.9	28.0	41.9	14.72	0.35	Eclipse Id., WA
CSIRO PROS 237	35.57	65.4	42.5	100.35	103.96	50.9	25.8	84.05	26.63	34.72	27.7	42.8	14.58	0.34	Eclipse Id., WA
CSIRO PROS 961	–	69.33	44.12	107.3	111.18	49.86	27.86	–	–	–	–	–	–	–	Coffin Id., WA
BMNH S/1964.14.19	39.52	71.67	45.0	110.46	114.81	54.34	–	89.1	28.67	34.4	30.5	49.56	15.35	0.31	Discovery Bay, Victoria
BMNH S/1964.14.18	38.6	68.1	43.27	106.65	109.33	52.73	27.98	86.74	27.7	35.44	29.5	45.5	16.3	0.36	Discovery Bay, Victoria
BMNH 1848.8.31.39	38.35	68.7	43.0	106.3	109.43	53.26	29.04	91.1	28.43	34.07	28.5	47.05	14.9	0.32	South Atlantic
BMNH 1848.8.31.40	38.5	67.72	43.16	107.36	111.76	52.4	29.31	88.28	28.88	35.48	28.86	45.56	16.12	0.35	South Atlantic

Recent *Pterodroma macroptera gouldi* from the New Zealand region.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Lac W	PO W	ZP W	Pmx L	Pmx W	Pmx W/L
Mean	39.24	70.56	43.8	109.93	114.34	53.83	28.46	89.47	28.79	34.66	29.86	45.92	16.43	0.36
Standard deviation	1.05	1.34	0.80	2.42	2.10	1.21	0.90	1.99	0.62	0.97	0.66	1.72	0.88	0.02
Minimum	38.0	68.4	42.7	105.5	110.7	51.5	27.2	86.2	27.7	33.4	28.9	43.1	15.0	0.33
Maximum	40.7	73.3	45.6	114.5	118.9	56.1	30.0	91.8	29.9	36.1	30.9	48.5	18.0	0.39
Sample size	14	14	14	14	14	14	14	13	13	11	12	13	13	13

Appendix 2

Summary statistics for *Pterodroma mollis*

(Measurements are in mm. Abbreviations are defined in "Methods.")

Fossil *Pterodroma mollis* from Amsterdam Island.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Lac W	PO W	ZP W	Pmx L	Pmx W	BCL	Pmx W/L
Mean	28.20	53.14	33.35	78.60	80.95	39.06	21.53	69.70	22.59	27.99	23.01	32.72	11.68	33.33	0.36
Standard deviation	0.83	1.44	0.84	2.25	2.42	0.92	0.56	1.82	0.83	0.64	0.69	0.73	0.48	1.00	0.02
Minimum	26.53	48.48	31.23	73.1	74.7	36.5	20.2	67.5	21.2	27.0	21.6	31.3	11.0	31.3	0.33
Maximum	31.5	55.22	35.3	84.0	84.2	41.4	23.0	73.0	24.4	28.9	24.2	34.3	12.8	35.3	0.41
Sample size	54	20	39	78	75	74	87	6	15	7	19	13	15	23	12
Coefficient of variation	2.94	2.71	2.52	2.86	2.99	2.35	2.60	2.61	3.67	2.29	3.00	2.23	4.11	3.00	5.56

Modern *Pterodroma mollis* from Gough Island and New Zealand (NZ).

Catalog number	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Lac W	PO W	ZP W	Pmx L	Pmx W	Pmx W/L	Locality
MNZ 22424	30.1	57.5	36.3	83.1	85.7	40.9	23.2	72.0	22.6	27.7	22.9	35.0	11.5	0.33	Gough Id.
MNZ 22423	30.7	58.5	35.3	83.4	86.8	41.6	23.0	72.7	23.3	29.7	23.5	35.4	10.8	0.31	Gough Id.
MNZ 22419	30.4	58.3	35.1	82.1	83.3	39.9	22.3	73.7	23.3	28.9	24.5	35.6	12.3	0.36	Gough Id.
MNZ 16583A	29.5	57.6	34.8	83.1	86.6	40.6	22.8	73.5	23.3	29.7	24.2	34.3	11.7	0.34	NZ, Rangitikei River
MNZ 21454	29.8	57.5	35.3	82.2	85.3	41.7	23.3	–	–	–	–	–	–	–	NZ, Petone Beach

Appendix 3

Summary statistics for *Pachyptila*

(Measurements are in mm. Abbreviations are defined in "Methods.")

Fossil *Pachyptila macgillivrayi* from Amsterdam Island.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Lac W	PO W	ZP W	Pmx L	Pmx W	BCL	Pmx W/L
Mean	24.35	49.53	32.83	57.26	56.94	30.41	19.08	65.98	17.33	22.09	20.05	36.25	16.30	27.05	0.45
Standard deviation	0.81	1.51	1.20	1.59	1.41	0.89	0.65	1.47	0.86	0.55	0.74	1.40	0.74	0.63	0.02
Minimum	22.58	45.60	30.40	53.30	52.30	28.60	17.50	62.9	15.8	21.1	18.7	33.1	14.9	25.8	0.40
Maximum	26.21	52.04	35.50	60.80	61.70	32.80	20.90	69.3	18.6	23.2	22.5	39.4	17.7	28.2	0.52
Sample size	51	36	71	120	127	110	90	18	27	20	31	32	31	19	28
Coefficient of variation	3.33	3.05	3.65	2.78	2.48	2.93	3.41	2.23	4.96	2.49	3.69	3.86	4.54	2.33	4.44

Modern *Pachyptila vittata*[*] from the New Zealand region.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Lac W	PO W	ZP W	Pmx L	Pmx W	Pmx W/L
Mean	26.86	52.65	35.16	61.92	61.78	33.04	20.53	71.88	21.54	23.78	21.66	40.89	18.99	0.46
Standard deviation	0.78	1.24	0.94	1.12	1.16	0.81	0.65	1.54	0.96	0.83	0.59	1.43	1.64	0.036
Minimum	25.40	50.80	33.90	60.00	60.20	31.50	19.50	68.50	19.8	22.20	20.60	37.90	15.50	0.382
Maximum	28.30	55.10	37.20	64.70	64.30	34.60	21.90	74.40	23.10	24.70	22.40	43.40	20.50	0.507
Sample size	17	17	17	16	16	16	16	16	14	15	16	15	15	15

[*] Included within the above statistics for *P. vittata* are data from MNZ 12481 and MNZ 12482, from Phillip Island, Australia, and the west coast of Wellington, New Zealand, respectively. These specimens are similar in size to the rest of the sample but have markedly narrower bills. Pmx W/L=0.40 mm and 0.38 mm, respectively, compared to data for the other 13 specimens: mean=0.48, standard deviation=0.022, minimum=0.45, maximum=0.51, *n*=13.

Modern *Pachyptila salvini* from the New Zealand region.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Lac W	PO W	ZP W	Pmx L	Pmx W	Pmx W/L
Mean	24.87	50.25	33.00	58.38	56.75	30.61	19.34	65.46	19.01	22.62	20.21	35.78	14.06	0.39
Standard deviation	1.15	2.21	1.36	2.22	2.71	1.25	0.63	3.47	1.05	0.87	0.88	2.58	1.21	0.01
Minimum	23.6	48.3	31.6	56.0	52.6	28.5	18.3	61.2	17.7	21.1	18.6	33.1	12.5	0.37
Maximum	27.9	56.3	36.1	64.1	62.8	32.6	20.5	73.1	21.2	23.7	21.6	41.6	16.0	0.41
Sample size	10	10	10	10	10	10	10	9	9	10	10	9	8	8

Appendix 4

Summary statistics for *Procellaria cinerea*

(Measurements are in mm. Abbreviations are defined in "Methods.")

Fossil *Procellaria cinerea* from Amsterdam Island.

Statistic	Fem L	Tib TL	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Preorb W	PO W	ZP W	Pmx L	Pmx W	BCL	Pmx W/L
Mean	46.60	104.73	90.88	58.85	130.60	126.89	61.03	34.02	101.50	17.04	37.88	32.70	52.08	16.33	46.45	0.31
Standard deviation	1.21	2.41	1.62	1.35	2.61	2.54	1.38	1.02	3.40	0.71	0.98	1.02	1.46	0.61	1.16	0.01
Minimum	45.00	100.30	87.70	56.20	124.50	122.90	58.90	32.40	97.8	15.82	36.3	31.08	50.3	15.4	44.5	0.30
Maximum	48.75	107.70	93.30	60.70	136.60	131.50	64.10	36.00	106.0	18.3	38.8	34.0	54.5	17.3	48.5	0.34
Sample size	16	9	15	13	24	19	19	17	6	14	5	10	9	10	9	9
Coefficient of variation	2.60	2.30	1.78	2.29	2.00	2.00	2.26	3.00	3.35	4.17	2.59	3.12	2.80	3.73	2.50	3.22

Modern *Procellaria cinerea* from the New Zealand region.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Preorb W	PO W	ZP W	Pmx L	Pmx W	Pmx W/L
Mean	48.44	95.67	62.23	136.59	134.93	64.12	35.94	106.78	16.70	39.04	33.75	56.70	16.25	0.29
Standard deviation	1.65	1.78	1.19	2.45	2.43	1.19	0.58	2.89	1.16	1.16	0.71	1.89	1.14	0.02
Minimum	43.7	92.2	60.0	132.6	131.5	61.8	34.7	101.1	12.5	36.7	32.4	53.3	13.2	0.24
Maximum	51.2	98.8	64.3	141.5	140.1	66.1	36.8	113.0	18.1	40.9	35.2	60.4	18.2	0.32
Sample size	21	22	21	24	23	23	23	22	22	21	21	23	23	23

Appendix 5

Summary statistics for *Puffinus assimilis*

(Measurements are in mm. Abbreviations are defined in "Methods.")

Fossil *Puffinus assimilis* from Amsterdam Island.

Statistic	Fem L	Tib TL	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L	Skull TL	Preorb W	PO W	ZP W	Pmx L	Pmx W	BCL	Pmx W/L
Mean	25.58	71.31	56.73	40.39	62.78	55.20	33.36	22.62	65.25	8.57	25.92	20.40	30.77	9.17	31.50	0.30
Standard deviation	0.94	0.43	1.30	1.38	1.56	1.28	0.94	0.64	0.64	0.45	0.95	0.69	0.95	0.26	0.58	0.02
Minimum	23.78	71.00	54.45	35.16	59.60	52.10	31.60	21.20	64.8	7.6	24.3	19.2	29.3	8.8	30.6	0.28
Maximum	27.30	71.61	58.60	43.46	65.60	57.80	35.10	24.10	65.7	9.4	27.7	22.0	32.0	9.4	33.2	0.32
Sample size	32	2	21	36	45	45	33	43	2	21	13	15	7	6	20	6
Coefficient of variation	3.67	0.60	2.29	3.42	2.48	2.32	2.82	2.83	0.98	5.25	3.66	3.38	3.09	2.84	1.84	6.67

Modern *Puffinus assimilis elegans* from the Antipodes.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	26.34	58.56	40.83	64.76	56.53	34.01	23.09
Standard deviation	0.74	1.45	0.92	1.47	1.47	0.99	0.57
Minimum	25.1	55.6	39.2	62.3	53.6	32.0	21.9
Maximum	27.3	59.9	41.7	66.5	57.9	34.8	23.6
Sample size	7	7	7	7	7	7	7

Modern *Puffinus assimilis assimilis* from Norfolk Island.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	23.20	49.90	35.15	55.90	49.45	29.55	18.76
Standard deviation	–	1.98	2.05	2.40	3.46	1.06	–
Minimum	23.2	48.5	33.7	54.2	47.0	28.8	18.76
Maximum	23.2	51.3	36.6	57.6	51.9	30.3	18.76
Sample size	1	2	2	2	2	2	1

Recent *Puffinus assimilis haurakiensis* from Northland, New Zealand.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	23.80	54.00	37.95	58.25	51.65	31.55	21.95
Standard deviation	0.85	3.68	2.19	0.92	0.92	1.77	0.49
Minimum	23.2	51.4	36.4	57.6	51.0	30.3	21.6
Maximum	24.4	56.6	39.5	58.9	52.3	32.8	22.3
Sample size	2	2	2	2	2	2	2

Recent *Puffinus assimilis kermadecensis* from the Kermadec Islands.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	24.02	53.95	38.25	59.82	54.16	32.00	21.16
Standard deviation	0.57	1.71	1.46	1.79	1.85	0.96	0.87
Minimum	23.1	51.9	36.1	57.0	51.8	30.7	20.0
Maximum	25.0	56.8	40.7	62.9	56.4	33.4	22.6
Sample size	10	10	10	10	10	10	10

Recent *Puffinus assimilis* ssp. from New Zealand west-coast beaches.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	23.48	52.14	36.61	57.97	52.68	30.93	20.74
Standard Deviation	0.53	1.40	0.57	1.25	1.36	0.71	0.60
Minimum	22.6	49.7	35.5	56.0	51.0	30.2	20.0
Maximum	24.2	55.0	37.5	61.1	56.3	32.8	21.7
Sample size	10	10	10	12	12	12	11

Appendix 6

Summary statistics for storm-petrels

(Measurements are in mm. Abbreviations are defined in "Methods.")

Fossil *Pelagodroma marina* from Amsterdam Island.

Statistic	Fem L	Tib TL	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	17.23	59.48	54.19	40.91	25.02	22.32	16.88	14.17
Standard deviation	0.41	2.07	1.66	1.18	0.81	0.57	0.51	0.61
Minimum	15.92	56.30	51.86	37.30	22.84	21.01	16.03	13.25
Maximum	17.93	65.73	60.32	43.36	26.59	23.80	18.13	15.10
Sample size	37	31	46	87	49	73	40	15
Coefficient of variation	2.38	3.48	3.06	2.88	3.24	2.55	3.02	4.30

Modern *Pelagodroma marina* from the New Zealand region.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	16.86	53.92	40.90	25.09	22.93	16.82	13.72
Standard deviation	0.19	1.16	0.99	0.46	0.58	0.47	0.49
Minimum	16.5	52.1	39.33	24.12	21.6	15.76	13.05
Maximum	17.1	56.5	42.68	25.8	23.96	17.72	14.58
Sample size	12	14	14	14	14	14	14

Fossil *Fregetta grallaria* from Amsterdam Island.

Statistic	Fem L	Tib TL	Tib AL	Tmt L	Hum L	Ulna L	Cmc L
Mean	18.94	50.98	47.77	37.57	27.03	23.17	17.76
Standard deviation	0.06	1.91	1.66	1.09	0.38	0.54	–
Minimum	18.9	49.61	46.18	36.15	26.6	22.43	17.76
Maximum	18.98	53.16	49.4	39.13	27.31	23.76	17.76
Sample size	2	3	4	12	3	5	1

Modern *Fregetta* from the New Zealand region.

Specimen	Fem L	Tib TL	Tib AL	Tmt L	Hum L	Ulna L	Cmc L	Tmt SW as % length
Fregetta grallaria								
MNZ 16071	17.6	53.0	49.06	37.4	25.72	23.58	17.82	5.08
Fregretta tropica								
MNZ 18963	19.02	57.73	53.40	42.45	26.06	23.15	17.5	4.55
MNZ 19277	18.26	57.05	52.70	40.69	24.94	22.26	16.9	4.67
MNZ 22254	18.02	57.52	52.70	41.42	25.02	22.56	17.14	4.68
MNZ 23798	18.62	58.70	54.32	42.54	25.54	23.28	17.60	4.61

Appendix 7

Summary statistics for *Pelecanoides* species and subspecies

(Measurements are in mm. Abbreviations are defined in "Methods.")

Modern *Pelecanoides georgicus* from Heard Island.

Statistic	Fem L	Tib TL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	21.60	43.75	23.44	40.18	30.30	21.79	22.54
Standard deviation	0.23	0.69	0.50	0.67	0.70	0.47	0.65
Minimum	21.2	42.6	22.5	39.3	29.4	21.1	21.6
Maximum	21.9	44.8	23.9	41.0	31.1	22.5	23.7
Sample size	8	8	7	8	8	8	7

Modern *Pelecanoides urinatrix exsul* from Auckland and Heard islands.

Statistic	Fem L	Tib TL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	23.46	47.41	25.74	42.43	33.23	24.03	23.85
Standard deviation	0.49	0.74	0.63	0.64	0.29	0.64	0.99
Minimum	22.9	45.9	24.6	41.8	32.9	23.0	22.6
Maximum	24.2	48.2	26.5	43.3	33.7	24.9	25.1
Sample size	7	7	7	7	7	7	6

Modern *Pelecanoides urinatrix chathamensis* from Southeast Island, Chatham Group.

Statistic	Fem L	Tib TL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	22.74	45.99	24.99	40.80	32.31	23.18	22.80
Standard deviation	0.67	1.35	0.89	0.68	0.81	0.50	0.41
Minimum	21.5	43.7	23.5	39.8	30.8	22.5	22.0
Maximum	23.4	48.1	26.3	41.9	33.3	23.8	23.2
Sample size	7	7	7	7	7	6	7

Modern *Pelecanoides u. urinatrix* from beaches near Wellington, New Zealand.

Statistic	Fem L	Tib TL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	24.01	48.45	26.16	44.43	35.66	25.24	23.83
Standard deviation	0.61	0.89	0.90	0.73	0.61	0.67	0.61
Minimum	22.9	46.9	25.3	43.1	34.7	24.3	22.8
Maximum	24.7	49.6	27.7	45.7	36.4	26.3	24.8
Sample size	8	8	8	8	8	8	8

Fossil *Pelecanoides urinatrix* from Amsterdam Island.

Statistic	Fem L	Tib TL	Tmt L	Hum L	Ulna L	Cmc L	Cor L
Mean	22.51	43.43	24.42	40.77	31.91	22.57	22.95
Standard deviation	0.35	1.38	0.40	1.09	0.50	0.11	0.90
Minimum	22.05	42.45	23.8	39.6	31.1	22.46	22.1
Maximum	23.13	44.4	24.8	42.14	32.36	22.7	24.1
Sample size	7	2	5	6	9	4	4

Appendix 8

Summary statistics for *Catharacta* spp.

(Measurements are in mm. Abbreviations are defined in "Methods.")

Modern *Catharacta maccormicki* from the Antarctic.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L
Mean	60.56	103.01	66.41	135.54	139.56	69.60
Standard deviation	2.03	3.05	1.81	4.15	4.45	2.36
Minimum	58.5	100.3	64.0	130.6	133.4	66.4
Maximum	64.1	108.1	69.8	141.6	144.8	73.7
Sample size	7	7	7	7	7	7

Modern *Catharacta skua lonnbergi* from New Zealand Subantarctic islands.

Statistic	Fem L	Tib AL	Tmt L	Hum L	Ulna L	Cmc L
Mean	73.55	126.18	81.50	152.02	153.88	76.40
Standard deviation	3.76	4.22	1.99	5.15	4.40	1.80
Minimum	69.6	122.0	79.2	145.1	148.4	74.1
Maximum	78.8	132.5	84.6	158.0	159.5	78.4
Sample size	6	5	5	6	5	5

Fossil *Catharacta* bones from Amsterdam Island.

Location	Hum L	Ulna L	Cmc L	Fem L	Tib AL	Tmt L
Site 8.4	–	–	–	–	–	74.4
Site 9	–	–	–	–	–	76.5
Site 13.5	–	–	71	–	–	–
Site 19	–	144.1	–	–	–	–
Site 15.2	–	–	–	–	–	75.9

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Comparison of Paleoecological Patterns in Insular Bird Faunas: A Case Study from the Western Mediterranean and Hawaii

Bartomeu Seguí and Josep Antoni Alcover

ABSTRACT

A comparison among the Pleistocene avifaunas from the western Mediterranean islands (Menorca, Mallorca, and Cabrera (Gymnesic Islands); Eivissa (=Ibiza) and Formentera (Pityusic Islands); Corsica; Sardinia) shows great differences between those islands with terrestrial mammals (Gymnesic Islands, Corsica, Sardinia) and those lacking them (Pityusic Islands). A close parallel is found between the late Pleistocene avian communities of the Pityusics and the prehuman avifauna of the Hawaiian Islands, whereas the communities from the remaining western Mediterranean islands were similar ecologically to those of the eastern Mediterranean islands. A key factor for the understanding of avian community structure is the presence or absence of middle-sized herbivorous mammals (*Myotragus balearicus* Bate on the Gymnesic Islands and *Megaceros cazioti* (Depéret) on Corsica and Sardinia).

Introduction

Since the works of Darwin (1859) and Wallace (1881), the study of islands has been a powerful tool for the advancement of many fields of biology (Vitousek et al., 1995). The recent inclusion of fossils in the study of insular faunas has conferred a historical dimension to previous analyses of insular biogeography and ecology. This new component enables us to test the validity of faunal composition and biogeographic concepts derived from the study of present faunas, allowing new kinds of analyses of the components and the structure of paleocommunities (Alcover and McMinn, 1994; James, 1995).

The study of insular fossil faunas has already changed several paradigms of insular biogeography and ecology. Thus, the actual existence of ecological processes of "faunistic turnover" for the establishment of an "insular equilibrium" (MacArthur and Wilson, 1967) has been seriously questioned (e.g., Olson and James, 1984; Steadman, 1986, 1995; James, 1995). Recent findings also have questioned ecological processes, such as the so-called "taxon cycle" (see Pregill and Olson, 1981), or postulates to the effect that insular communities harbor species of predators exhibiting lesser body size than those from the closest mainland (Blondel and Frochot, 1976).

Typical insular communities are characterized by their disharmony, by so-called "insular poverty," and by their high degree of endemism (Wallace, 1895). These factors imply that ecological communities assemble on islands in a peculiar way, with an organization of ecological relationships between species that is different from that on continents. Before human colonization, island communities were even more peculiar than at present (James, 1995).

The western Mediterranean islands (Figure 1) have provided moderately rich Quaternary avifaunas (Alcover et al., 1992) as well as prehuman faunas of mammals, reptiles, and amphibians (see Table 1). To date, the late Pleistocene paleornithological record consists of 55 or 56 species in Mallorca, eight in Menorca, 60 to 65 in Eivissa, two in Formentera, 74 in Corsica, and 49 in Sardinia. The fossil avifauna of Eivissa is considered to be the best represented of prehuman bird communities of any island in the Mediterranean region. The late Pleistocene record of Eivissa is based on more than 150,000 fossil bird specimens, mainly coming from a single deposit, Es Pouàs (McMinn, in prep.), as well as from another six sites of lesser importance. In Mallorca, more than 3000 bird bones have been exhumed to date from 14 late Pleistocene and Holocene sites (Seguí, 1997). The fossil record from Corsica and Sardinia, in spite of not being as representative of its Quaternary avifaunas, displays several features that allows the characterization of its prehuman native faunas. The late Pleistocene fossil record of Menorca and Formentera is still very limited. Because we do not consider the fossil records of these islands to be as representative of

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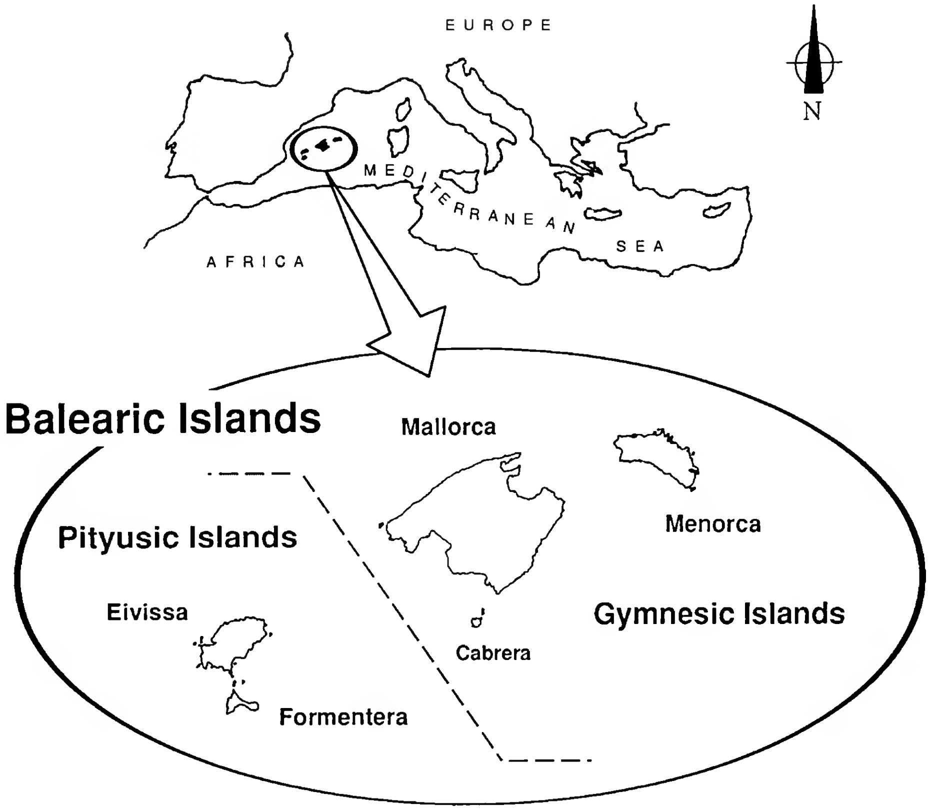

FIGURE 1.—Map of the Mediterranean region showing the position and nomenclature of the Balearic Islands used in this paper. Eivissa is the Catalan name for the island known in other languages as Ibiza.

native, prehuman avifaunas as those of the other islands, we have excluded Menorca and Formentera from our analysis. The numbers of fossil bones presented above, together with data on species distribution in the different deposits, allow a rough estimate of relative species abundance on the islands, taphonomic biases included.

The very different vertebrate paleofaunas of the Mediterranean-basin archipelagos are of interest for comparison with other insular faunas worldwide. Herein we present a preliminary analysis of the paleoecology of the late Pleistocene bird communities of the western Mediterranean islands based on the known trophic ecology of the different species recorded on the islands. We emphasize parallels with other known prehuman native-bird communities worldwide. The Pleistocene bird communities of the western Mediterranean mainly include extant species, even though many have recently vanished from several or all the islands considered. They also include at least four or five extinct species: *Tyto balearica* Mourer-Chauviré, Alcover, Moyà, and Pons, a nonendemic species found on Mallorca, Menorca, Corsica (Mourer-Chauviré, pers. comm., 1996), and in some mainland deposits from France and the Iberian Peninsula; *Bubo insularis* Mourer-Chauviré and Weesie, endemic to Corsica and Sardinia; an undescribed species of *Athene* endemic to Corsica (Mourer-Chauviré, pers. comm., 1996); an undescribed species of *Rallus* endemic to Eivissa; and *Grus primigenia* Milne-Edwards, a nonendemic species widely distributed during the European Pleistocene, also present on Eivissa and Mallorca, which is probably conspecific with *Grus grus* (J.R. Stewart, pers. comm., 1996). Some taxa previously considered as possible endemics (e.g., Fringillidae, species undescribed, and Corvidae, species undescribed; see Alcover et al., 1992) have been deleted after taxonomic reappraisal. Nomenclature for binomials of modern birds follows Sibley and Monroe (1990).

Even though the determination of the feeding habits and specializations of extinct species may be imprecise or speculative, the allocation of these species to broad trophic categories can allow us to undertake a more general analysis. These kinds of inferences are applicable to all the extinct Mediterranean species considered above, but they cannot be extended indiscriminately, especially in the case of bizarre small Passeriformes without known analogs (e.g., *Vangulifer* from Maui, Hawaiian Islands; James and Olson, 1991).

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TABLE 1.—Vertebrate fauna, excluding birds, from the late Pleistocene and the Holocene of the main western Mediterranean islands.

Fauna	Eivissa	Mallorca	Corsica and Sardinia
Amphibians	–	*Alytes* (*B.*) *muletensis*	*Euproctus* spp. *Speleomanthes* spp. *Discoglossus* spp. *Hyla sarda*
Reptiles	*Podarcis pityusensis*	*Podarcis lilfordi*	*Phyllodactylus europaeus* *Podarcis tiliguerta* *Archaeolacerta bedriagae* *Algyroides fitzingeri*
Mammals	bats	*Nesiotites hidalgo* *Hypnomys morpheus* *Myotragus balearicus* bats	*Nesiotites* spp. *Rhagamys orthodon* *Microtus henseli* *Prolagus sardus* *Lutrini* spp. *Megaceros* (*D.*) *cazioti* bats

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Bird Trophic Type (BTT)

Initially, we defined the main Bird Trophic Types (BTTs) present on the western Mediterranean islands. Afterwards, we identified the taxa present in the fossil record of each island and assigned them to their respective BTT. The distribution of the taxa among BTTs was analyzed at different taxonomic levels (species, genus, or family) to enable comparisons with other insular faunas, even those from other biogeographical regions.

In Table 2 the basic BTTs considered in this work are defined. These do not include all the actual trophic types of birds, especially those of passerines, and they exclude others, such as aerial planctophagous species (e.g., swifts) or coastal generalists (e.g., gulls). Nevertheless, the majority of bird species of the Mediterranean islands fit well in these BTTs (see Table 3). Trophic types considered are as follows: predators of vertebrates (superpredators, nocturnal predators, ornithophagous diurnal predators, generalist diurnal predators, fish-eaters); scavengers; sea birds; herbivorous nonpasserines; malacophagous, insectivorous, and herbivorous nonpasserines; and three BTTs within the Passeriformes (large-sized omnivores, small-sized omnivores, granivores).

The assignment of each taxon to a BTT was based on the main components of their diet, according to various general

TABLE 2.—Main BTTs (Bird Trophic Types) in the Pleistocene-Holocene fossil record from the western Mediterranean Islands.

<table>
<tr><td rowspan="11">Nonpasseriforms</td><td rowspan="5">Vertebrate predators</td><td colspan="2">Superpredators</td><td>large-sized birds that prey mainly on middle- and large-sized vertebrates</td></tr>
<tr><td colspan="2">Nocturnal predators</td><td>nocturnal birds that prey mainly on small-sized vertebrates during the night and twilight</td></tr>
<tr><td rowspan="2">Diurnal predators</td><td>specialized ornithophagous</td><td>diurnal birds specialized for preying on middle- and small-sized birds, mainly small Passeriformes</td></tr>
<tr><td>generalist</td><td>diurnal birds for which birds are just a part of the diet, which consists mainly of small-sized vertebrates, insects, and carrion</td></tr>
<tr><td colspan="2">Fish-eaters</td><td>specialized fish-catchers that feed in inland and littoral waters</td></tr>
<tr><td colspan="3">Scavengers</td><td>diurnal birds that feed totally or partially on carrion and bone fragments of large carcasses</td></tr>
<tr><td colspan="3">Sea birds</td><td>pelagic birds that feed mainly on crustaceans, cephalopods, and fish from the upper layers of the water column</td></tr>
<tr><td colspan="2" rowspan="2">Herbivores</td><td>large-sized</td><td>middle- and large-sized browsers, grazers, and frugivores</td></tr>
<tr><td>small-sized</td><td>small-sized browsers, grazers, and frugivores</td></tr>
<tr><td colspan="2" rowspan="2">Malacophages, insectivores, and herbivores</td><td>large-sized</td><td>large-sized birds that feed mainly on terrestrial snails and insects as well as on varied vegetable sources</td></tr>
<tr><td>small-sized</td><td>medium- and small-sized birds that feed mainly on terrestrial snails and insects as well as on varied vegetable sources</td></tr>
<tr><td rowspan="3">Passeriforms</td><td colspan="2" rowspan="2">Omnivores</td><td>large-sized</td><td>large-sized passeriformes that feed on varied animal and vegetable sources</td></tr>
<tr><td>small-sized</td><td>middle- and small-sized passeriformes that feed on varied animal and vegetable sources</td></tr>
<tr><td colspan="3">Granivores</td><td>small passeriformes that feed mainly on seeds</td></tr>
</table>

TABLE 3.—The main BTTs (Bird Tropic Types) on islands with terrestrial mammals (Corsica, Sardinia, Mallorca) compared with islands without terrestrial mammals (Eivissa, Hawaiian Islands). Taxa in parentheses are known only from very scarce remains. On islands with terrestrial mammals, some of the BTTs are not present because the niches that they represent are practically monopolized by mammals (see shaded boxes). Data are from the authors; Alcover et al., 1992; Olson and James, 1991; and James and Olson, 1991.

Bird trophic types				Islands with terrestrial mammals			Islands without terrestrial mammals	
				Corsica and Sardinia	Mallorca	Eastern Mediterranean islands	Eivissa	Hawaiian Islands
Nonpasseriforms	Vertebrate predators	Superpredators		*Aquila*	*Aquila*	*Aquila*	*Haliaeetus*	*Haliaeetus*
		Nocturnal predators		*Bubo*, *Asio*, *Tyto alba*	*Tyto alba*/ *Tyto balearica*	*Tyto alba*, *T. melitensis*, *Athene cretensis*, *Aegolius*, (*Ketupa*) (*A. flammeus*)	*Asio flammeus*	*Grallistrix*
		Diurnal predators	specialized ornithophagous	*Accipiter*	*Accipiter*	*Accipiter*	*Accipiter*	*Circus dossenus*
			generalists	*Falco*, *Milvus*, *Buteo*, *Circus*	*Falco*	*Buteo*	*Falco* (*Circus*)	*Buteo*
		Fish-eaters		*Haliaeetus*	–	*Haliaeetus*	*Haliaeetus*, *Pandion*	*Haliaeetus*
	Scavengers			*Gypini*	*Gypini*	*Gypini*	*Haliaeetus*	*Haliaeetus*
	Sea birds			Procellaridae spp.	–	(*Puffinus*)	Procellaridae spp.	Procellaridae spp.
	Herbivores	large-sized		Cervidae	Bovidae	Cervidae, Elephantidae, Hippopotamidae	*Anser*/*Branta*	*Branta*, moa-nalos
		small-sized		Rodentia, Lagomorpha	Rodentia	Rodentia	–	–
	Malacophages, insectivores, detritivores, herbivores	large-sized		(*Otis*)	(*Grus*)	(*Otis*) *Grus melitensis*	*Otis*, *Grus*	*Apteribis*
		small-sized		(*Rallus*) (*Porzana*) (*Gallinula*) (*Crex*)	(*Porzana*)	(*Porzana*) (*Gallinula*) (*Fulica*)	*Rallus*, *Crex*	*Porzana*
Passeriforms	Omnivores	small-sized		*Sturnus*, *Pyrrhocorax*	(*Sturnus*), (*Corvus*), *Pyrrhocorax*	(*Sturnus*), *Corvus*, *Pyrrhocorax*, *Garrulus*	*Pyrrhocorax*	*Aidemedia*
		large-sized		(*Corvus corax*)	–	(*Corvus corax*)	*Corvus*	*Corvus viriosus*, *Corvus impluviatus*, *Corvus hawaiiensis*
	Granivores			several Fringillidae, Passeridae, Emberizidae	several Fringillidae, Passeridae, Emberizidae	several Fringillidae and Emberizidae	several Fringillidae, Passeridae, Emberizidae	several Drepanidini

works (Cramp and Simmons, 1977, 1980; Cramp, 1985; Hoyo et al., 1992, 1994, 1996). Usually, each taxon was referred only to a single BTT, although a small group of species occupied more than one type (e.g., *Haliaeetus* on Eivissa, which is considered to have been the superpredator on the island but was simultaneously the main fish predator and the main scavenger).

The absence of medium-sized herbivorous mammals on Eivissa is related to the presence of an abundant goose, probably derived from *Anser erythropus*. The tribe Anserini is usually underrepresented, due to taphonomic conditions, in nonanthropogenic cave sites, excepting on some islands. Because of the great number of remains that have been exhumed from speleological sites on Eivissa, the extinct goose must have been very abundant in Pityusic paleornithological communities. This species was probably the main medium-sized herbivorous vertebrate on the island and must be considered to be the key species in understanding Pityusic paleoecosystems.

The occupation of the browsing- or grazing-herbivore trophic type by mammals (Bovidae and Cervidae) on all the Mediterranean islands has further implications for trophic webs. Thus, the islands with ungulates have eagles of the genus *Aquila* as superpredators and have vultures (*Aegypius*, *Gyps*) as the chief large scavengers. On the other hand, on islands without these mammals but with abundant Anseriformes and Procellariiformes, the role of superpredators is taken by sea-eagles of the genus *Haliaeetus*, which also must be considered the main scavengers there. This relationship, confirmed on the Mediterranean islands, also applies to other islands in the world (Alcover and McMinn, 1992, 1994). Sea-eagles must have been very abundant in the Pityusic Islands before human colonization. In just one fossiliferous site, remains of at least nine individuals have been found, including several practically complete associated skeletons. On Corsica and Sardinia, on the other hand, very few remains of *Haliaeetus* have been recovered.

As far as vertebrate nocturnal predators are concerned, the absence of Tytonidae in the fossil record of Eivissa, as is the case in the Hawaiian Islands, is particularly noteworthy. Tytonidae are present in the early Pleistocene and the Holocene of

Mallorca, probably in prehuman levels, and in the late Pleistocene from Corsica-Sardinia (Alcover et al., 1992). Their presence is probably related to the presence of small mammals on these islands (*Hypnomys* and *Nesiotites* in the Gymnesic Islands, *Nesiotites, Rhagamys, Microtus,* and *Prolagus* in Corsica-Sardinia), whereas small mammals are absent from Eivissa. It is not possible, however, to infer in a strict sense the absence of Tytonidae on islands without small mammals. For example, in the Galápagos and Canary islands different small mammals have been recorded on some of the islands but not on all of them. In these archipelagos, tytonids have even been obtained in prehuman deposits on islands without small mammals (Steadman, 1986; Alcover, unpublished).

Strigid owls that prey on vertebrates are unknown in the fossil record of Mallorca. Although *Otus scops* and *Athene noctua* do occur in the fossil record, these species feed mainly on insects. *Asio flammeus* and *Bubo insularis* are present in the fossil record on Sardinia, and *Bubo insularis, Asio otus,* and a new, undescribed species of *Athene* have been found as fossils on Corsica (Mourer-Chauviré, pers. comm., 1996). Several remains of *Asio flammeus* and those of a single individual of a large species of Strigidae, probably *Bubo bubo,* have been found in the late Pleistocene of Eivissa (Alcover et al., 1992; Sondaar et al., 1995). *Asio flammeus,* the more abundant strigid on Eivissa, is more diurnally active than other Palearctic species of owls of the same size, like *Asio otus* or *Strix aluco* (Cramp, 1985). This behavioral pattern may have been advantageous for preying on birds, which were the primary food available on Eivissa before human colonization. Circadian rhythms might differ between insular and continental systems (Granjon and Cheylan, 1990, 1993, gave an example of change of circadian rhythms in a mammalian species). *Asio flammeus* may have been more diurnal on Eivissa than in other areas of its range.

The endemic genus *Grallistrix* lived in the Hawaiian Islands (Olson and James, 1991). This genus shows anatomical specializations for bird-catching (elongated legs and shortened wings). Its ornithophagous habits have been confirmed by fossil pellets (Olson and James, 1991). The main activity period of *Grallistrix* is unknown, but its ability to catch and kill birds in flight suggests that the species of this genus may have been more diurnal than other Strigidae.

Hawks and falcons are widely distributed on western Mediterranean islands and have been found as fossils on all those islands studied herein. In the Hawaiian Islands this BTT is occupied by *Circus dossenus,* a species convergent with bird-eating hawks of the genus *Accipiter* (Olson and James, 1991). On Mediterranean islands with mammals, species of *Buteo* (with a diet of small mammals and small- and medium-sized reptiles), species of *Circus* and *Milvus* (each with a varied diet), and small species of the genus *Falco* (mainly herpetophagous and entomophagous) have been found (Alcover et al., 1992). This BTT is occupied by *Buteo solitarius* in the Hawaiian Islands (Olson and James, 1991), whereas in Eivissa it is represented by *Circus cyaneus,* which is scarce in the fossil record, and by small species of the more abundant *Falco* (Sondaar et al., 1995).

Pelagic sea birds are not found on the large western Mediterranean islands with mammals, being unknown in Corsica and Sardinia (Alcover et al., 1992). On the other hand, the small island of Tavolara, near Sardinia, has yielded fossil remains of *Calonectris diomedea* and *Puffinus yelkouan* (Mayaud and Schaub, 1950). Significantly, Procellariiformes were abundant in the Pityusic Islands. Many fossil bones of *Puffinus mauretanicus* and scarcer remains of *Calonectris diomedea* and *Hydrobates pelagicus* have been found in Eivissa (Sondaar et al., 1995). Similarly, abundant remains of procellariforms, such as the extinct, small-sized gadfly petrel *Pterodroma jugabilis* (Olson and James, 1991), have been found in Oahu and Hawaii, and many other Procellariidae are commonly encountered.

The BTT that includes the nonpasseriform species with a wide diet (malacophagous, insectivorous, detritivorous, and herbivorous birds) has a better representation on the Pityusic and Hawaiian islands than on the other western Mediterranean islands. Two or more flightless species of ibis belonging to the extinct genus *Apteribis* lived on the Hawaiian islands Molokai, Maui, and Lanai, which constituted the Pleistocene island of Maui Nui (Olson and James, 1991). The genera *Otis* (bustards) and *Grus* (cranes) can be considered to be the Palearctic ecological analogs of these species. Both are common in the Eivissan fossil record but are not as common on the other western Mediterranean islands: so far, only a few remains of one specimen of *Grus* have been obtained in Mallorca (Mourer-Chauviré et al., 1975), and a few remains of *Otis* have been found on Corsica (Mourer-Chauviré, pers. comm., 1996).

Among the rails, only a few remains of *Porzana* have been recorded on Mallorca, and no rails have been found in the Sardinian fossil record. Four species of rails are infrequently encountered in the fossil record of Corsica (Alcover et al., 1992), whereas rails are well represented in the late Pleistocene of Eivissa as well as on the Hawaiian Islands. Endemic species have evolved on the Hawaiian Islands and on Evissa but not on the other western Mediterranean islands. An endemic undescribed form of *Rallus* lived on Eivissa (McMinn, in prep.), whereas the genus *Porzana* underwent a significant radiation in the Hawaiian Islands (Olson and James, 1991).

The BTTs occupied by Passeriformes are not as easily defined as those occupied by nonpasserines. Thus, only three BTTs were considered for the Passeriformes. Some patterns, coming mainly from corvids, emerged from our analysis. On all the islands studied, corvids played an important role. *Pyrrhocorax* was present during the late Pleistocene on all the western Mediterranean islands. At least one small-sized species of *Corvus* also was present in Corsica, Sardinia, and Mallorca. Large-sized species of *Corvus* are scarce in the fossil record of Mallorca, Corsica, and Sardinia. In contrast, on Eivissa abundant remains of a large *Corvus,* initially identified as *C. antecorax* (Florit et al., 1986), but whose identity is now under revision (McMinn, in prep.), have been recorded. In the Pleistocene of the Hawaiian Islands three large-sized species of

Corvus have been found: the extinct *C. impluviatus* James and Olson (1991) and *C. viriosus* James and Olson (1991) and the extant *C. hawaiiensis.* Probably all the large Hawaiian and Mediterranean species of *Corvus* represent roughly the same BTT. The scarcity of large crows on the Mediterranean islands with terrestrial mammals, in contrast with their abundance in Eivissa and the Hawaiian Islands, reinforces the parallels between the two archipelagos.

The BTT that includes small-sized corvids on the Mediterranean islands is tentatively paralleled by the Hawaiian genus *Aidemedia,* which on the basis of its jaws was thought to have dietary habits similar to those of *Sturnus* (James and Olson, 1991). *Sturnus* is present in the fossil records of Mallorca (Seguí et al., 1997), Corsica, and Sardinia (Alcover et al., 1992), although it is considerably scarcer than *Pyrrhocorax.* The living representatives of both genera have opportunistic dietary habits and eat lots of fleshy fruits.

The small Passeriformes (perching birds) are included in a very wide range of BTTs that are more difficult to characterize than the larger species, compounded by the fact that they often change their BTT through the year. Because of these and other considerations we have omitted them from Table 3, except for small granivorous species, which are included to show that the members of a variety of families occupy the same BTT on the Mediterranean islands as do some granivorous species of Drepanidini in the Hawaiian Islands. A similar pattern among granivorous passerines in the Galápagos Islands (all belonging to a single radiation) and in the Canary Islands (where species belonging to different families occupy this BTT) has been recorded.

Discussion

The peculiarity of the Eivissan paleoavifauna within the Mediterranean region is clearly supported by the preceding analysis. The late Pleistocene fauna of Eivissa was structured along similar lines to that of the Hawaiian Islands: Anseriformes as the most important middle-sized grazers, sea-eagles as superpredators, mammal-eating tytonids absent, bird-catching strigids with more diurnal behaviour present, diurnal birds of prey (bird-catching specialists or more generalists) present, ground-dwelling species with varying food habits (i.e., medium- and small-sized malacophagous, insectivorous, detritivorous, and herbivorous species), along with flying, omnivorous, medium-sized passerines (large corvids). In the faunas of the other Mediterranean islands, where land mammals were present, the paleornithological communities were structured in very different ways.

One of the main points to be emphasized is that the greatest parallel to the late Pleistocene bird community of Eivissa is not on the other Mediterranean islands, the Atlantic or Indian oceanic islands that lack terrestrial mammals, or on the majority of Pacific islands, but on the very distant and isolated Hawaiian Islands. Conversely, the most accurate parallel to the Hawaiian paleoavifauna, according to the assignment of the different BTTs, is not to found among the other Pacific Islands, or among the Atlantic Islands, but rather in the late Pleistocene fauna from Eivissa. The significance of such an ecological relationship is currently unknown. Nevertheless, there is no doubt that an accurate study of the Eivissan fossil avifauna will be useful for the understanding of the development of the Hawaiian avifauna, and vice versa. In any case, the striking similarity between the avian paleocommunities of the Hawaiian Islands and the Pityusic Islands reinforces criticisms of the randomness of the ecological processes of immigration and extinction in the development of insular communities.

One point of interest of the present analysis is its predictive character. We have an accurate knowledge of the late Pleistocene fauna from Eivissa, contrasting with scarce data on late Pliocene/early Pleistocene bird fauna of the island (Alcover, 1989, and unpublished data). During this earlier period, a vertebrate fauna, including a giant tortoise and at least two terrestrial mammals, lived on Eivissa. In addition, a varied mollusk fauna of at least 22 species also was present. These faunas suffered a dramatic, early or middle Pleistocene extinction event (Alcover et al., 1994). The avifauna associated with the giant tortoise episode is as yet poorly known, although it likely was substantially different from the late Pleistocene avifauna. The mass extinction on Eivissa must have forced a change in the composition and structure of the bird communities.

Study of the fossil bird fauna from Menorca also should be enlightening. This island, which is about same size as Eivissa, was occupied by *Myotragus balearicus* Bate, a terrestrial ungulate that must be considered a key species in the ecosystem. If the size of the island alone was the key factor in determining its fauna, the late Pleistocene fossil avifauna from Menorca would have been similar to that of Eivissa. But if the island's ecology has greater importance in determining its fauna, as we postulate, the late Pleistocene avifauna from Menorca will cluster with that of Mallorca, where *Myotragus* also was present.

CATALAN SUMMARY

La comparació entre les avifaunes pleistocèniques de les illes de la Mediterrània occidental (Gimnèsies, Pitiüses, Massís cirnosard) documenta l'existència de dues castes de comunitats ornítiques en el passat: una a les illes habitades per mamífers terrestres (Gimnèsies, Còrsega, i Sardenya) i l'altra a les illes que no en contenen (Pitiüses). Les comunitats ornítiques pitiüses troben el seu paral.lelisme més evident a les comunitats ornítiques prehumanes de les Hawaii, mentre que les comunitats ornítiques de les altres illes de la Mediterrània Occidental s'addiuen més amb les de les illes de la Mediterrània Oriental. El factor clau per entendre l'estructuració de les comunitats ornítiques insulars mediterrànies del Pleistocè sembla esser la presència/absència de mamífers herbívors de talla mitjana (*Myotragus balearicus* Bate a les Gimnèsies i *Megaceros caziotti* (Depéret) al massís cirno-sard).

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A New Species of Extinct Barn Owl (Aves: *Tyto*) from Barbuda, Lesser Antilles

David W. Steadman and William B. Hilgartner

ABSTRACT

A new species of extinct barn owl, *Tyto neddi*, is described from six bones discovered in a late Quaternary cave deposit on Barbuda, Lesser Antilles, West Indies. *Tyto neddi* is the first extinct species of barn owl known from the Lesser Antilles. It appears to be most closely related to the several large, extinct species of *Tyto* known from late Quaternary cave deposits in the Greater Antilles and Bahamas. By far, the most abundantly represented species of vertebrate at the type locality of *T. neddi* is a large, extinct oryzomyine rodent (genus and species undescribed) that probably was the primary prey item of *T. neddi*. A single pedal phalanx from the type locality of *T. neddi* represents a much smaller species of *Tyto* that is the size of the extant *T. alba* (Scopoli). Bones of the Burrowing Owl, *Athene* (*Speotyto*) *cunicularia* (Molina), also occur commonly in Barbudan caves. Thus Barbuda, where no species of owl occurs today, once supported at least three species.

Introduction

During 16–24 January 1983, DWS was part of a team (see Acknowledgments) that surveyed modern and prehistoric vertebrates on Barbuda, Leeward Islands, Lesser Antilles (Figure 1). Although no deep, stratified bone deposits were found, we did collect hundreds of vertebrate fossils from several small, shallow, sediment accumulations in a limestone cave system at Gun Shop Cliff on Barbuda's northeastern coast. At least 42 indigenous species of reptiles, birds, and mammals are known from these and other prehistoric sites on Barbuda, which has a fossil vertebrate fauna exceeded in the Lesser Antilles only on nearby Antigua (Pregill et al., 1994).

The most common species in the Barbudan sites by far is a large, undescribed, extinct cricetid rodent (Oryzomyini, genus and species undescribed), which would suggest that a large owl was responsible for the bone deposits in these caves. Bones of owls, however, are often scarce in Quaternary fossil deposits on islands, even in deposits that the owls helped to create (Steadman, 1986). In spite of the abundance of cricetid rodent bones in prehistoric sites from both Barbuda and Antigua (Ray, 1962; Steadman et al., 1984; Watters et al., 1984), evidence of any large species of owl was lacking on these islands and elsewhere in the Lesser Antilles until we found six bones of a large species of *Tyto* in a small solution cavity at Gun Shop Cliff known as "Rat Pocket."

Five extinct species of barn owls (Tytonidae: *Tyto*) are known from bone deposits in the Greater Antilles and Bahamas. Four of these are larger than any extant West Indian spe-

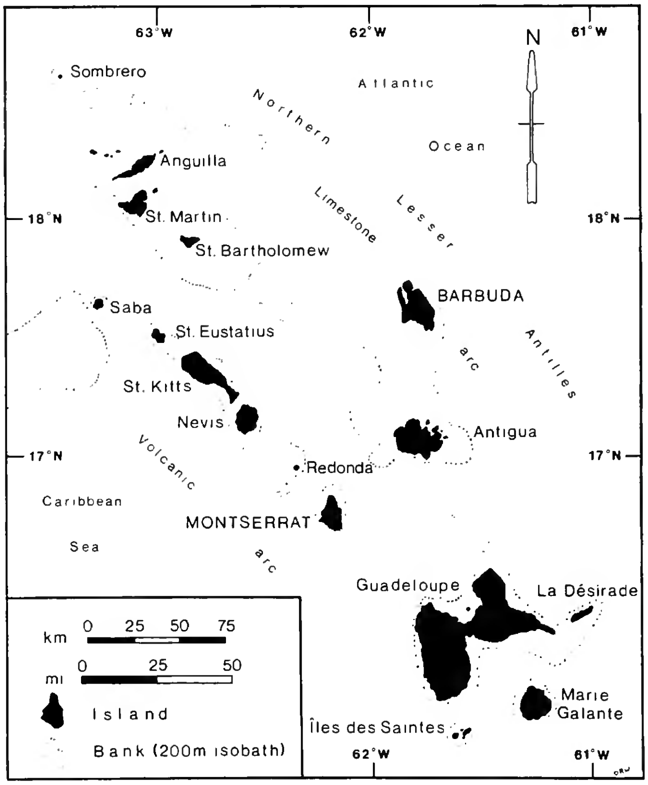

FIGURE 1.—The Leeward Islands of the Lesser Antilles, West Indies.

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cies of *Tyto* (see "Discussion"). In this paper we describe from Barbuda a fifth large West Indian species of *Tyto*. We note as well the bones of two other species of owls from Barbuda, an island that lacks owls today.

MATERIALS AND METHODS.—The partially mineralized bones of *Tyto* from Barbuda are housed in the Vertebrate Paleontology Collection of the National Museum of Natural History, Smithsonian Institution (housing the collections of the former United States National Museum (USNM)). Modern comparative skeletons are from the USNM, the Florida Museum of Natural History (UF), and the New York State Museum. Prehistoric bones of *T. ostologa* Wetmore (1922b) from Hispaniola are from the USNM (especially St. Michel, Cave 1, Haiti, collected in 1928 by A.J. Poole; see Wetmore, 1922b, 1959; Miller, 1926, 1929; Wetmore and Swales, 1931) and the UF (sorted by DWS from various sites excavated from 1978 to 1984 by C.A. Woods and colleagues; see Woods et al., 1985). Specimens of *T. punctatissima* (G.R. Gray) from Holocene cave deposits in the Galápagos Islands are housed at the USNM (Steadman, 1986; Steadman and Zousmer, 1988). Certain osteological nomenclature follows Baumel et al. (1993).

ACKNOWLEDGMENTS.—We thank the government and people of Barbuda, especially Hillborn Frank, Morris Nedd, and Johnny DiSouza for their generous cooperation during our visit. Able field associates on Barbuda were R.I. Crombie, J.P. Dean, G.K. Pregill, C.L. Watters, and D.R. Watters. Field work was sponsored by the National Science Foundation (grant DEB-8207347 to G.K. Pregill), the Smithsonian Institution (Scholarly Studies Program, Alexander Wetmore Fund), and the Carnegie Museum of Natural History. Museum research was supported in part by the National Science Foundation (grant BSR-8607535 to DWS). S.L. Olson (USNM) and C.A. Woods (UF) kindly provided access to collections. L.J. Justice and E.S. Wootan helped to prepare the manuscript. For comments on the manuscript, we thank M.R. Browning, S.L. Olson, G.K. Pregill, D.R. Watters, and C.A. Woods. The photographs are by V.E. Krantz (USNM).

Systematics

Class AVES

Order STRIGIFORMES

Family TYTONIDAE

The bones are referred to the Tytonidae and the genus *Tyto* rather than to the Strigidae because of the following characters.

Femur with proximal portion of crus condylus lateralis rather pointed (not squared) in posterior aspect; condylus lateralis extends farther posteriorly beyond trochlea fibularis in lateral aspect. Coracoid with foramen nervus supracoracoidei relatively small; processus procoracoideus sterno-humerally elongate; facies articularis clavicularis nonpneumatic and confined to humeralmost portion of bone. Pedal phalanges with condyles (distal articulations) narrow relative to overall size of bones.

Tyto neddi, new species

HOLOTYPE.—Right femur, USNM 359240 (Figure 2), collected on 19–20 January 1983 by D.W. Steadman, G.K. Pregill, D.R. Watters, R.I. Crombie, and J.P. Dean.

TYPE LOCALITY.—Rat Pocket, Gun Shop Cliff, Two Foot Bay, Barbuda.

HORIZON AND AGE.—Unstratified; late Quaternary, probably late Pleistocene or early Holocene.

Because the deposit lacked organic materials, such as charcoal or unmineralized bone for radiocarbon dating, we were unable to refine the chronology of this site beyond being late Quaternary.

PARATYPES.—Left coracoid, USNM 359245 (Figure 3); left pedal digit I, phalanx 1, USNM 359242 (Figure 4); left pedal digit II, phalanx 1, USNM 359243 (Figure 5); left pedal digit III, phalanx 2, USNM 359241 (Figure 6); juvenile pedal phalanx (either digit II, phalanx 1; digit III, phalanx 3; or digit IV, phalanx 4), USNM 359244 (not figured).

FIGURE 2.—Right femur of *Tyto* in caudal aspect: A, *T. ostologa*, St. Michel (Cave 1), Haiti, USNM uncataloged; B, *T. neddi*, holotype, Barbuda, USNM 359240; C, *T. alba furcata*, male, Jamaica, USNM 553575. (Scale=10 mm.)

All material collected 19–20 January 1983 by D.W. Steadman, G.K. Pregill, D.R. Watters, R.I. Crombie, and J.P. Dean.

ETYMOLOGY.—We name this species after Mr. Morris Nedd, a resident of Barbuda generally known by his nickname "Tomac." Barbuda's premier naturalist, Tomac guided us to many caves in 1983, including the type locality of *Tyto neddi.*

DIAGNOSIS.—A large species of *Tyto* that is slightly smaller than *T. ostologa,* slightly larger than *T. noeli* Arredondo (1972a), and either much larger or much smaller than all other New World insular species of *Tyto* (Tables 1–5).

Compared to *Tyto ostologa,* femur with larger and deeper impressio ansae musculo iliofibularis, deeper depression on medial side of condylus medialis, and tuberculum musculo gastrocnemius lateralis placed more proximally; coracoid with larger foramen nervus supracoracoidei; and pedal phalanges proportionately more robust.

Discussion

BIOGEOGRAPHY.—*Tyto neddi* is part of a late Quaternary Barbudan avifauna that included 15 species of birds that no longer occur on the island (Pregill et al., 1994). Antigua and Barbuda were coalesced into a single, large island during Quaternary glacial intervals (Pregill et al., 1988). Thus it is likely that *T. neddi* also occurred on Antigua. *Tyto neddi* also is the sixth extinct species of barn owl to be described from West Indian Quaternary fossil deposits and is the first described from the Lesser Antilles. Arredondo (1976) reviewed the large extinct tytonids in the Greater Antilles and Bahamas, particularly those from Cuba, where two large species once existed (*T. noeli* and the extremely large *T. riveroi* Arredondo, 1972b). Single large species of *Tyto* are known from Hispaniola (*T. ostologa,* which is geographically the closest to *T. neddi* of all large congeners (see Figure 8)) and the Bahamas (*T. pollens* Wetmore, 1937). A smaller extinct species (*T. cavatica* Wetmore, 1920) inhabited Puerto Rico (see also Wetmore, 1922a). Although no extinct species of *Tyto* are known from Jamaica (Olson and Steadman, 1977; Pregill et al., 1991), this may be an artifact reflecting how few avian fossils have been recovered and studied from Jamaica.

From the same bone deposit as the type material of *Tyto neddi* is an ungual phalanx (digit II, phalanx 3), USNM 453559 (Figure 7), that we cannot distinguish quantitatively (Table 6) or qualitatively from digit II, phalanx 3, of modern specimens of *T. alba* (Scopoli). We assign the specimen to digit II, phalanx 3, based on the uniform roundness of the dorsal surface, the relatively flattened ventral surface, and the relatively rounded (less oblong) articular surface. USNM 453559, which represents an adult bird, is not an adequate basis for species-level identification. Its similarity in size to the same phalanx in *T. alba* means that USNM 453559 is smaller than in *T. neddi,* even though digit II, phalanx 3, is not available for *T. neddi.*

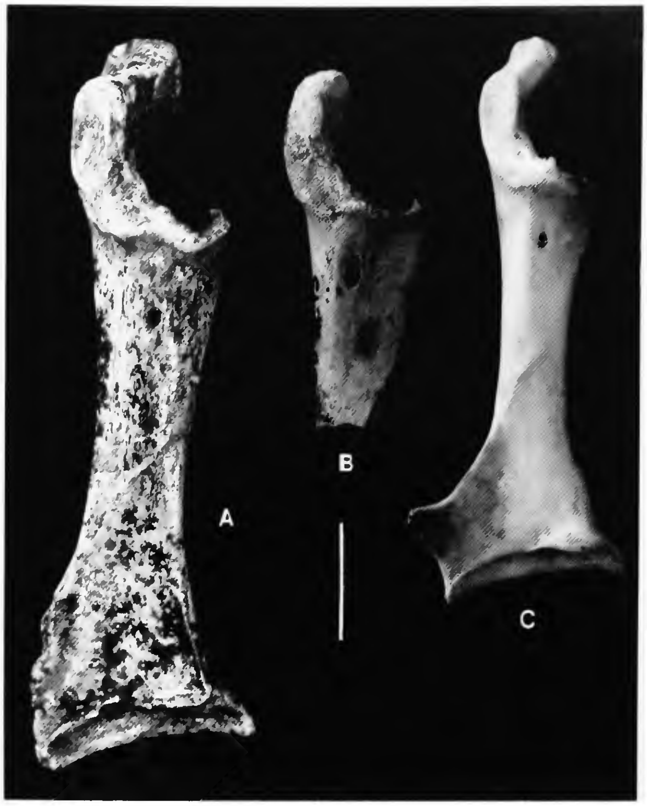

FIGURE 3.—Left coracoid of *Tyto* in dorsal aspect: A, *T. ostologa,* St. Michel (Cave 1), Haiti, USNM uncataloged; B, *T. neddi,* paratype, Barbuda, USNM 359245; C, *T. alba furcata,* male, Jamaica, USNM 553575. (Scale=10 mm.)

The taxa of *Tyto* that reside today in the Greater Antilles are

TABLE 1.—Measurements (mm) of the coracoid in New World species of *Tyto,* with mean ($\bar{x}$), range, and sample size (*n*). (Glenoid facet=facies articularis humeralis; coracoidal foramen=foramen nervus supracoracoidei.)

Species	Locality	Length of glenoid facet			Width at coracoidal foramen			Depth at coracoidal foramen		
		$\bar{x}$	range	*n*	$\bar{x}$	range	*n*	$\bar{x}$	range	*n*
T. neddi	Barbuda	9.4		1	7.4		1	3.9		1
T. ostologa	Hispaniola	10.7	10.6–10.7	4	8.9	8.7–9.3	3	5.2	4.6–5.7	6
T. alba pratincola	North America	7.3	6.7–8.2	11	6.2	5.5–6.6	11	3.7	3.1–4.0	11
T. alba furcata	Jamaica, Haiti, Cuba	7.8	7.0–8.8	8	6.4	5.9–7.0	8	4.1	3.7–4.4	8
T. glaucops	Hispaniola	6.2	5.6–6.8	2	6.1	6.0–6.2	2	3.4	3.3–3.5	2
T. punctatissima	Galápagos Islands	5.2	4.9–5.4	4	4.9	4.8–5.0	2	2.9	2.8–3.0	4

FIGURE 4.—Left pedal digit I, phalanx 1, of *Tyto* in dorsal (A–C), plantar (D–F), and lateral (G–I) aspects: A,D,G, *T. ostologa*, St. Michel (Cave 1), Haiti, USNM uncataloged; B,E,H, *T. neddi*, paratype, Barbuda, USNM 359242; C,F,I, *T. alba furcata*, male, Jamaica, USNM 553575. (Each scale=10 mm.)

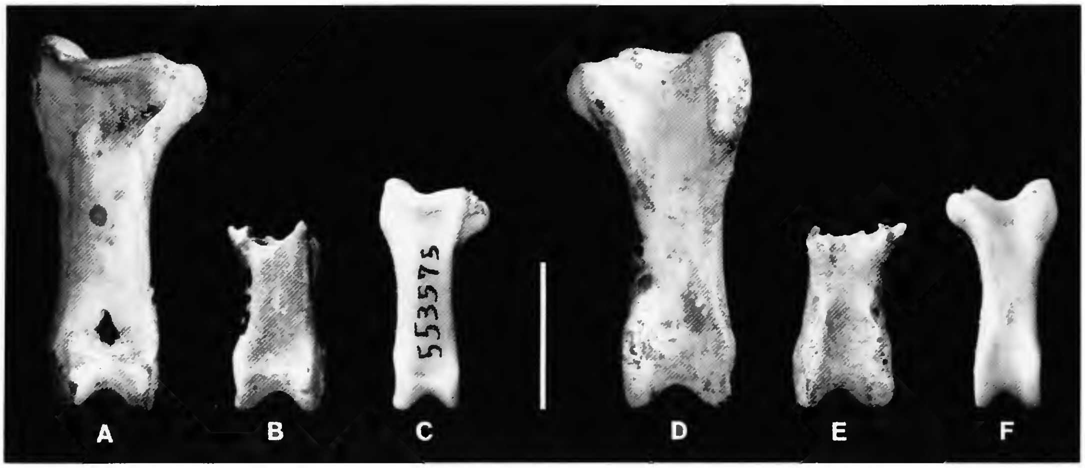

FIGURE 5.—Left pedal digit II, phalanx 1, of *Tyto* in dorsal (A–C) and plantar (D–F) aspects: A,D, *T. ostologa*, St. Michel (Cave 1), Haiti, USNM uncataloged; B,E, *T. neddi*, paratype, Barbuda, USNM 359243; C,F, *T. alba furcata*, male, Jamaica, USNM 553575. (Scale=10 mm.)

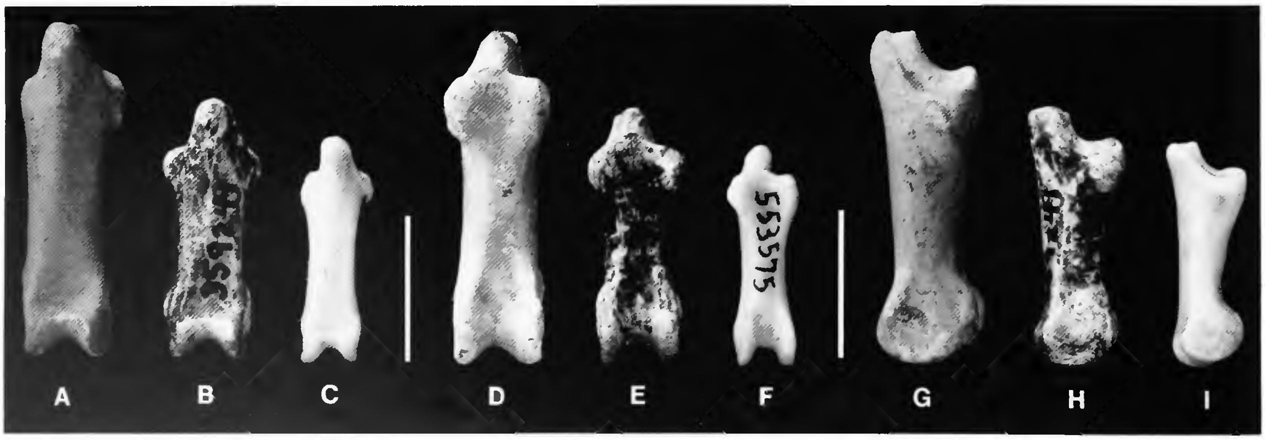

FIGURE 6.—Left pedal digit III, phalanx 2, of *Tyto* in dorsal (A–C), plantar (D–F), and lateral (G–I) aspects: A,D,G, *T. ostologa*, St. Michel (Cave 1), Haiti, USNM uncataloged; B,E,H, *T. neddi*, paratype, Barbuda, USNM 359241; C,F,I, *T. alba furcata*, male, Jamaica, USNM 553575. (Each scale=10 mm.)

T. alba furcata (Temminck) in the Bahamas, Cuba, Jamaica, and Cayman Islands, *T. alba niveicauda* Parkes and Phillips (1978) on Isle of Pines, and *T. glaucops* (Kaup), endemic to Hispaniola (Ridgway, 1914:612–613; Wetmore and Swales, 1931; Parkes and Phillips, 1978). The only race of *T. alba* currently recognized for North American populations, *T. a. pratincola* (Bonaparte), has been recorded in the nonbreeding season on Cuba (Garrido, 1978) and Hispaniola (Schwartz and Klinikowski, 1965). In the Lesser Antilles, *T. alba* may be represented by *T. "a." nigrescens* (Lawrence) on Dominica and *T. "a." insularis* (Pelzeln) on St. Lucia, St. Vincent, Bequia, Carriacou, Union, and Grenada (Peters, 1940; Bond, 1956, 1980; Evans, 1990). These two forms are smaller and darker than other Antillean subspecies of *T. alba* and, like *T. glaucops*, may deserve recognition as a single distinct species (Ridgway, 1914:613–615). The current absence of *Tyto* on the northern (leeward) islands of the Lesser Antilles (including Barbuda) is without obvious ecological or biogeographic explanation. Thus it is not surprising that a smaller species of *Tyto* (but larger than *T. "a." nigrescens* or *T. "a." insularis*) once occurred on Barbuda.

The West Indian species of *Tyto* can be arranged into a size progression (see references above and Tables 1–6, herein) from smallest to largest, as follows (*=extinct): (1) *T. glaucops;* (2) **T. cavatica;* (3) *T.* [*alba*?] *nigrescens, T.* [*alba*?] *insularis;* (4) *T. alba furcata, T. alba pratincola, T.* sp. (Barbuda); (5) **T. noeli;* (6) **T. neddi;* (7) **T. ostologa;* (8) **T. pollens;* and (9) **T. riveroi.* We have not seen skeletons of *T. nigrescens* or *T. insularis,* although skins of these taxa are consistently smaller than those of *T. alba furcata* or *T. a. pratincola* in all external measurements (Ridgway, 1914:601–615). Also, whereas measurements of the skeletal elements in Tables 1–6 are not available for *T. riveroi,* the measurements and photographs of other elements of *T. riveroi* reveal a size about 10% larger than that of *T. ostologa* and 30%–40% larger than that of *T. noeli* (Arredondo, 1972a, 1972b, 1976, 1982). The only other New World species of tytonid is *T. punctatissima,* which is endemic to the Galápagos Islands (Steadman, 1986) and is smaller than any of the West Indian species (Tables 1, 2).

Large extinct species of *Tyto* are not confined to the West Indies. *Tyto balearica* Mourer-Chauviré, Alcover, Moya, and Pons (1980) and *T. melitensis* (Lydekker, 1891) were described from middle and late Pleistocene deposits on the Mediterranean islands of Mallorca and Menorca and of Malta, respectively (Alcover et al., 1992). The geochronologic and geographic range of *T. balearica* has been extended to the late Miocene and Pliocene of mainland Spain (Mourer-Chauviré and Sánchez, 1988; Cheneval and Adrover, 1995). From the Miocene of the Gargano Peninsula in Italy are two species of *Tyto* (*robusta* Ballmann, 1973, *gigantea* Ballmann, 1976) that are each larger than any living congeners (Ballmann, 1973, 1976; Olson, 1978; Mourer-Chauviré et al., 1980). In spite of a

TABLE 2.—Measurements (mm) of the femur in New World species of *Tyto*, with mean ($\bar{x}$), range, and sample size (*n*). Values for *T. noeli* are from Arredondo (1976).

Species	Locality	Distal width			Depth of inner condyle			Least depth between condyles		
		$\bar{x}$	range	*n*	$\bar{x}$	range	*n*	$\bar{x}$	range	*n*
T. neddi	Barbuda	15.4		1	11.1		1	5.1		1
T. ostologa	Hispaniola	17.3	16.5–18.3	9	12.9	12.5–13.6	5	6.4	6.0–6.7	5
T. noeli	Cuba	14.4	14.0–14.8	2	–	–	–	–	–	–
T. pollens	Bahamas	18.1		1	–	–	–	–	–	–
T. alba pratincola	North America	11.8	10.9–12.9	11	8.4	7.8–9.4	11	4.0	3.6–4.7	11
T. alba furcata	Jamaica, Haiti, Cuba	11.9	11.4–12.8	8	7.7	7.1–8.9	8	4.7	4.4–5.1	8
T. glaucops	Hispaniola	11.0	10.8–11.1	2	6.6	6.5–6.7	2	4.2	4.1–4.4	2
T. punctatissima	Galápagos Islands	8.5	8.4–8.6	4	5.4	5.2–5.6	4	3.6	3.5–3.8	5

TABLE 3.—Measurements (mm) of pedal digit I, phalanx 1, in New World species of *Tyto*, with mean ($\bar{x}$), range, and sample size (*n*).

Species	Locality	Statistic	Total length	Proximal width	Proximal depth	Least width shaft	Least depth shaft	Distal width	Distal depth
T. neddi	Barbuda	$\bar{x}$	18.3	7.3	7.6	4.6	3.7	5.5	6.1
		range							
		n	1	1	1	1	1	1	1
T. ostologa	Hispaniola	$\bar{x}$	23.5	7.7	9.1	5.3	4.5	6.1	6.0
		range	23.1–24.3	7.5–7.9	8.7–9.6	5.2–5.3	4.4–4.9	6.0–6.3	6.8–7.1
		n	5	5	5	5	5	5	5
T. alba pratincola	North America	$\bar{x}$	14.0	4.9	5.4	3.0	2.5	3.6	4.4
		range	13.4–14.9	4.6–5.2	4.9–5.9	2.8–3.3	2.2–2.8	3.1–4.1	4.1–4.8
		n	11	11	11	11	11	11	11
T. alba furcata	Jamaica, Cuba	$\bar{x}$	15.1	5.2	5.8	3.3	2.7	3.7	4.7
		range	14.0–15.8	4.9–5.3	5.5–6.0	3.1–3.4	2.4–2.9	3.6–3.8	4.4–4.9
		n	4	4	4	4	4	4	4
T. glaucops	Hispaniola	$\bar{x}$	12.0	4.6	4.5	2.7	2.1	3.2	3.8
		range							
		n	1	1	1	1	1	1	1

TABLE 4.—Measurements (mm) of pedal digit II, phalanx 1, in New World species of *Tyto*, with mean ($\bar{x}$), range, and sample size (n).

Species	Locality	Least shaft width			Least shaft depth			Distal width		
		$\bar{x}$	range	n	$\bar{x}$	range	n	$\bar{x}$	range	n
T. neddi	Barbuda	5.1		1	4.3		1	6.2		1
T. ostologa	Hispaniola	6.0	5.9–6.0	3	5.4	5.3–5.4	3	7.0	6.9–7.1	3
T. alba pratincola	North America	3.5	3.3–3.8	11	3.1	2.6–3.6	11	4.1	3.8–4.5	11
T. alba furcata	Jamaica, Cuba	3.7	3.6–3.8	4	3.3	3.2–3.4	4	4.5	4.3–4.7	4
T. glaucops	Hispaniola	3.2		1	2.6		1	3.7		1

TABLE 5.—Measurements (mm) of pedal digit III, phalanx 2, in New World species of *Tyto*, with mean ($\bar{x}$), range, and sample size (n).

Species	Locality	Statistic	Total length	Proximal width	Proximal depth	Least shaft width	Least shaft depth	Distal width	Distal depth
T. neddi	Barbuda	$\bar{x}$	18.0	7.0	6.5	4.4	3.8	6.1	5.6
		range							
		n	1	1	1	1	1	1	1
T. ostologa	Hispaniola	$\bar{x}$	23.8	7.5	7.9	5.0	4.6	6.4	7.3
		range	22.8–24.4	7.2–8.0	7.5–8.5	4.7–5.5	4.4–4.8	5.9–6.7	7.0–7.6
		n	11	13	11	13	13	13	11
T. alba pratincola	North America	$\bar{x}$	14.6	4.5	5.0	3.0	2.7	3.8	4.4
		range	14.2–15.6	4.3–5.1	4.9–5.3	2.7–3.3	2.5–3.0	3.6–4.2	4.1–4.7
		n	11	11	11	11	11	11	11
T. alba furcata	Jamaica, Cuba	$\bar{x}$	15.6	4.9	5.4	3.2	2.8	4.0	4.6
		range	14.9–16.3	4.7–5.1	5.2–5.5	3.1–3.3	2.7–2.9	3.7–4.3	4.5–4.7
		n	4	4	4	4	4	4	4
T. glaucops	Hispaniola	$\bar{x}$	12.4	4.1	4.2	2.8	2.3	3.2	3.4
		range							
		n	1	1	1	1	1	1	1

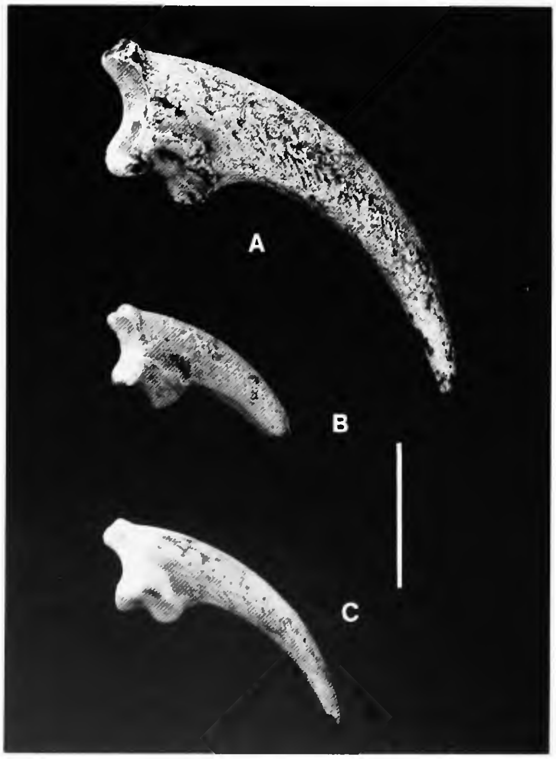

FIGURE 7.—Ungual phalanx (digit II, phalanx 3) of *Tyto* in lateral aspect: A, *T. ostologa*, St. Michel (Cave 1), Haiti, USNM uncataloged; B, *Tyto* sp., Barbuda, USNM 453559; C, *T. alba furcata*, male, Jamaica, USNM 553575. (Scale = 10 mm.)

TABLE 6.—Measurements (mm) of the ungual phalanx (digit II, phalanx 3) in New World species of *Tyto*, with mean ($\bar{x}$), range, and sample size (n).

Species	Locality	Articulation width			Articulation depth		
		$\bar{x}$	range	n	$\bar{x}$	range	n
T. ostologa	Hispaniola	7.6	7.2–8.1	6	9.6	9.4–9.8	6
T. alba pratincola	North America	4.7	4.4–5.0	8	5.6	5.2–5.9	8
T. alba furcata	Jamaica, Cuba	4.8	4.5–5.0	4	5.7	5.2–6.1	4
Tyto sp.	Barbuda	5.3		1	5.9		1
T. glaucops	Haiti	4.4		1	5.0		1

fairly rich fossil record of birds, no large extinct species of *Tyto* have been reported from the Canary or other island groups in the North Atlantic (Báez, 1992; Alcover and McMinn, 1995).

No species of owls live on Barbuda today, where the prehistoric bones now reveal the former occurrence of at least three owl species (two tytonids and one strigid). Nowhere in the West Indies today does more than a single resident species of tytonid owl survive. Prehistorically, however, three species of *Tyto* are known from Cuba (Arredondo, 1976, 1982) and two from Hispaniola (Wetmore and Swales, 1931). The single species of strigid owl from the Barbudan caves, *Athene cunicularia* (Molina), is the only species of strigid recorded anywhere in the Lesser Antilles, whereas individual major islands in the Greater Antilles once sustained at least three to seven species of strigid owls in the genera *Otus, Gymnoglaux, Bubo, Ornimegalonyx, Glaucidium, Athene, Pulsatrix, Asio,* and *Pseudoscops* (Arredondo, 1976, 1982; Arredondo and Olson, 1994).

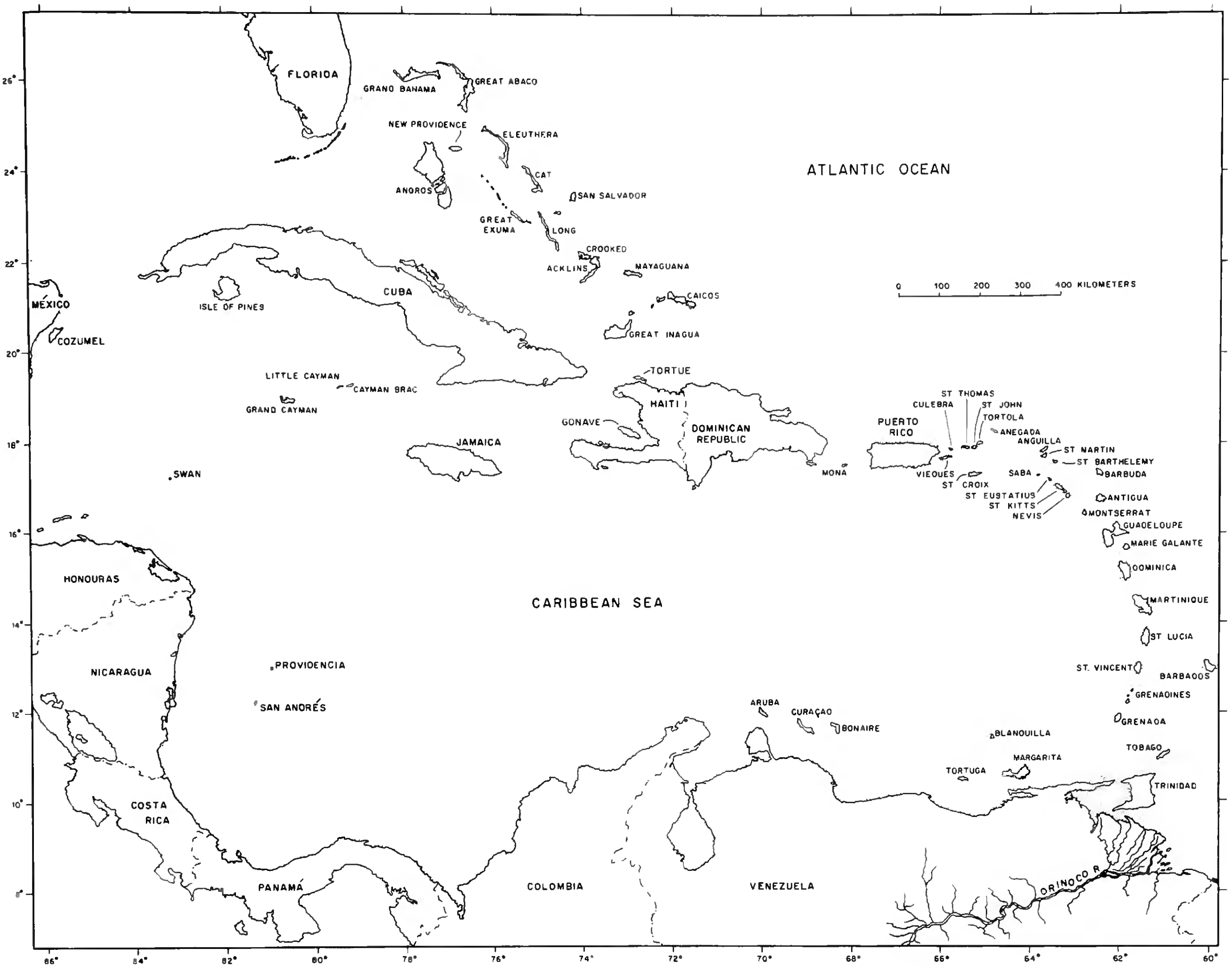

FIGURE 8.—The West Indies.

EVOLUTION AND PALEOECOLOGY.—The available specimens of *T. neddi* are not adequate to evaluate whether it is derived from a Greater Antillean large species of *Tyto* or whether it evolved autochthonously from a smaller Lesser Antillean species. The evolution of tytonid owls in the West Indies may be linked to their prey (primarily rodents and insectivores, to a lesser extent ground sloths, primates, bats, amphibians, reptiles, and birds) and perhaps as well to interactions with strigid owls. This can be evaluated only through the fossil record because most indigenous species of West Indian barn owls and nonvolant mammals became extinct in the late Quaternary.

West Indian insectivores, primates, and ground sloths were confined to the Greater Antilles (Morgan and Woods, 1986; MacPhee and Iturralde-Vinent, 1994, 1995). The short toes of *T. neddi* (relative to those of *T. ostologa*) may reflect a diet focused more exclusively on rodents. The longer toes of the Hispaniolan *T. ostologa* may have been advantageous when hunting arboreal primates or thick-skinned edentates.

Two great radiations of rodents occurred in the West Indies: caviomorphs, mainly in the Greater Antilles and Bahamas (Woods, 1989), and oryzomyines, primarily in the Lesser Antilles (Ray, 1962; Woods, 1989; Pregill et al., 1994). Nearly all of the species in the former radiation and every species in the latter one are now extinct. All of the extinct caviomorph rodents and many of the extinct oryzomyine rodents are larger than the typical prey of *Tyto alba* today. Thus an approximate correlation with size of prey, especially of rodents, might account for the large size of most of the extinct West Indian species of *Tyto*. The undescribed, extinct oryzomyine from Barbuda (and Antigua) was larger than a large packrat (*Neotoma* spp.) but smaller than a muskrat (*Ondatra zibethicus* (Linnaeus)). Considering age-related size variation, adults of this rodent seem well suited as prey for *T. neddi,* whereas the juveniles would be appropriate for the smaller species of *Tyto* that lived on Barbuda.

The extinction of the various large species of *Tyto* was probably related to loss of their preferred prey species. Because the stratigraphy and/or chronology of West Indian fossil *Tyto* are so poorly documented, it is uncertain whether most of the extinct tytonids survived into the Holocene or became extinct in the late Pleistocene. Extensive anthropogenic change has occurred in the terrestrial habitats of Barbuda and Antigua, both in prehistoric and in historic times (Harris, 1965; Steadman et al., 1984; Pregill et al., 1988). On both Barbuda and Antigua, the extinct oryzomyine rodent survived into the late Holocene, being recorded commonly in archaeological sites (Watters et al., 1984, 1992; Pregill et al., 1994). This would suggest that *Tyto neddi* also may have survived into the last millennium or two.

The Burrowing Owl is too small to have fed upon the large extinct cricetid rodent that dominates the Barbudan fossil assemblages. In the West Indies, *Athene cunicularia* seems to have eaten mainly insects, amphibians, and reptiles (Steadman et al., 1984). Conversely, predation from the much larger *Tyto neddi* and *Tyto* sp. may explain why bones of *A. cunicularia* occur commonly in the bone deposits on Barbuda and Antigua.

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The History of the Chatham Islands' Bird Fauna of the Last 7000 Years—A Chronicle of Change and Extinction

Philip R. Millener

ABSTRACT

Over the past 150 years, thousands of fossil bones of extinct and living species of birds have been collected from the Chatham Islands, an isolated island group some 860 km east of New Zealand. Recent field research (1988–1993) has dramatically augmented the earlier collections and has provided, for the first time, a sound stratigraphic and radiometric chronology for this rich subfossil avifauna. Most of these bones have been found naturally deposited in the buried soil horizons of coastal sand dunes or in limestone caves, but some are of archeological origin, deposited by human agency in coastal dune middens or, occasionally, in dwelling caves. Most, if not all, of the avian remains are of early Holocene or younger age, as indicated by a series of some 65 accelerator-mass-spectometry radiocarbon dates ranging from ca. 7000 yrs BP to ca. 300 yrs BP. The Holocene fossil record for, and patterns of evolution and extinction within, the Chatham Islands' avifauna are documented and discussed. Taxonomic studies indicate that several taxa, all extinct, can no longer be considered inseparable from their mainland counterparts; among these are as yet undescribed species of *Eudyptes, Tadorna, Mergus,* and *Nestor.*

Introduction

Dune sands and cave sediments on the Chatham Islands (Figure 1) have yielded thousands of Holocene fossil bones of extinct and living species of birds (Forbes, 1892a, 1892b, 1892c, 1893a, 1893b; Andrews, 1896a, 1896b; Scarlett, 1955; Dawson, 1957, 1958, 1959, 1960, 1961a, 1961b; Simmons, 1964; Olson, 1975, 1984, 1990; Sutton and Marshall, 1977; Sutton, 1979, 1982; Millener, 1981, 1991, 1996; Tennyson and Millener, 1994). The Museum of New Zealand, Wellington, for example, holds more than 250,000 Chatham Islands fossil specimens, whereas extensive additional material is housed at the Canterbury Museum, Christchurch, and in the Natural History Museum, London. The diversity of this fossil avifauna, which included many endemic land birds (among them several flightless forms), numerous waterfowl, and colonies of breeding subtropical and subantarctic seabirds, contrasts markedly with that of the present. The total number of bird species, living and extinct, recorded from the Chatham Islands is more than 100. The majority of them, some 60 species, are marine birds; among them are albatrosses, petrels and shearwaters, penguins, cormorants, waders, and gulls and terns (see Table 1). Only about 25 of these marine species currently breed in the Chathams, although formerly perhaps as many as seven more did so (Bourne, 1967). The remaining seabirds are summer migrants, occasional visitors, or vagrants. The rest of the birds (those of terrestrial and freshwater habitat) can be divided into three groups: (1) those present prior to first human contact; (2) those that self-colonized more recently, some of them within the historic period (e.g., Welcome Swallow (*Hirundo tahitica*), White-faced Heron (*Ardea novaehollandiae*), Spur-winged Plover (*Vanellus miles*)); and (3) those that have been deliberately introduced by Europeans (e.g., Black Swan (*Cygnus atratus*), Weka (*Gallirallus australis*), House Sparrow (*Passer domesticus*), Blackbird (*Turdus merula*), Song Thrush (*Turdus philomelos*), Starling (*Sturnus vulgaris*)). This paper is primarily concerned with the composition of the prehistoric Chatham Island avifauna, so the recent self-colonists and the deliberately introduced species are not considered further. Nomenclature for species' binomials and English names of modern birds follows Turbott (1990) unless otherwise noted.

METHODS

Radiometric ages quoted in this paper were determined by the Rafter Radiocarbon Laboratory, Institute of Geological and Nuclear Sciences, Gracefield, New Zealand, using accelerator

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TABLE 1.—Avian taxa identified from fossil deposits in the Chatham Islands. Fossil bones often cannot be identified to subspecies. Nevertheless, the subspecific epithets given in this table are those of the subspecies known to occur, or to have occurred, in the Chathams region. Nomenclature follows Turbott (1990) and Olson (1973; Rallidae) except where more recent revisions apply. For common names, "Chatham Island" is used for taxa endemic, fossil or living, to any of the islands in the Chathams' group. (*=extinct in Chathams in prehistoric period; *c.=extinct in Chathams within historic period, with date of last sighting or specimen; B=breeding; FB=formerly breeding; V=visitor or vagrant.)

Species	Common Name	Status
PROCELLARIIFORMES		
Diomedea exulans/D. e. epomophora	Wandering/Southern Royal Albatross	V/V,?FB/?FB
D. e. sanfordi	Northern Royal Albatross	B
D. cauta eremita	Chatham Island Mollymawk	B
D. bulleri platei	Northern Buller's Mollymawk	B
Phoebetria palpebrata	Light-mantled Sooty Albatross	V
Puffinus carneipes	Flesh-footed Shearwater	V
P. bulleri	Buller's Shearwater	V
P. griseus	Sooty Shearwater	B
P. tenuirostris	Short-tailed Shearwater	V
P. gavia/huttoni	Fluttering/Hutton's Shearwater	V/V
P. assimilis elegans	Subantarctic Little Shearwater	B
Pelecanoides u. urinatrix	Common Diving-petrel	B
Procellaria ?cinerea	Grey Petrel	V
P. parkinsoni	Parkinson's Petrel	V
P. ?westlandica	Westland Petrel	V
P. ?aequinoctialis	White-chinned Petrel	V
Daption capense australe	Snares Cape Pigeon	V
Fulmarus glacialoides	Antarctic Fulmar	V
Macronectes ?halli	Northern Giant Petrel	B
Pachyptila turtur	Fairy Prion	B
P. crassirostris pyramidalis	Chatham Island Fulmar Prion	B
P. vittata	Broad-billed Prion	B
Pterodroma nigripennis	Black-winged Petrel	B
P. axillaris	Chatham Petrel	B
P. cf. *inexpectata*	cf. Mottled Petrel	?FB
P. macroptera gouldi	Grey-faced Petrel	V
P. magentae	Magenta Petrel (Taiko)	B
P. lessonii	White-headed Petrel	V
Oceanites nereis	Grey-backed Storm Petrel	B
Pelagodroma marina maoriana	New Zealand White-faced Storm Petrel	B
Fregetta tropica	Black-bellied Storm Petrel	V
SPHENISCIFORMES		
Aptenodytes patagonicus	King Penguin	V
Megadyptes antipodes	Yellow-eyed Penguin	V
Eudyptula minor	Blue Penguin	B
Eudyptes species undescribed	"Chatham Island Crested Penguin"	*FB
PELECANIFORMES		
Morus serrator	Australasian Gannet	V
Sula dactylatra	Masked Booby	V
Phalacrocorax carbo novaehollandiae	Black Cormorant	B
Leucocarbo onslowi	Chatham Island Shag	B
Stictocarbo featherstoni	Pitt Island Shag	B
Fregata ariel	Lesser Frigatebird	V
CICONIIFORMES		
Botaurus poiciloptilus	Australasian Bittern	*c. 1910, FB
Ixobrychus novaezelandiae	New Zealand Little Bittern	*?FB
ANSERIFORMES		
Cygnus sumnerensis	New Zealand Swan	*FB
Tadorna, species undescribed	Chatham Island Shelduck	*FB
Anas s. superciliosa	Grey Duck	B
A. chlorotis	Brown Teal	*c. 1915, FB
Anas, species undescribed	Chatham Island Teal	*FB
A. rhynchotis variegata	New Zealand Shoveler	*c. 1925, ?FB
Pachyanas chathamica	Chatham Island Duck	*FB
Aythya novaeseelandiae	New Zealand Scaup	*FB
Mergus, species undescribed	Chatham Island Merganser	*FB
FALCONIFORMES		
Circus approximans	Australasian Harrier	B
Haliaeetus australis	Chatham Island Sea-eagle	*?FB
Falco novaeseelandiae	New Zealand Falcon	*c.1890, FB
GRUIFORMES		
Gallirallus dieffenbachii	Dieffenbach's Rail	*c. 1840, FB
G. modestus	Chatham Island Rail	*c. 1900, FB
Diaphorapteryx hawkinsi	Hawkins' Rail	*FB
Porzana tabuensis	Spotless Crake	B
P. pusilla	Marsh Crake	V
Fulica chathamensis	Chatham Island Coot	*FB
CHARADRIIFORMES		
Haematopus chathamensis	Chatham Island Pied Oystercatcher	B
Thinornis novaeseelandiae	Shore Plover	B
Arenaria interpres	Turnstone	V
Coenocorypha pusilla	Chatham Island Snipe	B
C. chathamica	Extinct Chatham Island Snipe	*FB
Calidris canutus	Lesser Knot	V
Numenius phaeopus ?hudsonicus	American Whimbrel	V
Catharacta skua lonnbergi	Brown Skua	
Larus d. dominicanus	Southern Black-backed Gull	B
L. novaehollandiae scopulinus	Red-billed Gull	B
Sterna albostriata	Black-fronted Tern	V
S. striata	White-fronted Tern	B
S. vittata/paradisea	Antarctic/Arctic Tern	V/V
S. nereis	Fairy Tern	V
COLUMBIFORMES		
Hemiphaga chathamensis	Chatham Island Pigeon	B
PSITTACIFORMES		
Nestor, species undescribed	"Chatham Island parrot"	*FB
Cyanoramphus novaezelandiae chathamensis	Chatham Island Red-crowned Parakeet	B
C. auriceps forbesi	Chatham Island Yellow-crowned Parakeet	B
CUCULIFORMES		
Chrysococcyx l. lucidus	Shining Cuckoo	B
PASSERIFORMES		
Anthus novaeseelandiae chathamensis	Chatham Island Pipit	B
Bowdleria rufescens	Chatham Island Fernbird	*c. 1900, FB
Gerygone albofrontata	Chatham Island Warbler	B
Rhipidura fuliginosa penita	Chatham Island Fantail	B

TABLE 1.—Continued

Species	Common Name	Status
Petroica macrocephala chathamensis	Chatham Island Tomtit	B
P. traversi	Black Robin	B
Anthornis melanura melanocephala	Chatham Island Bellbird	*c. 1906, FB
Prosthemadera novaeseelandiae chathamensis	Chatham Island Tui	B
Palaeocorax moriorum	New Zealand Crow	*FB

mass spectrometry (AMS) techniques on avian-bone collagen or marine-shell carbonate. Within the text, the reported age given for a specific sample (assigned a Rafter Radiocarbon Laboratory reference number, prefixed by NZA) is the conventional radiocarbon age before present (Stuiver and Polach, 1977). Such ages are expressed in the form "age ± standard deviation (SD) yrs BP." Calibrated ages to which the appropriate terrestrial or marine calibrations have been applied are expressed in the form "CAL BP" (see Stuiver and Braziunas, 1993; Stuiver and Pearson, 1993). Within the Appendix, both conventional and calibrated ages are given for each of the samples listed. Locality names (see Figure 1) and grid references for sampled sites are from New Zealand Topographical Map, New Zealand Map Series (NZMS) 260, 1:50000 series, Chatham Islands, Edition 1, 1981 (Chatham Island, sheet 1; Pitt Island, sheet 2).

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Site Descriptions and Avifaunal Analysis

Our knowledge of the Chatham Islands' prehistoric bird fauna comes from the detailed examination of the abundant fossil bones naturally deposited in coastal sand dunes and limestone caves as well as the archeological material deposited by human agency in coastal dune middens or dwelling caves. The AMS radiocarbon dates for more than 60 bone and shell samples (see Appendix for data and localities) have provided, for the first time, a sound stratigraphic and radiometric chronology for a broad selection of avian remains from a variety of depositional environments. Comparison of these fossil assemblages with the recent fauna indicates that 21 of the original 36 species of land birds or waterfowl have become extinct since human settlement began about 450 years ago (McFadgen, 1994) and that breeding populations of several seabirds have been reduced or eliminated. Of the original 100 or so avian taxa recorded, fossil or living, from the Chathams, only 25 marine and 15 terrestrial species (a total of 40) now breed there (see Table 1).

Fossil bird bones are known only from Chatham, Pitt, and Mangere islands. The remaining islands and rock stacks are typically steeply cliffed and lack extensive sand dunes, swamps, or caves that could have acted as repositories for bones.

SAND DUNE SITES

Coastal dune belts, in the form of a series of rows of progradational sand dunes, generally running parallel to the shore, and sometimes extending several hundred meters inland of it, are important physiographic features fringing all but the southern coasts of Chatham and Pitt islands. These dunes now are eroded into sequences of discontinuous ridges and hillocks. They began to form in their present positions only about 6500–7000 years ago, after the sea reached its approximate current level following the last (Otira) glacial low sea level of perhaps –120 meters (Hay et al., 1970). At least four depositional episodes, consisting of unstable phases with high rates of deposition followed by stable phases with the establishment of vegetative cover and soil formation, seem to have taken place over the last 7000 years. It is clear that periodic denudation, followed by erosion, must have removed parts of the stratigraphic sequence. Buried soils are frequently exposed as undulating bands, following the surface contours of the dunes upon whose surfaces they were formed (Figures 2–5). These soils consist of variously pale yellow, orange, or chocolate-brown/black- stained sand up to two meters thick, usually overlain by unconsolidated drift sand, rapidly deposited and marking the onset of the first (unstable) phase of the next depositional cy-

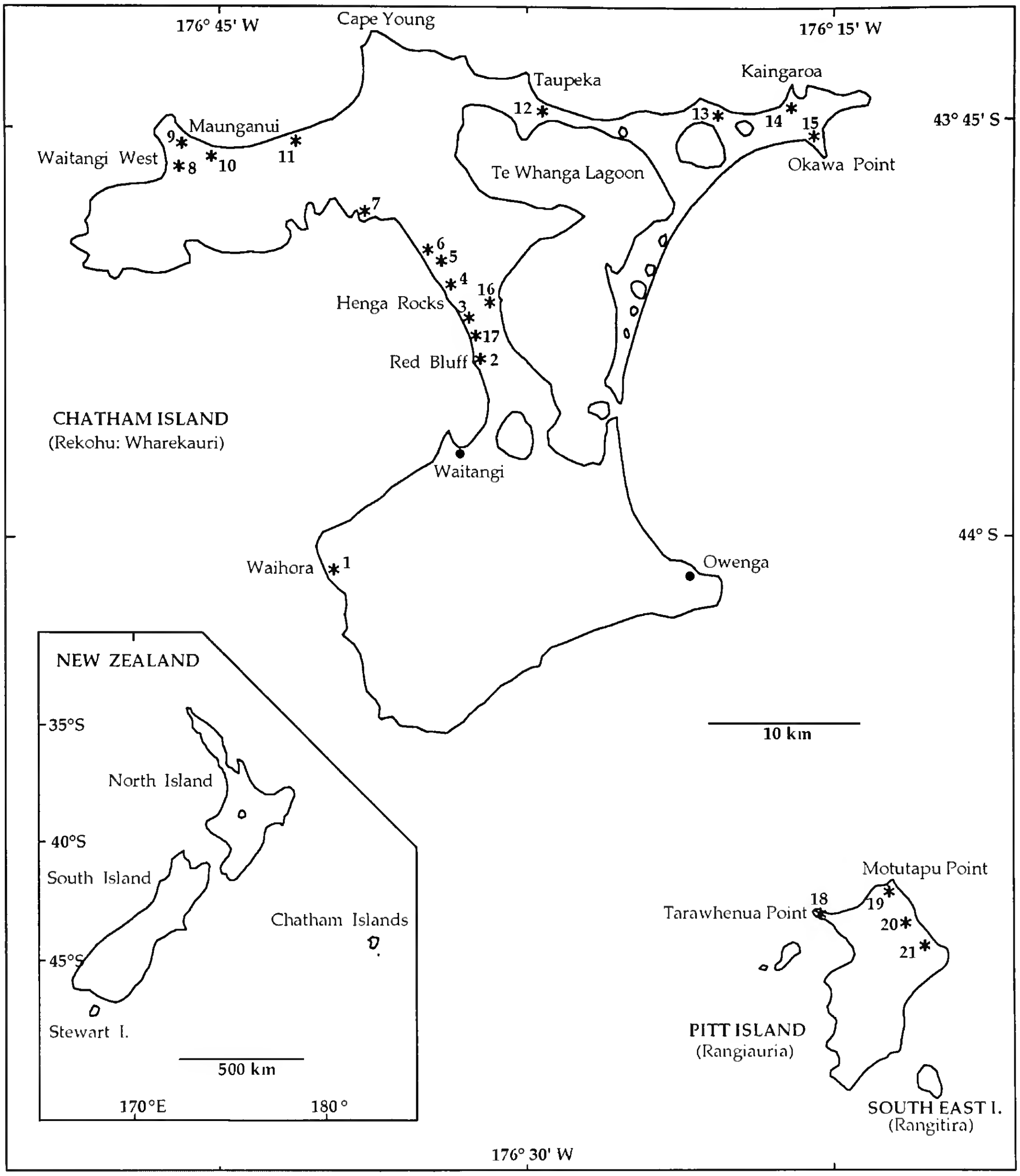


FIGURE 1.—Map of the Chatham Islands, showing their location relative to New Zealand (inset), and the positions of the 21 numbered sites from which radiocarbon dates (see "Appendix") were obtained.

cle. The older soils often exhibit quite complex soil profiles, indicative of lengthy stable periods. Such soils typically grade from a dark-stained, indurated erosion surface at the top, underlain by a grey-colored, strongly leached horizon, through variably consolidated, pale- to chocolate-brown sand, often markedly orange-stained through the formation of an incipient iron pan, and all underlain by unconsolidated, unstained sand at the base (see Wright, 1959; McFadgen, 1994). It seems likely that coastal forest vegetation clothed the slopes and ridges of these developing dunes for much of this period (especially during the stable, soil forming phases), whereas swamps and ephemeral brackish-water lakes filled interdune hollows, especially in low-lying areas behind the active foredunes. It was this mosaic of coastal forest, scrub, and swampland that provided habitat suitable for the various land birds, waterfowl, breeding seabirds, and land snails whose remains are now preserved within the sands. The abundant fossil bones are found in the sands and soils, often in situ as complete associated skeletons in (or recently eroded from) buried soil sequences on the flanks of hillocks or in lag deposits on the floors of the often

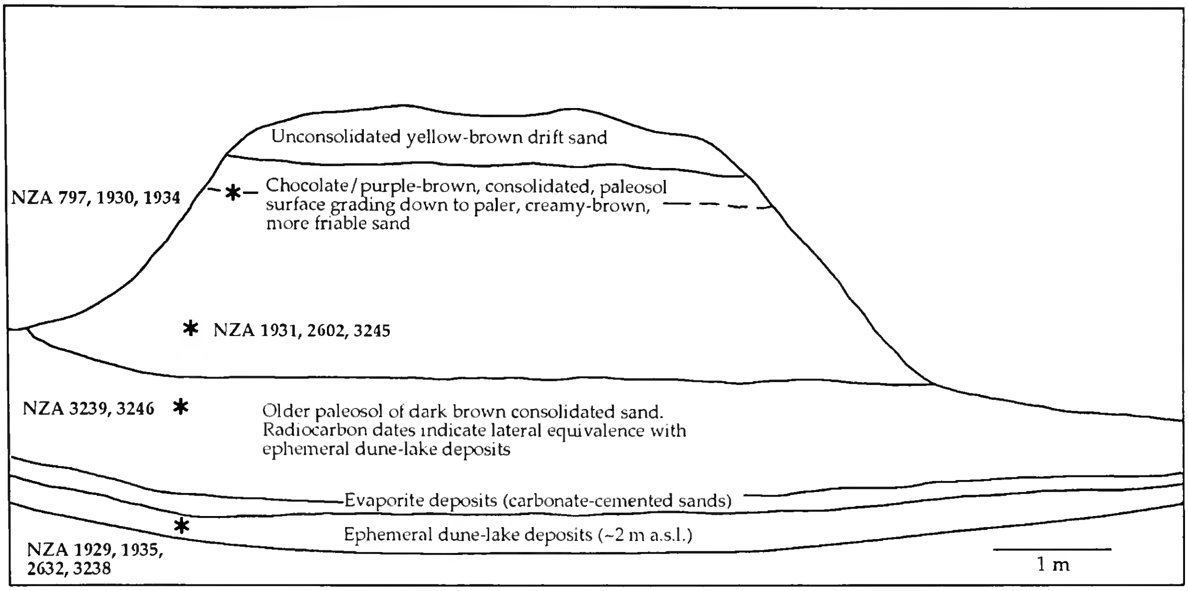


FIGURE 2.—Schematic stratigraphic cross section of dune sands at Long Beach (localities 3, 4). Locations of radiocarbon-dated samples (including those from comparable stratigraphic horizons at other sites within the same dune series) are marked by asterisks (*) and are identified by their Rafter Radiocarbon Laboratory reference (NZA) numbers.

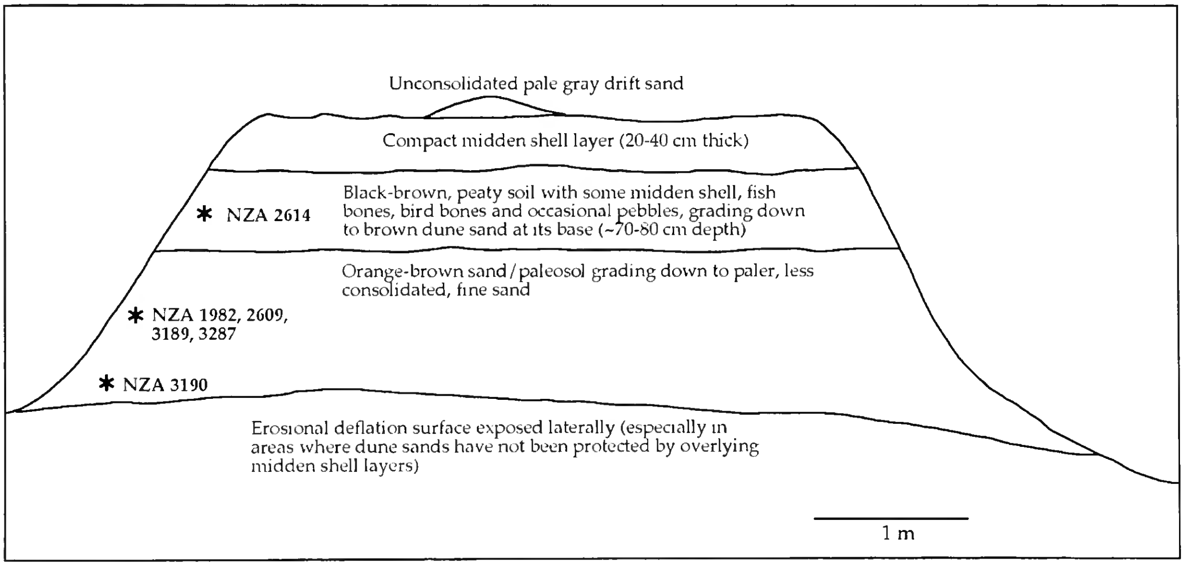


FIGURE 3.—Schematic stratigraphic cross section of the Eastern Maunganui Dunes (locality 11), drawn from a photograph. Locations of radiocarbon-dated samples (including those from comparable stratigraphic horizons at other sites within the same dune series) are marked by asterisks (*) and are identified by their Rafter Radiocarbon Laboratory reference (NZA) numbers.

extensive blow-out deflation hollows. These noncultural death assemblages represent birds whose remains were buried relatively quickly after death by drift sand and were thus preserved as fossils, but no doubt the bones of many more, which were not so fortuitously interred, have decayed completely.

In low-lying areas, where ephemeral dune lakes probably once existed (Figure 2), the most common bird remains are those of the extinct Chatham Island Coot (*Fulica chathamensis;* see Andrews, 1896c; Millener 1980, 1981), the extinct swan (*Cygnus sumnerensis*), and various species of duck. A

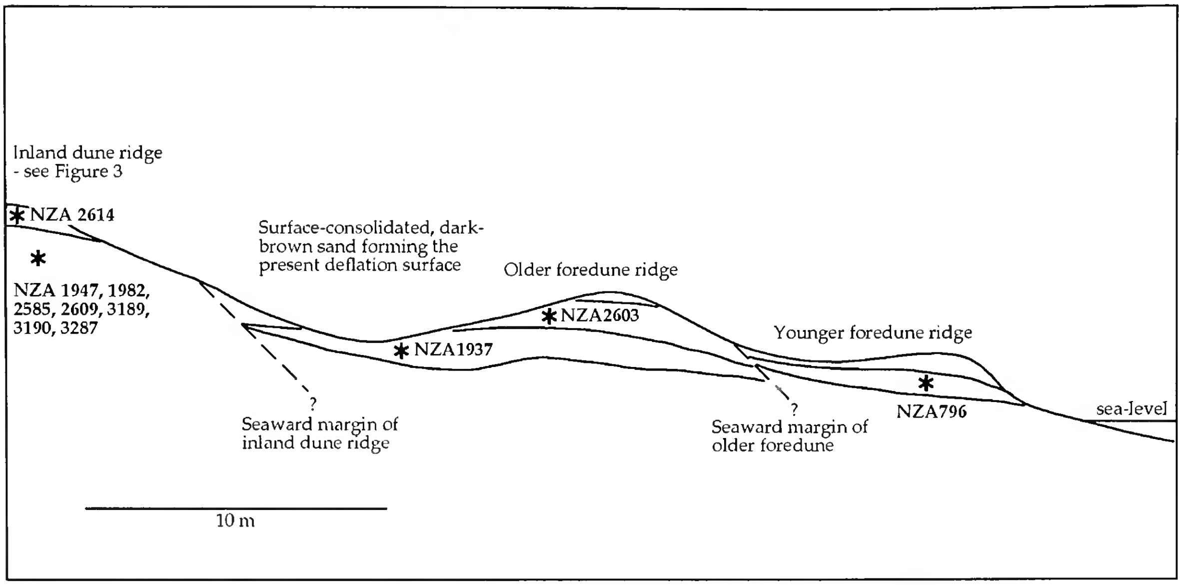


FIGURE 4.—Schematic stratigraphic cross section of dunes at Tahatika Creek in the Eastern Maunganui Dunes (locality 11). Locations of radiocarbon-dated samples are marked by asterisks (*) and are identified by their Rafter Radiocarbon Laboratory reference (NZA) numbers. Samples listed for the inland dune ridge include those from comparable stratigraphic horizons at several sites along the ridge.

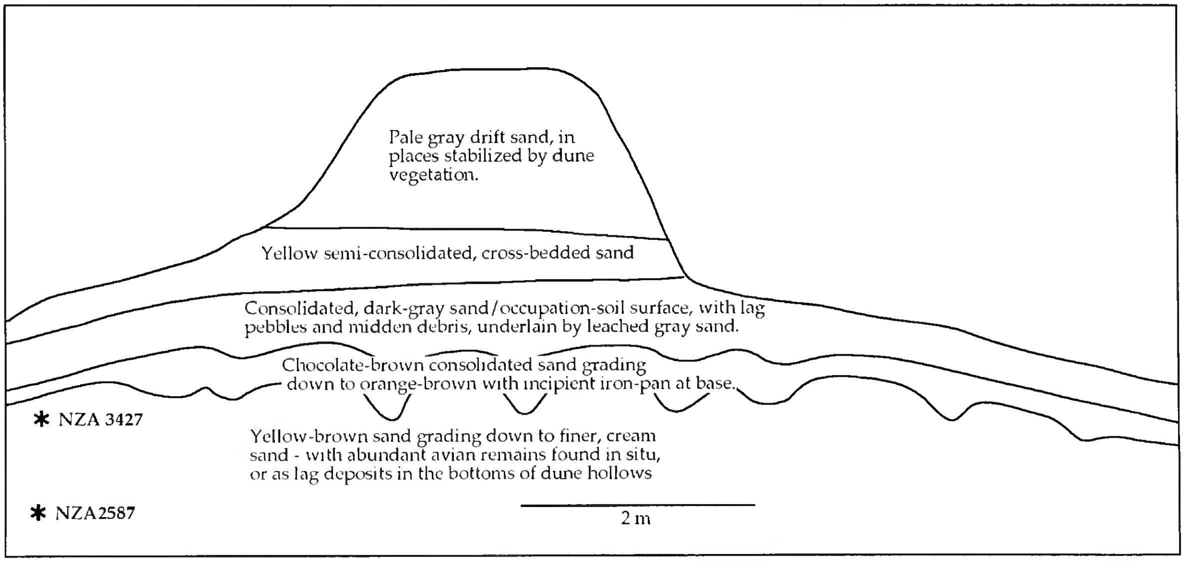


FIGURE 5.—Schematic stratigraphic cross section of the Taupeka inland dunes (locality 12), drawn from a photograph. Locations of radiocarbon-dated samples are marked by asterisks (*) and are identified by their Rafter Radiocarbon Laboratory reference (NZA) numbers.

specimen of *Fulica* from one of these lake beds yielded the oldest radiocarbon age (NZA 3238, locality 4; 6879 ± 68 yrs BP) so far obtained for bird bones on main Chatham Island. The undulating dune slopes and buried soils in the broad zone between foredune and ridge crests yielded the greatest variety of species, both marine and terrestrial, but with forest-dwelling birds such as the Chatham Island Pigeon (*Hemiphaga chathamensis*), Dieffenbach's Rail (*Gallirallus dieffenbachii*), the extinct Chatham Island Snipe (*Coenocorypha chathamica*), *Nestor* (*Nestor*, species undescribed, Figure 10), parakeets (*Cy-*

anoramphus spp.), Chatham Island Tui (*Prosthemadera novaeseelandiae chathamensis*), and Chatham Island Bellbird (*Anthornis melanura melanocephala*) most often represented. Radiocarbon dates from this complex physiographic zone cover a broad range, from ca. 700 to ca. 6500 CAL BP, the oldest dates coming from the eroded older inland dunes, and the youngest dates from younger foredune sites, typically only a short distance inland of the present, unconsolidated, active dune/beach zone (see Appendix: locality 2, NZA 1930, NZA 1931; locality 8, NZA 3285, NZA 3426; locality 9, NZA 3608; locality 12, NZA 2587; locality 14, NZA 2588).

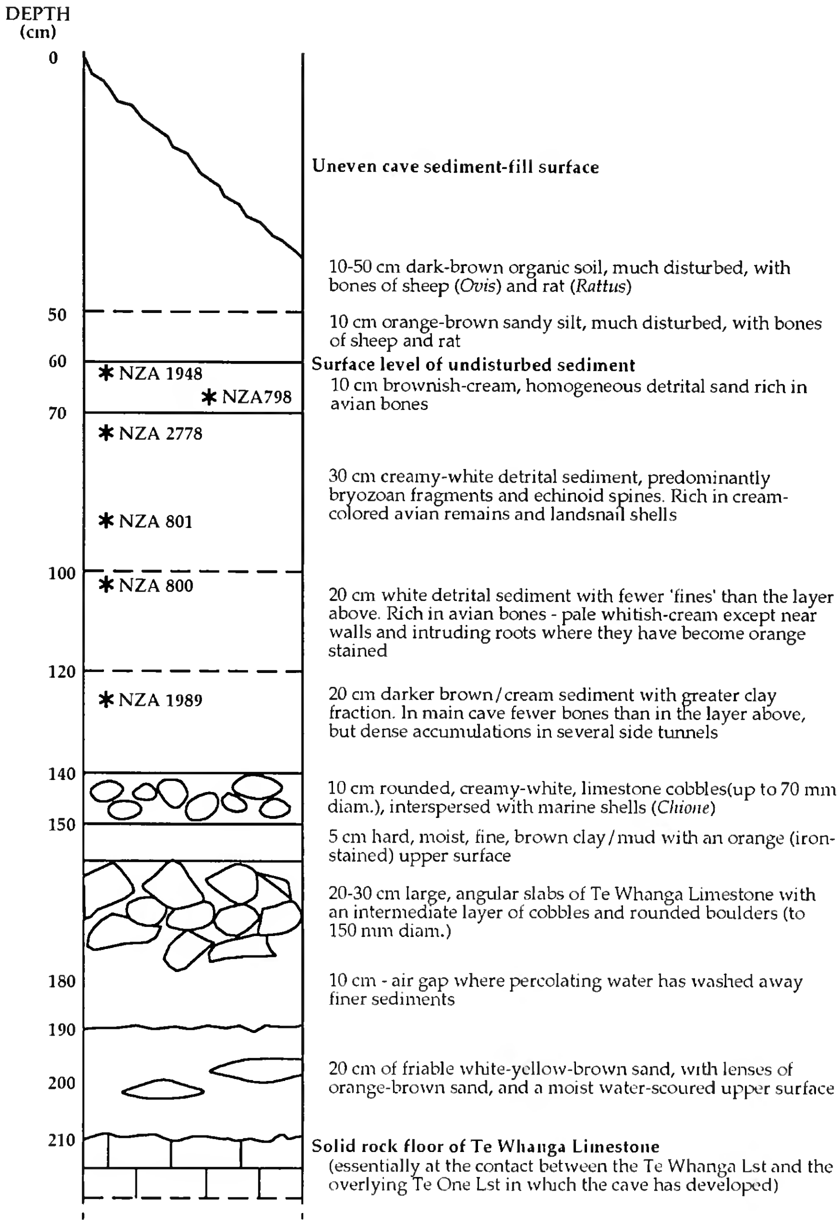
On the higher slopes and ridge crests, and especially in blowouts in pasture land up to several hundred meters inland, bones of many of these same forest birds occur, but they are outnumbered by bones of seabirds, especially Taikos (*Pterodroma magentae*), Sooty Shearwaters (*Puffinus griseus*), Common Diving-petrels (*Pelecanoides urinatrix*), and various prions (*Pachyptila* spp.) and storm-petrels (*Oceanites, Pelagodroma, Fregetta*). The presence of eggshell fragments and the bones of nestlings of all these seabirds (Bourne, 1967) indicates that these widespread fossil sites, dated at between ca. 700 and ca. 3300 CAL BP, mark the locations of former breeding colonies (see Appendix: locality 4, NZA 794; locality 5, NZA 1932, NZA 1933; locality 6, NZA 795; locality 17, NZA 2777).

MIDDEN SITES

The prehistoric Moriori left extensive faunal remains at numerous, widely spread sites in the dunes and as surface scatters on them (Simmons, 1964; see also Figures 3–5). These kitchen middens are generally dominated by marine shells, but bones of sea lions, seals, fish, and birds also occur, particularly in the oldest sites (those dating between ca. 400 and ca. 450 CAL BP). Some earlier archeological workers, who collected much of their material from lag deposits in deflation hollows and who did not have access to radiocarbon dating, failed to distinguish between natural and midden deposits and tended to ascribe a midden origin to virtually all the bird remains they found (e.g., Coutts, 1969). Recent stratigraphic studies, supported by a large number of radiocarbon dates on bird bones, demonstrate that much of this so-called midden material has been eroded from naturally accumulated deposits that considerably predate human occupation by hundreds to thousands of years. An example is the abundant material from Sutton's main Waihora site (see Sutton, 1976, 1979, 1981, 1982; Marshall et al., 1987), which, apparently, was obtained by excavation of intact strata and was assumed to be entirely of midden origin, but which has yielded dates of ca. 5750 and ca. 5950 CAL BP (for Dieffenbach's Rail bones from Sutton's Layers I (NZA 3193) and III (NZA 3194), respectively; see Appendix, locality 1). In a few sites, notably Sutton's CHA and CHB sites at Waihora, and at Tupuangi and Waipaua on Pitt Island, bird remains of genuine midden provenance certainly do occur, often in great abundance. No dates of greater than ca. 450 CAL BP have yet been obtained for in situ midden material at these and other sites. My data corroborate McFadgen's (1994) suggestion that first Polynesian settlement of the Chathams group did not occur until about 450 years ago. The assemblages at these sites indicate that the Moriori hunted a wide range of species but that certain species (e.g., Taiko, Chatham Island Pigeon, Common Diving-petrel, Dieffenbach's Rail) were sought more intensively than the rest. There can be little doubt that prehistoric hunting had a profoundly deleterious effect on the Chatham Islands bird fauna. It appears, however, that the Moriori neither constructed permanent dwellings nor lived in long-term encampments, and perhaps it is because they led a rather more itinerant life style that they have left less evidence of their hunting (in the form of extensive bird bone middens) than did, for example, the Maori hunters of mainland New Zealand (see Trotter and McCulloch, 1984).

CAVE SITES

In several places on Chatham and Pitt islands are limestone crevices and cavities that contain bone deposits because they were used as shelters and nest sites by terrestrial and marine birds. There also are larger caves that acted as pit-fall traps, and these have yielded far more abundant fossil remains. The most significant of these is a small, single-chambered cave on the western edge of the Te Whanga Lagoon, Chatham Island. This cave, Te Ana a Moe (see Simmons, 1964), is developed near the base of a 15 m high cliff of Eocene Te One Limestone (typically creamy yellow in color, relatively soft, and rich in bryozoan fragments), immediately above its contact with the underlying Te Whanga Limestone (typically grey white, hard, crystalline and, here, where it forms the raised shore-platform, strongly karstic; see Hay et al., 1970; Campbell, 1996). The cave has a single walk-in entrance about 3 m above present lagoon level and is filled in with stratified sediment to a depth of at least 2 m (see Figure 6). Above the almost unfossiliferous basal layers (sands overlain by angular limestone slabs), a distinctive layer of water-rounded limestone cobbles is overlain by more than a meter of stratified sediment containing shells of at least 17 species of land snails (Table 2) and an extraordinary abundance of avian bones of some nine marine and 21 terrestrial or freshwater species (Table 3). Radiocarbon dates range from ca. 1150 CAL BP (NZA 1948, locality 16, at only 15 cm below the base of the disturbed surface soil) to ca. 3900 CAL BP (NZA 1989, locality 16, at a depth of 1.3 m). Bird remains were found to be particularly concentrated within several short (~2 m), narrow (~0.5 m diameter), blind tunnels leading off the main chamber, at depths of 0.9–1.5 m. Faunal material in these tunnels has yielded radiocarbon ages within the range of 2300–3900 CAL BP (NZA 801, NZA 1989, locality 16). Although a wide



Uneven cave sediment-fill surface

10-50 cm dark-brown organic soil, much disturbed, with bones of sheep (*Ovis*) and rat (*Rattus*)

10 cm orange-brown sandy silt, much disturbed, with bones of sheep and rat

Surface level of undisturbed sediment

10 cm brownish-cream, homogeneous detrital sand rich in avian bones

30 cm creamy-white detrital sediment, predominantly bryozoan fragments and echinoid spines. Rich in cream-colored avian remains and landsnail shells

20 cm white detrital sediment with fewer 'fines' than the layer above. Rich in avian bones - pale whitish-cream except near walls and intruding roots where they have become orange stained

20 cm darker brown/cream sediment with greater clay fraction. In main cave fewer bones than in the layer above, but dense accumulations in several side tunnels

10 cm rounded, creamy-white, limestone cobbles(up to 70 mm diam.), interspersed with marine shells (*Chione*)

5 cm hard, moist, fine, brown clay/mud with an orange (iron-stained) upper surface

20-30 cm large, angular slabs of Te Whanga Limestone with an intermediate layer of cobbles and rounded boulders (to 150 mm diam.)

10 cm - air gap where percolating water has washed away finer sediments

20 cm of friable white-yellow-brown sand, with lenses of orange-brown sand, and a moist water-scoured upper surface

Solid rock floor of Te Whanga Limestone
(essentially at the contact between the Te Whanga Lst and the overlying Te One Lst in which the cave has developed)

FIGURE 6.—Schematic stratigraphic section of sedimentary deposits within Te Ana a Moe Cave (locality 16). Locations of radiocarbon-dated samples are marked by asterisks (*) and are identified by their Rafter Radiocarbon Laboratory reference (NZA) numbers.

range of taxa are represented in the deposits, in total many thousands of bones from hundreds of individuals, the following species predominate in the assemblages: Chatham Island Rail (*Gallirallus modestus*), Dieffenbach's Rail, a merganser (*Mergus*, species undescribed, Figures 12–14), Chatham Island Fernbird (*Bowdleria rufescens*), Magenta Petrel, or Taiko, Fairy Prion (*Pachyptila turtur*), and Common Diving-petrel. One particularly important find was that of an almost complete individual skeleton of the flightless Chatham Island Duck, *Pachyanas chathamica* Oliver (1955) (Figure 7). Bones were more abundant in the lower levels (particularly in the 2300–3900 CAL BP strata), but species composition varied little with depth. The fact that the youngest dates obtained for in situ faunal material were ca. 1150 CAL BP (e.g., NZA 1948, locality 16) is taken to indicate that at about this time, when the infilling sediment reached the level of the single walk-in entrance, the cave ceased to be an effective pit-fall trap for birds.

TABLE 2.—Land snails (Gastropoda: Pulmonata) identified from Te Ana a Moe Cave, Chatham Island (Locality 16 (Figure 1)). Taxonomy follows Climo (pers. comm., 1993). Sample 1 (PRM sample 155/91) is from brown sand/soil in the uppermost 20 cm of undisturbed sediment; sample 2 (PRM sample 156/91) is from creamy white bryozoan detrital sand, at 1 m depth (~40 cm below upper surface of undisturbed sediment); sample 3 (PRM sample 120A/91) is from brown gray bryozoan detrital sand at 1.2–1.4 m depth (60–80 cm below upper surface of undisturbed sediment) in a side tunnel in SW quadrant. For each sample, abundance of each species is expressed as a percentage of sample size (*n*). (See also Figure 6.)

Family	Species	Sample		
		1 (*n*=164)	2 (*n*=110)	3 (*n*=128)
TORNATELLINIDAE	*Lamellidea novoseelandica*	0.6	–	1.6
PUNCTIDAE	*Serratopunctum serratocostata*	–	0.9	–
	Litopunctum rakiura	74.4	18.2	40.6
	Punctum lateumbilicata	–	4.5	4.7
	Alexaoma chathamensis	–	–	0.6
	Dellopsis stewartensis	–	–	0.8
	Pryhina chathamensis	10.4	21.8	13.3
CHAROPIDAE	*Phenacharopa pseudanguicula*	1.2	–	1.6
	Charopa coma	–	6.4	2.3
FLAMMULINIDAE	*Flammocharopa mayhillae*	–	–	0.8
	Sinployea parva	0.6	–	1.6
ROTADISCIDAE	*Huonodon hectori*	–	2.7	1.6
	Mitodon wairarapa	–	2.7	–
	Basimocella maculata	5.5	35.5	18.8
	Discocharopa eta	0.6	–	–
	Cavellia buccinella	2.4	8.2	7.0
CAMAENIDAE	*Thalassohelix* sp.	4.3	1.8	3.9

TABLE 3.—Bird species identified from Te Ana a Moe Cave, Chatham Island (Locality 16 (Figure 1)). See "Appendix" and Table 1. (A=abundant (minimum number of individuals (MNI) >100); C=common (MNI ≥ 10); R=rare (MNI < 10); *=extinct.)

Taxon	Abundance
MARINE SPECIES	
Pelecanoides urinatrix	A (at all levels)
Pachyptila turtur	A (at all levels)
Pachyptila crassirostris	R
Pterodroma nigripennis	R
Pterodroma axillaris	C
Pterodroma magentae	A (at all levels)
Pelagodroma marina	R
Eudyptula minor	C
Larus dominicanus	R (upper level only)
TERRESTRIAL AND FRESHWATER SPECIES	
*_Tadorna_, species undescribed	R (MNI=2, in upper level only)
*_Anas_, species undescribed	R
*_Pachyanas chathamica_	R (MNI=1, in lower level)
*_Mergus_, species undescribed	A (at all levels)
Falco novaeseelandiae	R
*_Gallirallus dieffenbachii_	A (at all levels)
*_Gallirallus modestus_	A (at all levels)
*_Diaphorapteryx hawkinsi_	R
*_Fulica chathamensis_	R
*_Coenocorypha chathamica_	C
Hemiphaga chathamensis	R
*_Nestor_, species undescribed	R
Cyanoramphus novaezelandiae	C
Cyanoramphus auriceps	R
Anthus novaeseelandioe	R
*_Bowdleria rufescens_	C (at all levels)
Gerygone albofrontata	R
Rhipidura fuliginosa	R
Petroica traversi	C (at all levels)
*_Anthornis melanura_	R
Prosthemadera novaeseelandiae	R

SWAMP SITES

Although peat deposits and more recent swamps are widespread on Chatham Island, the conditions in them appear to have been unsuitable for the preservation of bones. Peat fires burning to considerable depths have occurred frequently on the island. Furthermore, both peats and more recent swamps seem typically to have been too acidic to allow long-term preservation of bone.

Paleogeography, Ancestral Immigration, and Avifauna Change

It is possible that the Chatham Islands, although isolated by a broad oceanic gap from the New Zealand mainland since the Late Cretaceous, some 80 million years ago, have provided a land mass capable of supporting viable bird populations more or less continuously for perhaps many millions of years (Fleming, 1962, 1975; Cooper and Millener, 1993). There is evidence, however, that during the late Eocene (40 Ma) and again during the Pliocene (5–2 Ma) the only emergent land in the entire Chathams group would have been a few volcanic peaks (Campbell, 1996:36). Thus colonization by the forerunners of the Holocene species may postdate the Pliocene. Further, there is some suggestion that later, in the Pleistocene, high interglacial sea-levels during the Castlecliffian (ca. 1.4–0.32 Ma) may have inundated all but the highest points of Chatham Island (see Hay et al., 1970). Therefore much, if not all, of any earlier established terrestrial avifauna may have been eliminated during this period. Any ancestral avian colonists that reached the Chathams since the Cretaceous, including those still arriving today, could have done so only by fly-

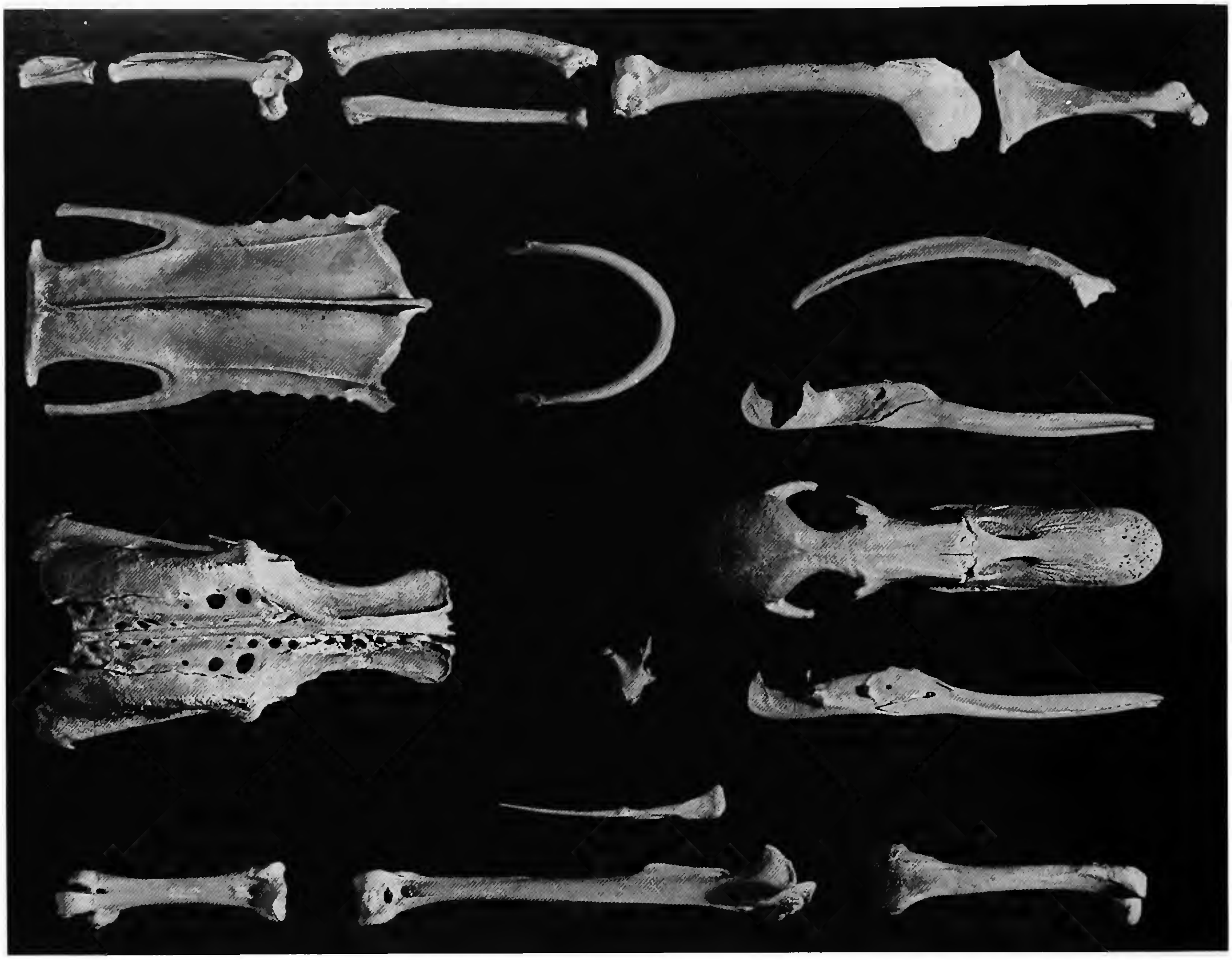


FIGURE 7.—Skeletal elements of *Pachyanas chathamica* (MNZ S29475, PRM sample #92/91) from Te Ana a Moe Cave, Te Whanga Lagoon, Chatham Island. Total length of cranium+premaxilla is 113.8 mm.

ing over water. In the absence, however, of any fossil record of birds on the Chathams beyond the last 7000 years, one can only speculate on the numbers and variety that may have reached the Chathams in earlier times and subsequently died out, leaving no trace of their passing. Possibly through extinction of early colonists, but more likely as a consequence of the serendipitous nature of transoceanic colonization ("sweepstakes dispersal"), some significant avian groups are absent from the known avifauna of the Chathams, including ratites (moas and kiwis), Podicipedidae, *Coturnix,* Strigidae, Alcedinidae, Acanthisittidae, Callaeidae, and *Turnagra.* No native frogs, tuatara, or geckos are known, fossil or living, from the Chathams. The one extant species of skink is possibly a geologically relatively recent arrival.

Both extant and extinct Chatham birds are presumably derived from the same ancestral stocks as are comparable species on the New Zealand mainland. They have, however, evolved in isolation and exhibit many of the same evolutionary features found in bird faunas on other small, isolated, oceanic islands, such as New Caledonia (Balouet and Olson, 1989), the Hawaiian Islands (Olson and James, 1982, 1991; James and Olson, 1991), and many other islands of Australasia and the southwest Pacific (van Tets et al., 1981; Meredith, 1991; Steadman, 1995). Typically, on oceanic islands such as these, which prior to human colonization lacked mammalian predators, birds exhibit increased body size and may lose their powers of flight (McNab, 1994). The evolutionary history of Chatham Islands birds has followed this same path. Most of the Chatham Islands land birds and waterfowl tend to be larger than their mainland counterparts, with some very much more so, such as Hawkins' Rail (*Diaphorapteryx hawkinsi*), the flightless Chatham Island Duck, the Chatham Island Pigeon, and the Chatham Island Bellbird. Further, of the 36 prehistorically known species, at least seven were flightless (two ducks, four rails, and the Chatham Island Fernbird; see Olson, 1990), and three more were weak fliers (a duck, a snipe, and a parrot).

With the exception of an apparently new species of crested penguin (*Eudyptes,* species undescribed; Figures 8, 9), no marine taxa are known to have become extinct. The seabirds have been affected, nevertheless, by the changes that occurred following human settlement. Fossil remains of numerous species of seabirds occur in large concentrations in many places, particularly along dune ridges and promontories, on Chatham Island and on Pitt. Few species of seabirds still breed on these two larger islands; most current breeding colonies are restricted to rugged, small, offshore islands or stacks. Fossil eggshells and bones of very immature chicks indicate the presence of former breeding colonies of a wide range of species. Radiocarbon dating of bones indicates that some of these colonies were occupied from at least 4500 years ago (NZA 1906, locality 18; 4300 ± 150 yrs BP=4545 CAL BP), and presumably much earlier. Some colonies continued to be occupied into the period of first human settlement, but there is no evidence of their persistence into the European era and, indeed, little evidence of viable colonies beyond about 300 years ago. These Chatham Island/Pitt Island breeding species included albatrosses (*Diomedea epomophora sanfordi* and at least one larger species); mollymawks; shearwaters; diving-petrels; several prions; gadfly petrels, especially the Taiko and another species, apparently similar but not identical to the Mottled Petrel (*Pterodroma inexpectata*); and storm-petrels.

FIGURE 8.—Skulls of *Eudyptes* spp. (dorsal views). Left to right: *Eudyptes pachyrhynchus* (MNZ 24546); *Eudyptes,* species undescribed (MNZ S26908, PRM sample #6/89), from Maunganui, Chatham Island; *Eudyptes sclateri* (MNZ 18897). (Scale bar=30 mm.)

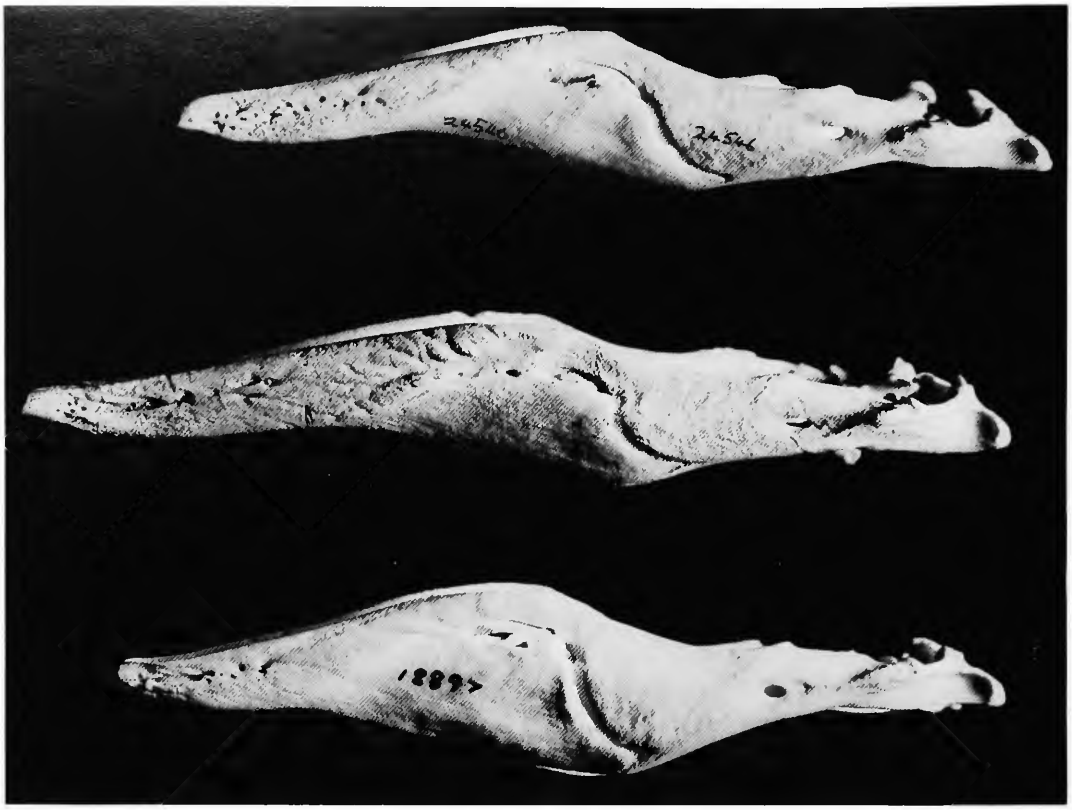


FIGURE 9.—Lower mandibles of *Eudyptes* spp. (left lateral views). Top to bottom: *Eudyptes pachyrhynchus* (MNZ 24546); *Eudyptes*, species undescribed (MNZ S30440, PRM sample #15/92), from Kaingaroa, Chatham Island; *Eudyptes sclateri* (MNZ 18897). Total length of MNZ S30440 is 119.1 mm.

THE COMPOSITION OF THE CHATHAMS AVIFAUNA

It is not possible to produce an entirely accurate catalog of the living and extinct birds of the Chathams because in many cases doubts have been raised (and may always exist) over reported occurrences of several taxa. The exact composition of the terrestrial and freshwater bird fauna is particularly difficult to ascertain. Several of the 45 recorded species appear to have been included by various authors as a result of errors of identification or locality (see van Bemmelen, 1993:32), whereas others, regarded by some as members of the indigenous Chathams fauna, seem more likely to have been introduced by humans.

Taxa that I exclude from the analysis of living and extinct fauna are considered below.

Apteryx sp. (kiwi): Travers (1866:358) stated that "formerly an apterix [sic], said by the Maoris to have been identical with a New Zealand species, and...a smaller species of the same bird...were found [in the Chathams], but have become extinct...." Hutton (1904), as had Wallace (1893), accepted this statement and included *Apteryx* in his catalog. Travers (1873:213), however, commented that his son "has now reason for believing that the weka..., the kakapo..., and the kiwi... were erroneously assigned to [it]" and later (Travers, 1883:183) that he himself was "not disposed to accept [these records]." No fossil bones of *Apteryx* have been found in the Chathams, and the record must remain unsubstantiated.

Gallirallus australis (Weka): Bones, reportedly identical to those of this species, have been recovered from several sites on Chatham Island, leading to the possibility that wekas were indigenous in the Chathams prior to the introduction of *G. australis hectori* in 1905 (Turbott, 1990). There is no unequivocal evidence that any of these bones predate the European introduction. A mounted specimen of a Weka in the Rijksmuseum van Natuurlijke Historie, Leiden (Temminck collection, accessioned in 1823), is said to be from the Chatham Islands, but this locality information may be spurious (van Bemmelen, 1993). On biogeographic grounds it seems highly unlikely that a population of *Gallirallus australis,* identical to the mainland form, would have evolved independently on the Chathams. If association with pre-European middens could be demonstrated, the most likely explanation would be that the species was taken to the Chathams from mainland New Zealand by the original Moriori inhabitants. Because there are no reports of Europeans having seen the species prior to 1905, it would seem that the population, if such existed, must have been eliminated in prehistoric times.

Gallirallus minor (extinct Weka): Several authors have reported bones of this species. Olson (1975:76) remarked that the presence of this species in the Chathams would be "a highly unlikely occurence" and indicated that at least the bones mentioned by Falla (1960) are well within the size range for *G. dieffenbachii. Gallirallus minor* is a species that has never been satisfactorily defined and may eventually prove to be no more than a smaller variant of *G. australis.*

Strigops habroptilus (Kakapo): Travers (1873) mentioned that kakapos (as well as kiwis and wekas, see above) were known to the Maori on the Chathams, and the record was followed by several subsequent authors. Although this statement was later disavowed, Forbes (1892c, 1893a) continued to accept the unsubstantiated myth. Dawson (1959), in a detailed analysis, concluded that the only material evidence for the former presence of *Strigops* rested with a single bone in the Travers collection, which perhaps had not come from the Chathams at all. Subsequently, Dawson (1960) discovered two further bones of *Strigops,* among uncataloged material in the British Museum, that had allegedly been collected by or for Forbes in the 1890s. Because these three bones are the only ones ever identified among the many thousands of bones obtained from the Chathams, it seems most likely that their locality, too, was incorrectly recorded, although there remains a possibility (in my view, highly implausible) that Kakapo were at some time taken to the islands from New Zealand by the Maori.

Nestor notabilis (Kea): The occurrence of fossil bones identified as those of the Kea was mentioned in several papers by Forbes (1892c, 1893a). Oliver (1955:542) obviously followed Forbes when remarking that "in pre-European times [the kea was present] on the Chatham Islands." Dawson (1959), however, considered all the Chatham Island bones of *Nestor* obtained by Forbes to belong to *N. meridionalis* (Kaka). My own research has shown that the Chatham Islands *Nestor* (Figure 10) is a new, undescribed species, poorly volant and now extinct, but it is structurally more like *N. meridionalis* than like *N. notabilis.*

Sceloglaux albifacies (Laughing Owl): Forbes (1892c) noted that among his Chatham Island material were bones that he identified as those of the Laughing Owl. Neither Dawson (in 1958) nor I (in 1984), however, recognized any bones attribut-

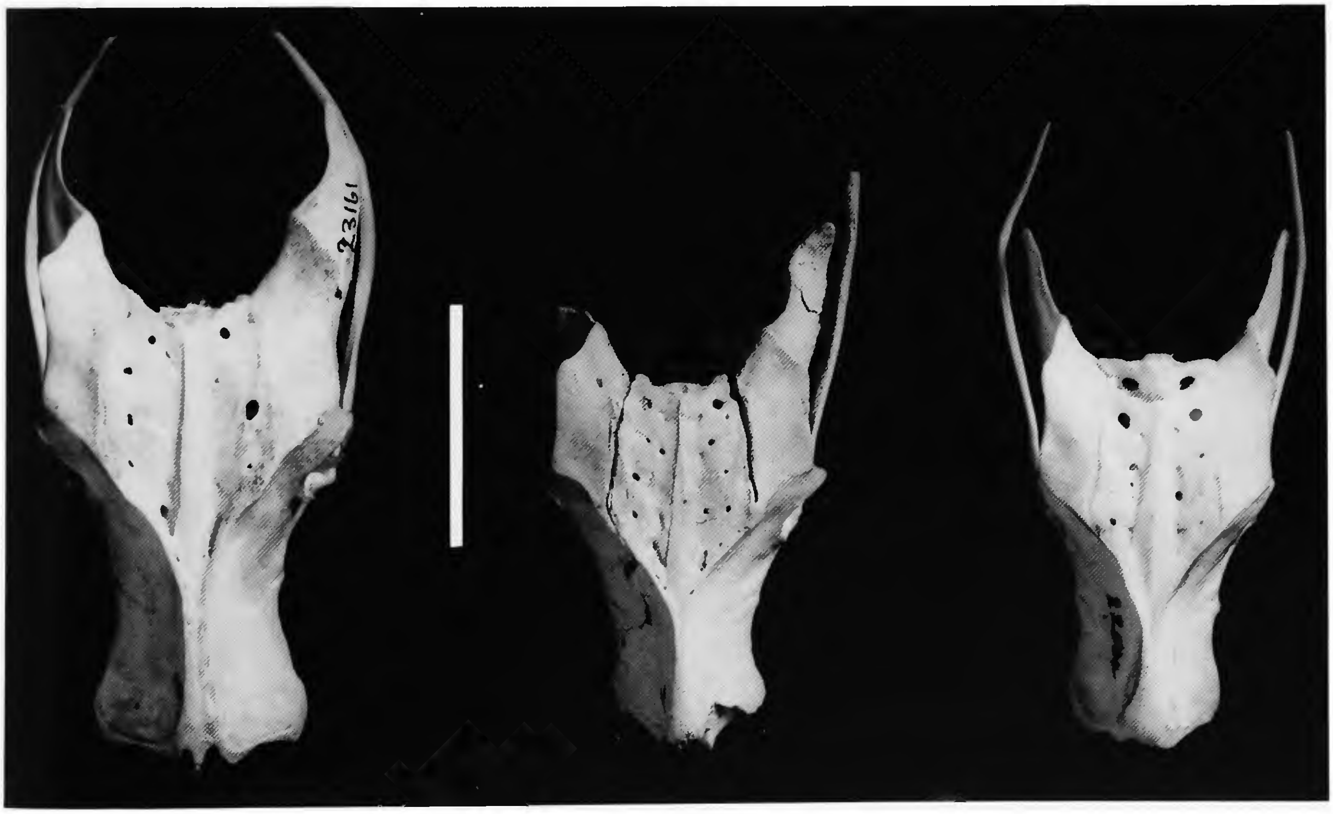


FIGURE 10.—Pelves of *Nestor* spp. (dorsal views). Left to right: *Nestor notabilis* (MNZ 23161); *Nestor,* species undescribed (NMZ S29990, PRM sample #152/91), from Te One, Chatham Island; *Nestor m. meridionalis* (NMZ 22504). (Scale bar=30 mm.)

able to *Sceloglaux* in Forbes' material in the Natural History Museum, London. It seems that this record is a case of mistaken identity. More recently (1993) I have examined a tarsometatarsus from Forbes' collection upon which is written in Forbes' distinctive hand "*Sceloglaux,* Ch.I., HOF." This specimen is clearly attributable to *Falco novaeseelandiae.* Several other bones of *Falco* have been recognized in Forbes' collection (see Dawson, 1961b) and many more have been collected from the Chathams in recent years, but none of *Sceloglaux.*

The Chatham Island Sea-eagle, originally described as *Ichthyophaga australis* (Harrison and Walker, 1973) but removed to *Haliaeetus* by Olson (1984), is a particular enigma, although it seems prudent to list it among the indigenous Chatham Islands birds until unequivocal evidence shows otherwise. Housed in the Natural History Museum, London, is a collection of about a dozen eagle bones found or otherwise acquired by H.O. Forbes in the 1890s, and labelled as being from the Chatham Islands. These bones, parts of four individual birds, certainly belong to the genus *Haliaeetus* (see Dawson, 1961a; Olson, 1984) and have been considered to differ somewhat from any existing species (although I could not distinguish them from bones of the Alaskan race of Bald Eagle, *H. leucocephalus alascanus* Townsend). There is reason to doubt that these bones came from the Chathams (some other bones in Forbes' collections are wrongly labelled) because it is extraordinary that among all the hundreds of thousands of bones collected subsequent to Forbes, not one of a sea-eagle has been recovered. Even the appearance of the bones is unlike that of other Chatham Islands fossils, as they seem to have a surface texture more like that of modern material. Another element of doubt about their authenticity is raised by a radiocarbon date (NZA 1548, locality uncertain) obtained from one of the paratypical bones (BMNH A3732). Depending on the calibration given, an age as young as ca. 1836 AD can be calculated. The enigma remains unresolved. Perhaps Forbes chanced upon the only bones yet known of an endemic Chatham Sea-eagle, or perhaps the bones are from an existing species, acquired as part of Forbes' reference collection of modern specimens.

NOTES ON SELECTED EXTINCT SPECIES FROM THE CHATHAM ISLANDS

Dieffenbach's Rail (*Gallirallus dieffenbachii*): This species is closely related to the widely distributed Banded Rail (*G. philippensis*) and is presumed to have evolved from the same ancestral stock (Olson, 1975). The anatomical differences between Dieffenbach's Rail and the Banded Rail (of which it has previously been considered only a subspecies; see Turbott, 1990) indicate that they are separate species (pers. obs.). Only one live specimen was ever collected, by Ernst Dieffenbach in 1840, who stated (1841:195) that the species "was formerly very common, but since cats and dogs have been introduced it has become very scarce" (see Forbes, 1893b). Dieffenbach's Rail was flightless, weighed perhaps 340–400 g (about twice as much as the Banded Rail, which is a capable flyer), and had a rather dull plumage and a distinctly down-curved bill (Atkinson and Millener, 1991). An inhabitant of forest and scrub, it probably consumed a wide range of foods, including soil invertebrates probed from soft earth, insects, seeds, and even eggs of ground-nesting birds.

Chatham Island Rail (*Gallirallus modestus*): This diminutive (body weight 50–70 g; Atkinson and Millener, 1991), flightless species may have evolved from the same stock as Dieffenbach's Rail (Olson, 1975). The type specimen was obtained by H.H. Travers from Mangere Island in 1871, but Oliver (1955:355–356) stated that "through the work of collectors... aided by cats... [it] was exterminated about twenty-five years after it was discovered." The bill of the Chatham Island Rail is very long and delicate and must surely have been used as a probe to capture small invertebrates in soft soil or leaf litter. The only observations of its habits are those of Hawkins (in Forbes, 1893b:532): "They nest in holes in the ground... [and] live on insects, principally the sandhoppers which travel into the bush a long way." Until recently, fossil bones of the Chatham Island Rail had not been commonly found, but they have now been recorded from Pitt and Mangere islands and from the Te Ana a Moe Cave beside the Te Whanga Lagoon on Chatham Island. From this one small cave, many thousands of bones, representing hundreds of individual birds (Table 3), have been excavated from sediments dating from about 1150 years to almost 4000 years ago.

Hawkins' Rail (*Diaphorapteryx hawkinsi*): Fossil bones of this species were first collected by W. Hawkins who sent them to H.O. Forbes in 1892 (see Forbes, 1892a, 1892b, 1892c, 1893a). This large (body weight ~2 kg; Atkinson and Millener, 1991), flightless rail is so distinct from the *Gallirallus* group that it is placed in its own genus. Its wings were greatly reduced, its legs robust, and its toes elongate. Its long, decurved bill may have been an adaptation for probing into soft earth for soil invertebrates. No living specimen of Hawkins' Rail was ever seen or collected by Europeans, but the substantial numbers of its bones in Moriori middens indicates that it was frequently hunted for food.

Chatham Islands waterfowl: The Chatham Islands formerly supported a wide range of waterfowl, including the extinct Chatham Island Swan and perhaps eight species of duck. The Chatham Island Duck (*Pachyanas,* Figure 7) and Merganser (*Mergus,* species undescribed, Figures 12–14) were flightless, and several of the other species (e.g., the Chatham Island Shelduck, *Tadorna,* species undescribed, Figure 11) show indications of having been weaker flyers than their mainland counterparts. All but the Grey Duck (*Anas superciliosa*) became extinct in the Chathams following human settlement. The extinct swan (*Cygnus sumnerensis*) would seem to have evolved from the same stock as the Australian Black Swan, which was introduced to the Chathams about 1890 and now flourishes on

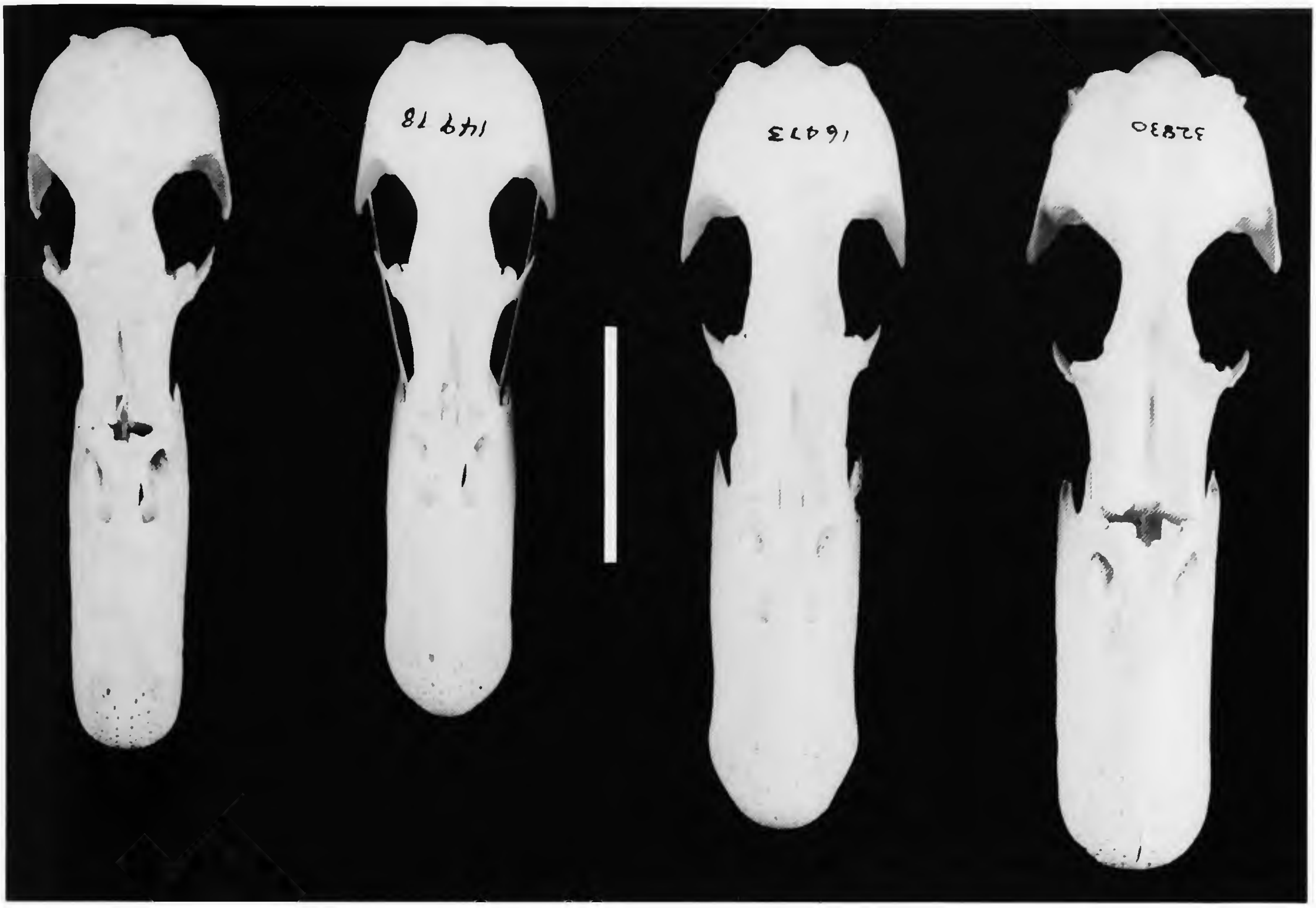


FIGURE 11.—Skulls of Anatidae (dorsal views). Left to right: *Anas*, species undescribed (MNZ S33298, ex. H.O. Forbes collection), from "Chatham Islands"; *Anas chlorotis* (MNZ 14978); *Tadorna variegata* (MNZ 16473, male); *Tadorna*, species undescribed (MNZ S32830, presumed male), from Maunganui, Chatham Island. (Scale bar=30 mm.)

the Te Whanga Lagoon (Turbott, 1990). The extinct species, known also from mainland New Zealand, differs in being somewhat larger, with a stouter bill and relatively shorter wings. Its bones have been found in greatest abundance at Waitangi West, at Tioriori, and at Te One Beach, near Red Bluff, in deposits ranging in age from ca. 7600 (cf. NZA 3238, locality 4) to ca. 700 (NZA 2603, locality 11) years old, but they also occur commonly in middens. The Chatham Island Duck, whose bones have been found at a considerable number of sites on Chatham Island, but not elsewhere, was robust, weighing as much as 2.5 kg (more than twice the weight of a Grey Duck), and yet with wings perhaps even a little smaller than in that species (pers. obs.). The new merganser (*Mergus,* species undescribed), whose bones have been found in abundance only in Te Ana a Moe Cave, was a little smaller than the recently extinct (ca. 1905), flightless Auckland Island Merganser (*Mergus australis;* see Kear and Scarlett, 1970) and had a shorter bill and even more reduced wings (Millener, pers. obs.).

EXTINCTIONS

The indigenous bird faunas of remote oceanic islands, having evolved in isolation from most or all vertebrate predators, are extraordinarily vulnerable to the impact of humans (see Milberg and Tyrberg, 1993; Steadman, 1995). The land birds and waterfowl of the Chatham Islands were well adapted to their island environment. Most became larger than their mainland counterparts, many became completely or nearly flightless, some probably laid smaller clutches, and none developed or retained a fear of mammalian predators. First human settlement was almost certainly accompanied by accidental or deliberate forest clearing, and on such small islands there would

FIGURE 12.—Bones of *Mergus*, species undescribed (MNZ S30049, PRM sample #113/91; all from 20 liters sediment), from Te Ana a Moe Cave, Te Whanga Lagoon, Chatham Island. (Scale bar=100 mm.)

have been few refuges for species whose habitat was destroyed. Hunting by humans and predation by rats (*Rattus exulans*) must have depleted the most vulnerable species, particularly the flightless and ground-nesting ones. Thirteen species (36% of the original terrestrial avifauna) were exterminated between about 450 years ago, the estimated date of first human arrival, and about 300 years ago, after which few, if any, bones of prehistorically extinct species are to be found in natural or midden deposits (Table 4). This group included nine species endemic to the Chathams: four ducks (three of which are undescribed,

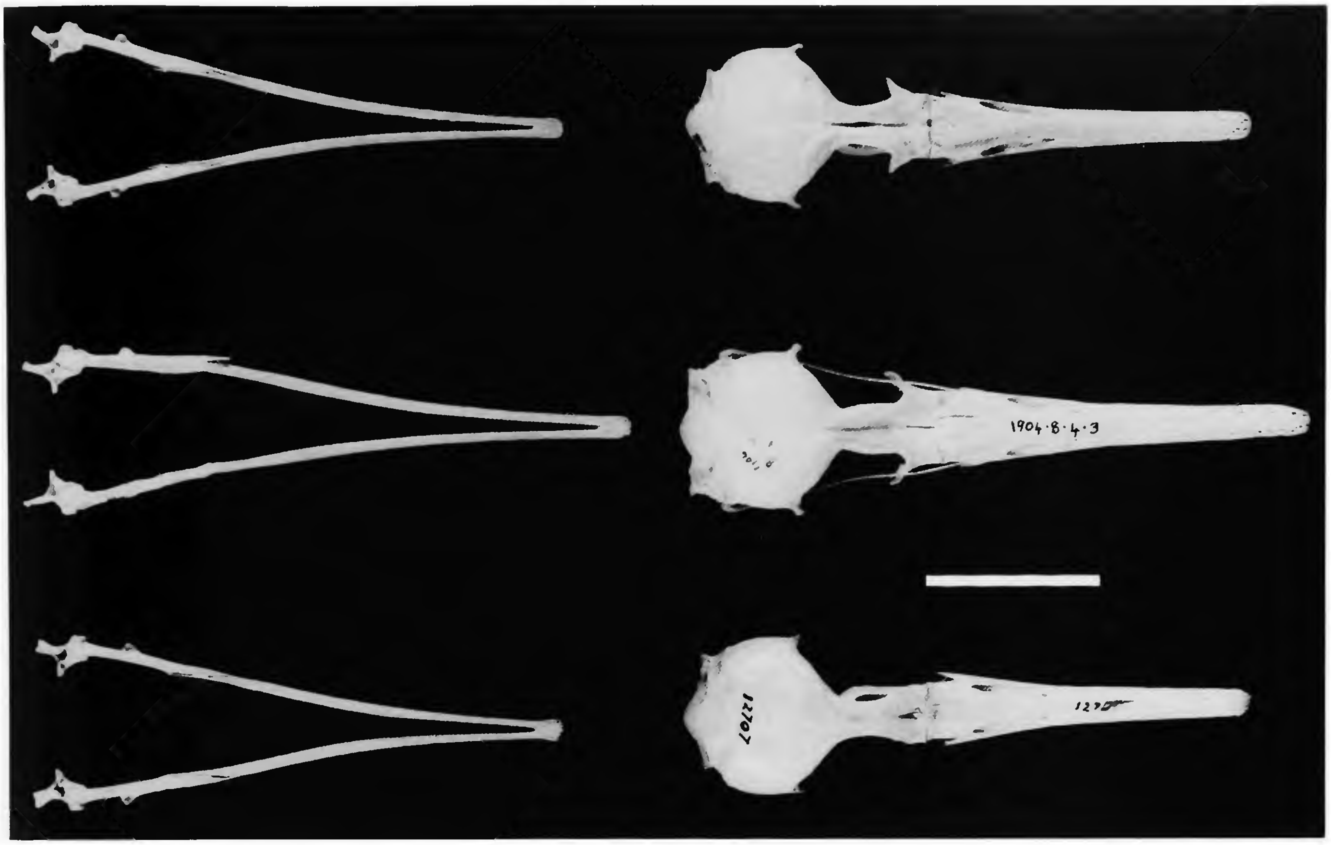


FIGURE 13.—Lower mandibles (left) and skulls (right) of *Mergus* spp. (dorsal views). Top to bottom: *Mergus*, species undescribed (MNZ S30049, PRM sample #113/91) from Te Ana a Moe Cave, Te Whanga Lagoon, Chatham Island; *Mergus australis* (BMNH 1904.8.4.3, male); *Mergus serrator* (MNZ 12707, female). Scale bar=30 mm.

see Figures 11–14), two rails, a snipe, the undescribed species of *Nestor* (Figure 10), and the putative Chatham Island Sea-eagle. Of the four other species rendered extinct on the Chathams in pre-European times, the swan and the crow (*Palaeocorax moriorum*) may have survived on the New Zealand mainland a little longer. The New Zealand Little Bittern (*Ixobrychus novaezelandiae*) survived on the mainland until early in the twentieth century. The New Zealand Scaup (*Aythya novaeseelandiae*) is the only one of this group of 13 species exterminated on the Chathams that still survives on the mainland.

European settlement brought further problems for the survival of the remaining Chathams avifauna; habitat destruction continued as forest and scrub were cleared for farming, two more species of rats, house mice, cats, and dogs were introduced, and human hunting no doubt continued. The four endemic species that became extinct between 1840 and 1906 were all of small size, three were flightless (and thus obligate ground nesters), and even the bellbird was a weak flyer. There can be little doubt their demise was hastened by a combination of habitat destruction and predation. Adults would have been particularly vulnerable to cat predation, and their eggs and young vulnerable to rats. The Brown Teal (*Anas chlorotis*) and New Zealand Shoveler (*Anas rhynchotis*), which were last seen in the Chathams in 1915 and 1925, respectively, would seem to have been the victims of recreational hunting.

TABLE 4.—Extinction of Chatham Islands terrestrial and freshwater birds. Of the 36 former breeding species, 13 were exterminated during the pre-European era, and eight were exterminated during the European era; total extinctions=21 (58%). There are now 15 breeding terrestrial species (excluding historic colonists and introductions) on the Chathams Islands.

Era	Total extinction (endemics)	Local extirpation
Pre-European	*Mergus*, species undescribed	*Cygnus sumnerensis*
	Pachyanas chathamica	*Aythya novaeseelandiae*
	Tadorna, species undescribed	*Ixobrychus novaezelandiae*
	Anas, species undescribed	*Palaeocorax moriorum*
	Haliaeetus australis	
	Diaphorapteryx hawkinsi	
	Fulica chathamensis	
	Coenocorypha chathamica	
	Nestor, species undescribed	
European	*Gallirallus dieffenbachii* (1840)	*Botaurus poiciloptilus* (1910)
	Gallirallus modestus (1900)	*Anas chlorotis* (1915)
	Bowdleria rufescens (1900)	*Anas rhynchotis* (1925)
	Anthornis melanura melanocephala (1906)	*Falco novaeseelandiae* (1900)

FIGURE 14.—Sterna of *Mergus* spp. (right lateral views). Top to bottom: *Mergus*, species undescribed (MNZ S30049, PRM sample #113/91), from Te Ana a Moe Cave, Te Whanga Lagoon, Chatham Island; *Mergus australis* (BMNH 1904.8.4.3, male); *Mergus serrator* (MNZ 12707, female). (Scale bar=30 mm.)

The Australasian Bittern (*Botaurus poiciloptilus*) may have suffered the same fate, although there is some doubt whether this species was ever really established in the Chathams. The New Zealand Falcon (*Falco novaeseelandiae*), from its subfossil record formerly abundant and reportedly seen as late as the 1890s, may have been vulnerable to rats and cats, particularly when nesting.

The elimination of these eight species during the historic period (34% of the 23 species that had survived through the Polynesian period) meant that since first human contact just over 400 years before, at least 58% of the Chatham Islands' original complement of land birds and waterfowl had become extinct. As a more positive adjunct to this sad record, it should be noted that without enlightened human intervention several more species, notably the Black Robin (*Petroica traversi*), the New Zealand Shore Plover (*Thinornis novaeseelandiae*), and the Chatham Island Pied Oystercatcher (*Haematopus chathamensis*), also might have become extinct.

Conclusions

Analysis of the abundant and well-dated fossil avian material found in sand-dune and cave deposits on several of the larger islands of the Chatham group indicates that these islands have supported a diverse, highly endemic avifauna since at least 7000 years ago. This avifauna, some 100 species in all, including many endemic land and freshwater birds, as well as a wide variety of seabirds, survived apparently unscathed until shortly after the first human arrival about 450 years ago.

Many birds of the Chatham Islands exemplify the evolutionary trend toward larger body size and diminished flying ability so typically found in small, isolated oceanic-island groups that, prior to human colonization, lacked mammalian predators. Most of the Chatham Islands land birds and waterfowl are larger than their mainland counterparts, and of the 36 prehistorically known species, at least seven were flightless and three more would have been weak fliers.

The land birds of the Chatham Islands were clearly no exception to the general rule that insular species tend to be "naive" toward humans and introduced predators (Milberg and Tyrberg, 1993:229). The lethal combination of weak flight and trusting attitude predisposed them to an extraordinary vulnerability to human interference. The fossil record of the last 7000 years gives no indication that any of the prehistorically known species became extinct, or even less abundant, prior to human arrival. All of the flightless and weak-flying species, and a further 11 flying species, however, became extinct within a few hundred years of first human settlement through the combined effects of human perturbations.

Appendix

This appendix provides an annotated listing of both conventional and calibrated radiocarbon ages for samples from Chatham and Pitt islands. Samples (bone collagen or marine-shell carbonate) are identified by their Rafter Radiocarbon Laboratory reference numbers (prefixed by NZA). Age data are presented as follows: conventional age based on the old (Libby) half-life of 5568 yrs (as "age ± standard deviation yrs BP"); calibrated (corrected) age, given as median age ("CAL BP") where possible; and calibrated (corrected) age as a range expressed in terms of the 95% confidence interval (age ± two standard deviations). Locality names and grid references (GR) given for sampled sites (see Figure 1, numbered sites 1–21) are from New Zealand Topographical Map, NZMS 260, 1:50000 metric series, Chatham Islands, edition 1, 1981 (Chatham Island (localities 1–17), sheet 1; Pitt Island (localities 18–21), sheet 2). (a.s.l.=above sea level.)

CHATHAM ISLAND

Locality 1, Waihora, Point Durham

NZA 3193: *Gallirallus dieffenbachii,* Sutton coll. WH/VII/2 Layer 1; GR 358470; Waihora Mound site, supposedly midden material; 5030 ± 68 yrs BP; ca. 5750 CAL BP; 5894–5605 CAL BP.

NZA 3194: *Gallirallus dieffenbachii,* Sutton coll. WH/VII/23 Layer 3; GR 358470; Waihora Mound site, supposedly midden material; 5237 ± 72 yrs BP; ca. 5950 CAL BP; 6173–5753 CAL BP.

Locality 2, Red Bluff

NZA 2610: *Hemiphaga chathamica,* MNZ S31065; GR 469603; back-beach sequence in embayment, ~800 m SSE of Te Whenuhau Trig, from uppermost stratum of coarse, yellow, shell sand (beneath windblown fine sand). Indicates minimum age for >2 m thick sequence; 985 ± 80 yrs BP; 843 CAL BP; 975–689 CAL BP.

Locality 3, Long Beach, S of Henga limestone bluffs (GR 450655)

NZA 1930: *Fulica chathamensis,* MNZ S27821; GR 465626; Long Beach, in typical, stratified, consolidated, dune hummock (~4 m a.s.l.), immediately beneath eroded surface of brown sand/soil horizon (30 cm thick), now overlain by drift sand; 2560 ± 145 yrs BP; 2254 CAL BP; 2666–1924 CAL BP.

NZA 1931: *Hemiphaga chathamensis,* MNZ S27822; GR 465626; Long Beach, in pale brown sand at 1.5 m depth (directly underlying sample NZA 1930); 3790 ± 150 yrs BP; 4109 CAL BP; 4511–3697 CAL BP.

NZA 1929: *Diaphorapteryx hawkinsi,* MNZ S27820; GR 456646; Long Beach, Milton's Gully site, embedded in gray brown, hard-pan deflation surface (former interdune lake deposit?); 6660 ± 150 yrs BP; 7456 CAL BP; 7693–7207 CAL BP.

NZA 3246: *Hemiphaga chathamensis,* MNZ S33158; GR 456646; Long Beach, Milton's Gully site, in horizontally bedded brown sand at inland margin of and stratigraphically above hard-pan deflation surface; 5355 ± 70 yrs BP; 6091 CAL BP; 6271–5935 CAL BP.

NZA 3239: *Gallirallus dieffenbachii,* MNZ S33146; GR 456646; Long Beach, Milton's Gully site, in consolidated brown sand at seaward margin of and stratigraphically above hard-pan deflation surface; 5779 ± 71 yrs BP; 6543 CAL BP; 6721–6405 CAL BP.

NZA 2632: *Hemiphaga chathamensis,* MNZ S32545; GR 454653; Long Beach, ~500 m N of Milton's Gully site. Orange brown bones in iron-stained sand. Site of former ephemeral dune lake? 4720 ± 87 yrs BP; ca. 5450 CAL BP; 5594–5057 CAL BP.

Locality 4, Long Beach, N of Henga limestone bluffs (GR 450655)

NZA 797: *Pterodroma magentae,* NMZ S26679; GR 447663; Long Beach, ~350 m N of Henga bluffs. From uppermost 20 cm of typical brown sand/soil exposed in eroding hillocks ~5 m a.s.l.; 3190 ± 130 yrs BP; 3025 CAL BP; 3321–2749 CAL BP.

NZA 1934: *Hemiphaga chathamensis,* MNZ S27825; GR 447663; Long Beach, ~350 m N of Henga bluffs. In situ in typical brown sand/soil exposed in eroding, seaward-extending ridge ~5 m a.s.l.; 2200 ± 150 yrs BP; 2139 CAL BP; 2702–1739 CAL BP.

NZA 2602: *Hemiphaga chathamensis,* MNZ S30584; GR 445669; Long Beach, in situ at ~5 m a.s.l. in extensive, consolidated brown-sand horizon exposed on large, seaward-sloping deflation surface; 4165 ± 92 yrs BP; ca. 4700 CAL BP; 4835–4418 CAL BP.

NZA 3245: *Hemiphaga chathamensis,* MNZ S33047; GR 445669; Long Beach, in situ at ~7 m a.s.l. in extensive, consolidated, gray brown sand horizon exposed on large, seaward-sloping deflation surface; 4493 ± 66 yrs BP; ca. 5050 CAL BP; 5282–4872 CAL BP.

NZA 3238: *Fulica chathamensis,* MNZ S33035; GR 445669; Long Beach, in situ at ~3 m a.s.l. in consolidated brown-sand horizon exposed on lower slopes of large, seaward-sloping deflation surface; 6879 ± 68 yrs BP; 7626 CAL BP; 7759–7529 CAL BP.

NZA 1935: *Fulica chathamensis,* MNZ S27819; GR 443675; Long Beach, associated skeleton on extensive deflation surface, ~2 m a.s.l. (former interdune lake?); 4990 ± 150 yrs BP; ca. 5737 CAL BP; 5988–5320 CAL BP.

NZA 794: *Pterodroma magentae,* NMZ S25362; GR 436683; Long Beach, on 30 m high dune ridge, ~200 m inland of shoreline. Site of former nesting colony? 3150 ± 150 yrs BP; 2982 CAL BP; 3351–2685 CAL BP.

Locality 5, Lake Marakapia

NZA 1932: *Pteodroma magentae,* MNZ S27823; GR 447677; Lake Marakapia, in situ (complete individual skeleton) in brown surface sand/soil of hilltop deflation area in farm pasture, ~15 m a.s.l. Site of former nesting colony? 2390 ± 140 yrs BP; 2047 CAL BP; 2351–1702 CAL BP.

NZA 1933: *Pteodroma magentae;* MNZ S27824: GR 447677; Lake Marakapia, in situ (complete individual skeleton) in yellow sand beneath brown surface sand/soil of hilltop deflation area in farm pasture. Site of former nesting colony?; 3310 ± 140 yrs BP; 3163 CAL BP; 3472–2814 CAL BP.

Locality 6, Tennant's Lake

NZA 795: *Pterodroma magentae,* MNZ S27008; GR 436693; Tennant's Lake, in situ (complete individual skeleton), ~200 m inland of shoreline, ~15 m a.s.l., on mosaic-cracked pan. Site of former nesting colony? 3420 ± 210 yrs BP; 3299 CAL BP; 3790–2798 CAL BP.

Locality 7, Ohira Bay

NZA 3430: *Hemiphaga chathamensis,* MNZ S (uncataloged); GR 384717; Ohira Bay, on eastern slope in brown sand, ~6 m a.s.l.; 4608 ± 66 yrs BP; ca. 5190 CAL BP; 5452–4989 CAL BP.

Locality 8, Waitangi West

NZA 2611: *Pterodroma magentae,* MNZ S31189; GR 252752; Waitangi West, in older consolidated dune series, ~50 m inland of shoreline, from dark brown sand/soil horizon, in places overlain by midden debris, ~3 m a.s.l.; 1114 ± 82 yrs BP; 690 CAL BP; 856–547 CAL BP.

NZA 3425: *Pachyanas chathamica,* MNZ S32638; GR 252752; Waitangi West, associated skeleton from low-lying deflation area, ~2 m a.s.l., between foredunes and inland consolidated dune series; 1913 ± 62 yrs BP; 1792 CAL BP; 1935–1625 CAL BP.

NZA 3285: *Gallirallus dieffenbachii,* MNZ S32639; GR 247764; Waitangi West, in inland dune series ~3–4 m a.s.l., in brown sand/soil immediately beneath occupation-midden shell stratum; 887 ± 59 yrs BP; ca. 730 CAL BP; 906–667 CAL BP.

NZA 3426: *Cygnus sumnerensis,* MNZ S (uncataloged); GR 247764; Waitangi West, in inland dune series ~3–4 m a.s.l., in pale brown sand/soil 30 cm beneath sample NZA 3285; 2306 ± 63 yrs BP; ca. 2250 CAL BP; 2358–2077 CAL BP.

NZA 2612: *Gallirallus dieffenbachii,* MNZ S31299; GR 250765; Waitangi West, from fine-grained, consolidated, pale brown sand (weathering to gray white), at ~3–4 m a.s.l. on N bank of Waihi Creek, ~200 m from outlet; 3625 ± 84 yrs BP; ca. 3880 CAL BP; 4088–3639 CAL BP.

Locality 9, Western Maunganui Dunes
(Cape Pattison E–Maunganui)

NZA 1950: *Paphies subtriangulatum,* MNZ S27830; GR 277761; Maunganui, Midden Site, 50 m E of Moravian Mission Stone Cottage. Marine midden shell from uppermost 10 cm of chocolate brown soil horizon (~35 cm thick) overlying natural dune sequence; 760 ± 140 yrs BP; 395 CAL BP; 634–121 CAL BP.

NZA 1949: *Gallirallus dieffenbachii,* MNZ S27831; GR 277761; Maunganui, Midden Site, 50 m E of Moravian Mission Stone Cottage. From brown, humic-stained dune sand, ~40 cm below NZA 1950; 1340 ± 150 yrs BP; ca. 1200 CAL BP; 1501–931 CAL BP.

NZA 1981: *Gallirallus dieffenbachii,* MNZ S27832; GR 277761; Maunganui, Midden Site, 50 m E of Moravian Mission Stone Cottage. From pale brown/gray, consolidated dune sand, ~70 cm below NZA 1950; 1830 ± 150 yrs BP; 1702 CAL BP; 2008–1353 CAL BP.

Locality 10, Mid-Maunganui Dunes
(Maunganui E–Washout Creek)

NZA 1947: *Diaphorapteryx hawkinsi,* MNZ S27828; GR 286760; Maunganui, in situ in pale brown, semiconsolidated foredune sand, 150 m E of Maunganui Bluff, ~3 m a.s.l.; 1860 ± 150 yrs BP; 1734 CAL BP; 2102–1400 CAL BP.

NZA 3608: *Gallirallus dieffenbachii,* MNZ S32892; GR 288760; Maunganui, ~4 m a.s.l., in back-beach dune face, from upper level of ~2 m thick, black brown (humic-stained) dune sand, here overlain by 50 cm thick layer of occupation-midden shell; 677 ± 60 yrs BP; ca. 600 CAL BP; 667–535 CAL BP.

NZA 2585: *Gallirallus dieffenbachii,* MNZ S29026; GR 289758; Maunganui, in brown sand of inland dune series, ~6 m a.s.l., ~300 m W of distinctive Basalt Knob; 4282 ± 89 yrs BP; ca. 4750 CAL BP; 5024–4523 CAL BP.

NZA 3189: *Hemiphaga chathamensis,* MNZ S32846; GR 289758; Maunganui, in brown sand of inland dune series, ~6 m a.s.l., ~300 m W of Basalt Knob. From fine, pale brown sand that seen laterally is overlain by thin (~10 cm) orange-colored sand layer (iron-stained) then 50 cm thick stratum of gray/black sandy soil. This sand/soil sequence here overlain by compact, 20 cm thick midden-shell layer, topped by recent drift sand; 4113 ± 67 yrs BP; ca. 4600 CAL BP; 4820–4411 CAL BP.

NZA 3191: *Diaphorapteryx hawkinsi,* MNZ S32834; GR 292758; Maunganui, immediately E of Basalt Knob, within inland dune series, from brown sand near base of N wall of ~8 m deep, nearly circular, steep-sided deflation hollow; 3857 ± 65 yrs BP; ca. 4200 CAL BP; 4406–3991 CAL BP.

NZA 3190: *Tadorna,* species undescribed, MNZ S32830; GR 292758; Maunganui, immediately E of Basalt Knob, from pale brown sand layer, 2 m below (stratigraphically) brown sand from which NZA 3191 was obtained; 5291 ± 66 yrs BP; ca. 6030 CAL BP; 6187–5902 CAL BP.

Locality 11, Eastern Maunganui Dunes
(Washout Creek E–Tahatika Creek)

NZA 1982: *Hemiphaga chathamensis,* MNZ S27832; GR 307758; Maunganui, in inland dune series, ~1.2 km E of Washout Creek (50 m W of Big Midden Site). From brown sand on south-facing deflation surface, ~5–6 m a.s.l. (stratigraphic equivalent of NZA 3189, NZA 3287); 3760 ± 160 yrs BP; 4067 CAL BP; 4510–3635 CAL BP.

NZA 2614: *Gallirallus dieffenbachii,* MNZ S32031; GR 308758; Maunganui, in inland dune series, ~1.25 km E of Washout Creek (Big Midden Site). From dark-stained sand ~30 cm beneath compact, 20 cm thick midden-shell horizon; 1390 ± 80 yrs BP; 1247 CAL BP; 1386–1069 CAL BP.

NZA 3287: *Diaphorapteryx hawkinsi,* MNZ S (uncataloged); GR 308758; Maunganui, in inland dune series, ~1.25 km E of Washout Creek (Big Midden Site). In situ in brown sand on south-sloping deflation surface, ~5–6 m a.s.l. (stratigraphic equivalent of NZA 1982, NZA 3189); 3966 ± 60 yrs BP; 4350 CAL BP; 4517–4152 CAL BP.

NZA 2609: *Hemiphaga chathamensis,* MNZ S30778; GR 347771; Maunganui, on ridge crest of inland dune series, ~500 m W of Tahatika Creek. In situ skeleton from pale brown sand at ~1.2 m, beneath ~10 cm thick, orange, iron-stained zone and brown black sandy soil, 30 cm thick, with rounded lag pebbles on surface; 3264 ± 84 yrs BP; ca. 3450 CAL BP; 3631–3218 CAL BP.

NZA 3286: *Pachyanas chathamica,* MNZ S32634; GR 349773; Tahatika, in situ in pale, gray brown sand, on low foredune (~2 m a.s.l.), ~250 m W of Tahatika Creek; 1529 ± 57 yrs BP; 1373 CAL BP; 1502–1293 CAL BP.

NZA 3284: *Fulica chathamensis,* MNZ S (uncataloged); GR 351772; Tahatika, from gullied, older red brown (iron-stained) sand, ~4 m a.s.l., on seaward (N) slopes of inland dune series, ~150 m W of Tahatika Creek; 3296 ± 59 yrs BP; ca. 3450 CAL BP; 3621–3361 CAL BP.

NZA 796: *Cygnus sumnerensis,* MNZ S26482; GR 354773; Tahatika, from seaward foredune slope, ~2 m a.s.l., 250 m E of Tahatika Creek (stratigraphic equivalent of NZA 3286); 1490 ± 130 yrs BP; 1351 CAL BP; 1606–1068 CAL BP.

NZA 1937: *Cygnus sumnerensis,* MNZ S27827; GR 354773; Tahatika, from brown sand forming nearly level deflation surface inland of foredune slope (cf. NZA 796), ~3 m a.s.l., 250 m E of Tahatika Creek; 1420 ± 140 yrs BP; 1276 CAL BP; 1533–985 CAL BP.

NZA 2603: *Cygnus sumnerensis,* MNZ S30709; GR 354773; Tahatika, from brown sand ridge upon main deflation surface (cf. NZA 1937), ~3 m a.s.l., ~300 m E of Tahatika Creek ; 792 ± 77 yrs BP; ca. 700 CAL BP; 891–549 CAL BP.

Locality 12, Taupeka Inland Dunes

NZA 2587: *Pelagodroma marina,* MNZ S30314; GR 517783; Taupeka inland dune series, ~2.5 km E of Taupeka. Excavated from face of large blowout hollow in consolidated, yellow brown sand ~3 m below present ground surface. As elsewhere along Taupeka inland dunes, fossiliferous sand lies beneath well-developed dune-soil sequence 1 m or so thick (see Figure 5); 6632 ± 98 yrs BP; 7127 CAL BP; 7330–6926 CAL BP.

NZA 3427: *Pterodroma* cf. *inexpectata,* MNZ S (uncataloged); GR 531778; Taupeka inland dune series, ~3 km E of Taupeka. From consolidated, pale brown sand ~2–3 m below present ground surface (cf. NZA 2587); 4935 ± 73 yrs BP; 5289 CAL BP; 5462–5048 CAL BP.

Locality 13, Lake Pateriki

NZA 3429: *Fulica chathamensis,* MNZ S (uncataloged); GR 660779; from pale, creamy white sand near base (~2–3 m a.s.l.) of sloping dune face at seaward end of E shore of Lake Pateriki; 2278 ± 70 yrs BP; ca. 2250 CAL BP; 2350–2053 CAL BP.

Locality 14, Kaingaroa

NZA 1983: *Fulica chathamensis,* MNZ S27834; GR 683787; SW of Kaingaroa on high dune ridge (~30 m a.s.l.). From depth of 50 cm in black peaty sand/soil forming seaward-sloping, lag-pebble strewn deflation surface (cf. NZA 1988, taken from 50 cm below); 2620 ± 160 yrs BP; 2623 CAL BP; 3062–2311 CAL BP.

NZA 1988: *Paleocorax moriorum,* MNZ S27835; GR 683787; SW of Kaingaroa on high dune ridge (~30 m a.s.l.). From depth of 1 m in brown-sand horizon (2 m+ thick), beneath 60-cm-thick black, peaty sand/soil that forms seaward-sloping, lag-pebble strewn deflation surface (cf. NZA 1983, taken from 50 cm above); 3410 ± 150 yrs; 3285 CAL BP; 3635–2898 CAL BP.

NZA 2588: *Cygnus sumnerensis,* MNZ S30421; GR 684796; W of Kaingaroa, at ~4 m a.s.l. in steep, beach-cut face of foredune. From yellow, unconsolidated sand, ~1 m below more compacted brown sand/soil horizon (buried occupation soil?), with midden shell debris upon it. This sequence exposed for >500 m southward along 2–10 m high, eroding, back-beach face; 1325 ± 84 yrs BP; ca. 1210 CAL BP; 1318–992 CAL BP.

Locality 15, Okawa Point

NZA 3428: *Hemiphaga chathamensis,* MNZ S (uncataloged); GR 706763; from extensive shallow deflation area (3–4 m a.s.l.) at S end of inland dune series, ~1.4 km N of Okawa Point. In pale brown sand beneath orange-colored incipient iron-pan, chocolate brown sand/soil, leached gray sand and, finally, loose yellow-white surface sand; 3938 ± 68 yrs BP; 4312 CAL BP; 4512–4093 CAL BP.

Locality 16, Te Ana a Moe Cave, W Shore of Te Whanga Lagoon

NZA 1948: *Gallirallus dieffenbachii,* MNZ S27829; GR 480652; Te Ana a Moe Cave, in SE quadrant, from ~60 cm depth immediately below surface of undisturbed sediments (Figure 6); 1250 ± 145 yrs BP; 1149 CAL BP; 1414–795 CAL BP.

NZA 798: *Gallirallus modestus,* MNZ S23708; GR 480652; Te Ana a Moe Cave, in SE quadrant, from ~65 cm depth in brownish cream bryozoan detrital sand, 5 cm below surface of undisturbed sediments (Figure 6); 1270 ± 120 yrs BP; ca. 1163 CAL BP; 1606–1068 CAL BP.

NZA 2778: *Tadorna,* species undescribed, MNZ S (uncataloged); 480652; Te Ana a Moe Cave, in NE quadrant, in brownish cream bryozoan detrital sand, ~15 cm below surface of undisturbed sediments (Figure 6); 1534 ± 62 yrs BP; ca. 1410 CAL BP; 1495–1338 CAL BP.

NZA 801: *Gallirallus modestus,* NMZ S27409; GR 480652; Te Ana a Moe Cave, in SW quadrant, in fine, pale cream, bryozoan detrital sand at ~90 cm depth (~30 cm below surface of undisturbed sediments; see Figure 6); 2290 ± 140 yrs BP; 2242 CAL BP; 2364–2003 CAL BP.

NZA 800: *Gallirallus modestus,* NMZ S27501; GR 480652; Te Ana a Moe Cave, in SW quadrant, in coarser, white, bryozoan detrital sand at ~1 m depth (~40 cm below surface of the undisturbed sediments; see Figure 6); 2950 ± 140 yrs BP; 3057 CAL BP; 3357–2768 CAL BP.

NZA 1989: *Pterodroma magentae,* MNZ S27836; GR 480652; Te Ana a Moe Cave, in SW quadrant at 1.25 m depth, in creamy brown sand, overlying rounded limestone cobbles (Figure 6), near end of short (~2 m long), blind-ending side tunnel; 3900 ± 150 yrs BP; 3904 CAL BP; 4308–3524 CAL BP.

Locality 17, Thomas Property, opposite Limestone Quarry, 4.5 km N of Te One

NZA 2589: *Hemiphaga chathamensis,* MNZ S30516; GR 469630; Lower Limestone Cave, excavated from sediments beneath overhang at base of exposed E face of outcrop; 2239 ± 87 yrs BP; 2188 CAL BP; 2348–1982 CAL BP.

NZA 2590: *Hemiphaga chathamensis,* MNZ S30516; GR 469630; Upper Limestone Cave, excavated from sediments beneath overhang 3–5 m above and 10 m W of NZA 2589; 2434 ± 88 yrs BP; ca. 2550 CAL BP; 2734–2187 CAL BP.

NZA 2777: *Pterodroma magentae,* MNZ S32593; GR 467630; ~400 m inland of S Long Beach, from dune sands mantling W portions of extensive outcrop of karstic Te Whanga Limestone. In situ skeleton from brown, surface-consolidated sand/soil overlying coarser, more friable yellowish sand (site of former nesting colony?); 2898 ± 64 yrs BP; 2691 CAL BP; 2814–2482 CAL BP.

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Locality 18, Tarawhenua Peninsula

NZA 2613: *Gallirallus dieffenbachii,* MNZ S31558; GR 690225; Tarawhenua Peninsula, from brown sands on W slope of narrow "neck" connecting peninsula to mainland; 2994 ± 83 yrs BP; 3104 CAL BP; 3336–2897 CAL BP.

NZA 1549: *Diomedea epomophora;* MNZ S27811; GR 679233; Tarawhenua Peninsula. Specimen from Lindsay collection (see Falla, 1960); 4440 ± 150 yrs BP; 4625 CAL BP; 4998–4224 CAL BP.

NZA 1906: *Diomedea epomophora,* MNZ S27817; GR 679233; from cliff-top exposure, at W extremity of Tarawhenua Peninsula. Bones of fledgling (indicative of former presence of nesting colony) from orange brown sandy soil (upon karstic Te Whanga Limestone), which underlies present pasture-grass surface; essentially same site as NZA 1549; 4300 ± 150 yrs BP; 4545 CAL BP; 4824–4059 CAL BP.

Locality 19, Motutapu Point

NZA 1907: *Diomedea epomophora,* MNZ S27818; GR 721248; from consolidated brown sand forming 50 cm thick surface layer, on steep S slope of Motutapu Point promontory, ~6–8 m a.s.l. Bones of fledgling (indicative of former presence of nesting colony); 1070 ± 150 yrs BP; 664 CAL BP; 935–436 CAL BP.

NZA 2586: *Fulica chathamensis,* MNZ S30949; GR 721248; from coarse, yellow sand, beneath 50 cm thick consolidated, brown-sand surface layer, ~15–20 m a.s.l., high on steep S slope of Motutapu Point promontory; 4419 ± 92 yrs BP; ca. 5000 CAL BP; 5292–4726 CAL BP.

Locality 20, Tupuangi

NZA 2631: *Hemiphaga chathamensis,* MNZ S31464; GR 741234; older dunes forming S bank of Tupuangi Creek estuary. From charcoal-blackened, greasy soil among oven stones at Moriori camp site. Indicates minimum date of first settlement of Pitt Island; 491 ± 80 yrs BP; ca. 450 CAL BP; 631–305 CAL BP.

NZA 3431: *Hemiphaga chathamensis,* MNZ S (uncataloged); GR 742235; older dune ridge, 200 m S of Tupuangi Creek estuary. From blowout hollow, in distinctive consolidated brown sand stratum, 1 m below present drift-sand surface; 1235 ± 60 yrs BP; ca. 1100 CAL BP; 1253–974 CAL BP.

Locality 21, Near Kokope Island

NZA 3461: *Hemiphaga chathamensis,* MNZ S (uncataloged); GR 756218; foredunes of Tupuangi dune series, just N of Kokope Island. Specimen in situ in brown-sand stratum stratigraphically below paler gray-sand horizon from which human (Moriori) skeletal remains were eroding. Indicates maximum age for human burial; 876 ± 62 yrs BP; 749 CAL BP; 906–663 CAL BP.

Locality Uncertain, Chatham Islands?

NZA 1548: *Haliaeetus australis;* BMNH A3732; "Chatham Islands," of uncertain provenance, from H.O. Forbes collection in The Natural History Museum, London; 1025 ± 51 yrs BP. Southern Hemisphere marine calibration, median 615 CAL BP; 679–533 CAL BP. Northern Hemisphere marine calibration, median 258 CAL BP; 406–114 CAL BP.

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The Role of Climate Change Versus Human Impacts—Avian Extinction on South Island, New Zealand

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ABSTRACT

The Late Quaternary avifaunas of South Island, New Zealand, reveal discrete faunal assemblages for the contrasting environments offered by wet, closed forest and open, grassland–shrubland–forest mosaics. These faunal associations are recognizable in deposits dating from the last glacial (Otiran) and the Holocene periods. Sites in western regions of South Island exhibit significant differences in the fauna's species composition between deposits formed in the last glacial period and those from the present interglacial period, but sites in the east do not. Several species became regionally extinct at the end of the glacial period, but all survived in the east until the present millennium. Although climate change caused the redistribution of species, all Late Quaternary extinctions in New Zealand were ultimately caused by humans during the last 1000 years.

Introduction

New Zealand has three main islands and numerous smaller ones, and it occupies the southernmost corner of Polynesia in the South Pacific Ocean. It is of continental origin but has been separated from other land masses for the last 80 million years and is now 1500 km from Australia. Its long isolation has resulted in a unique avifauna with a high degree of endemism and many flightless species (Fleming, 1979; Millener, 1990; Bell, 1991).

Fossil deposits have been known from New Zealand since the early nineteenth century; they are rich in material and are widely distributed (Atkinson and Millener, 1991; Worthy and Holdaway, 1993). Most early work sought to describe the unique elements of the fossil fauna, notably the various species of moa (Aves: Dinornithiformes; see references in Anderson, 1989), whereas paleoecological studies were lacking. Although fossil deposits in caves, swamps, and dunes provided extremely abundant remains, as recently as 1979 fossil avifaunas older than the Holocene in New Zealand were considered rare and limited in size (Fleming, 1979). Since then, extensive investigations of cave deposits combined with the intensive use of radiocarbon dating have shown that faunas of the last glacial age are common (Worthy, 1993a; Worthy and Holdaway, 1993, 1994a, 1995). Analysis of moa faunas throughout New Zealand showed that there was a pattern to the distribution of species that was related to habitat (Worthy, 1990).

This paper summarizes some of the important new information arising out of these and other recent studies of the Quaternary avifauna of New Zealand by the author and R.N. Holdaway. The primary purpose of the research has been to document fossil avifaunas and to describe the faunal changes brought about by climate during the last glacial–interglacial cycle, mainly during oxygen isotope stages 1 and 2. Study areas around South Island, New Zealand, were chosen for the range of climatic conditions each now has. Each area was kept small, usually 10–20 km across, to minimize geographic and present climate variation. These factors are assumed to have been instrumental in the control of vegetation physiognomies, so a relatively homogenous vegetation structure within each area is assumed and is related to the faunal composition. The distribution of birds was most affected by whether the vegetation was a closed-canopy forest or a mosaic of shrubland and grassland. The floral composition of the forest seems to have been of secondary importance to its structure, because closed forests, whether dominated by beech or by one of several podocarps, all had the same moa assemblage in the late Holocene. Also, grassland-shrubland associations in the subalpine zone have markedly different floras from those in lowland environments, but the same birds characterize both areas.

METHODS.—For each study area, all available fossil faunas of Holocene or Pleistocene age were examined, and extensive new collections were made. Efforts were made to obtain faunas

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with diverse taphonomic origins to offset the biases inherent in any one depositional environment. For example, pitfalls overly represent ground-dwelling species, and small, volant passerines are rare. The chronology of sites is based on 99 new and 27 preexisting radiocarbon dates obtained from bones (Worthy, 1993a, 1997; Worthy and Holdaway, 1993, 1994a, 1995, 1996). Most dates are based on accelerator-mass-spectrometry analysis of collagen or gelatin extractions from single bones as detailed in Worthy (1993a, 1997) and Worthy and Holdaway (1993, 1994a, 1995, 1996). Geologic ages cited hereafter are conventional radiocarbon ages. Nomenclature for species' binomials and English names of modern birds follows Turbott (1990).

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The Study Areas

GEOLOGY AND CLIMATE

FIGURE 1

WEST COAST.—The lowland (0–300 m) karst region between Punakaiki in the south and Charleston to the north, on the west coast of South Island, was studied by Worthy and Holdaway (1993). The area has a mild, humid climate, with mean monthly temperatures of 10°–18° C, and 2800–4000 mm of rainfall annually. A tall, closed-canopy, mixed beech (*Nothofagus*)/podocarp (dominated by *Dacrydium cupressinum* Lambert) rainforest characterizes the unmodified vegetation.

The fossil faunas are from sites in 42 caves and are up to 25,000 years old. Most faunas are from pitfalls. Some sites contained single skeletons lying on the surface; their origin is attributed to "vagrants" (individuals that entered the cave for any number of reasons and that often traveled 10–100 m from the entrance before dying). Often vagrants entered via large, horizontal entrances. The age of all such skeletons was considered individually because adjacent skeletons varied in age by thousands of years and may have been deposited during either the last glacial period or the present interglacial. There was only one fauna accumulated by the predatory Laughing Owl (*Sceloglaux albifacies*) (Worthy and Holdaway, 1994b).

HONEYCOMB HILL CAVE SYSTEM.—This cave system lies inland of Karamea, in the northwest part of South Island, in a valley at an altitude of about 300 m that receives 3000–4000 mm of rainfall annually. The present vegetation and temperatures are similar to those of the west-coast study area, although winter frosts occur.

There are more than 50 discrete fossil sites in this complex cave, which has about 14 km of passages and 70 entrances. The Graveyard and the Eagles Roost are the two most important sites (Worthy, 1993a). The fossil deposits are up to 20,000 years old.

TAKAKA HILL AND TAKAKA VALLEY.—Takaka Hill and Takaka Valley are in the northern part of South Island. Because southwesterly airflows prevail over New Zealand, and Takaka is east of a tract of mountains, it receives considerably less rainfall than the two previous study areas, about 2000–2500 mm annually. Temperatures are similar to those of the western sites (mean annual temperature for Takaka Valley is 12.7° C), although there is greater seasonality, with summer drought common, and on Takaka Hill snowfalls can be expected during winter. Sites in the valley (0–200 m) were compared to hill faunas (600–800 m) to detect altitudinal effects. The late Holocene vegetation of the valley was a tall, multitiered, closed-canopy mixed podocarp (dominated by *Podocarpus totara* D. Don) and broadleaf forest, compared with a closed-canopy (10–15 m), primarily beech (*Nothofagus* spp.) forest, with some Hall's Totara (*Podocarpus hallii* Kirk) and cedar (*Libocedrus* spp.) on the hill.

Fossil faunas were obtained from 43 caves in the combined hill and valley areas (Worthy and Holdaway, 1994a), although most were from the more extensive karst areas on the hill. Deposits are up to 30,000 years old and are mainly pitfalls, with only two significant faunas from Laughing Owl prey accumulations. None are in alluvial contexts.

NORTH CANTERBURY–MT. COOKSON.—The Mt. Cookson study area is a karst plateau at 400–600 m in the province of North Canterbury. Because it lies just east of the high Amuri Range and is about 20 km from the east coast, there is a marked rain-shadow effect. It has an annual rainfall of about 700 mm and a markedly seasonal climate; summers are hot (temperatures often >30° C), with drought common, and in winter snow lies on the ground for several weeks. The late Holocene vegetation was a closed-canopy beech forest.

Fossil faunas were from several pitfall sites and from three deposits accumulated by falcons (*Falco novaeseelandiae*) (Worthy and Holdaway, 1995). The sites are up to 38,000 years old.

NORTH CANTERBURY–WAIKARI.—All sites in the Waikari study area are at an altitude of 200–400 m and are within 10 km of Waikari in North Canterbury. The climate is dry, with annual rainfall of about 660 mm, and warm, with a mean annual temperature of 10.8° C. It is markedly seasonal; summer droughts are common, and in winter frosts and occasional snowfalls are normal. The late Holocene vegetation (5000–1000 years ago) was a tall podocarp (dominated by *Prumnopitys taxifolia* (Banks & Solander ex Lamb.) de Laub.) forest on the valley floors, with beech forest above this on the higher slopes (to 800 m). Areas of shrublands and grasslands were present on ridges and along river beds. The

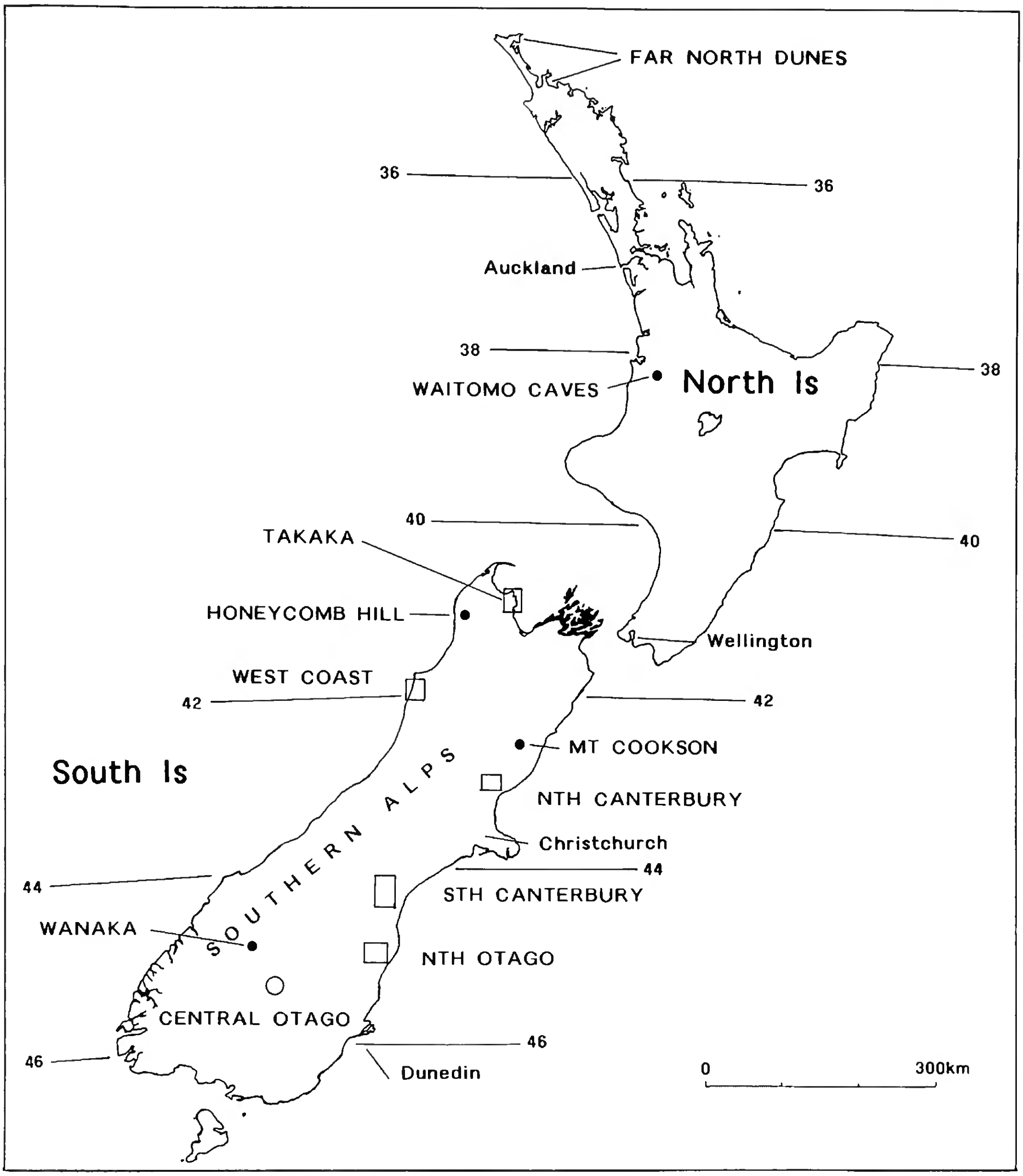

FIGURE 1.—Map of New Zealand showing the study areas on South Island, the four main cities (Auckland, Wellington, Christchuch, and Dunedin), major geographic features, and degrees of south latitude (numbered bars). Waitomo Caves and the Far North dunes are areas with important fossil deposits.

vegetation was characterized by its mosaic nature and differed markedly from the closed-canopy forests of western regions.

The faunas are from sites with diverse taphonomic histories: 10 sites are Laughing Owl deposits, five are swamps, one is a cave pitfall, two are archaeological, and several are rockshelters (Worthy and Holdaway, 1996). Most faunas are of Holocene age, but one is late glacial (10,000–12,000 years old). The oldest is from Otiran deposits (>24,000–<100,000 years old) in alluvial beds in the Waipara Valley.

SOUTH CANTERBURY.—The South Canterbury study area is at an altitude of 200–400 m and is located between Fairlie, Raincliff, and Bluecliffs Station (25 km southwest of Timaru). The climate is very similar to that of the Waikari study area, and the late Holocene vegetation is assumed also to have been very similar.

The 59 fossil sites include 27 Laughing Owl deposits, two falcon deposits, two swamps, and 28 cave pitfall or rockshelter deposits (Worthy, 1997). The deposits are up to 38,000 years old, although most are of late-Holocene age.

OTAGO.—Three study areas were chosen in Otago because this large region has a very varied geography and climate, including the driest regions of New Zealand.

1. *North Otago downlands* (<300 m; between Oamaru and Duntroon just south of the Waitaki River): The climate is mild, with an annual temperature of 11° C and low rainfall (500–550 mm annually). Summer drought is common but is not as extreme as in more inland regions of Otago. The late-Holocene vegetation was a tall podocarp (*Prumnopitys taxifolia* dominated) forest on the downlands, but in the alluvial valley floors *Dacrycarpus dacrydioides* (Rich.) de Laub. probably prevailed. The faunas are from fossil sites of diverse taphonomies: seven swamps, 11 Laughing Owl deposits, one falcon deposit, and 11 cave or rockshelter deposits of pitfall or vagrant derivation.

2. *Wanaka, western Otago:* Several sites are at altitudes between 300 m and 600 m in the lee of the Southern Alps near Wanaka. Most are pitfall deposits in fissures formed between large blocks of schist, but three have faunas accumulated by Laughing Owls, and two are swamps. Annual rainfall at Wanaka is low (419–952 mm, mean 682 mm). The late-Holocene vegetation of the hillslopes around most sites was a closed-canopy beech forest, but alluvial river flats had podocarp forests. Adjacent areas of higher altitude, and recently stable river flats, had shrubland and grassland.

3. *Alexandra to Cromwell, central Otago:* Fossil faunas are from isolated sites in fissures within schist, at altitudes from 300 m to 600 m. Only a few fissures had extensive faunas. Two swamp deposits are present, but no deposits accumulated by predators were found. Alluvial deposits at Chatto Creek contain the only fauna of Otiran age, although it is small. The incised gorges of the Clutha and Manuherikia rivers are up to 300 m deep and are notable features. Broad valleys at 200–300 m are surrounded by rounded ranges rising to 1700 m. In central Otago, rainfall varies from about 330 mm to 560 mm, with a mean of 409 mm. Mean annual temperature is about 11° C at Cromwell and Alexandra but rapidly decreases with altitude on the nearby ranges. There is marked seasonality; summer temperatures often exceed 30° C, with drought common, and in winter frosts are severe, and snowfalls are usual.

CLIMATIC AND VEGETATIONAL HISTORY

There are many data on the vegetation of the late Holocene but fewer for progressively older time periods. The following is an attempt to place successive fossil faunas in their contemporary habitat.

The period of time considered herein is roughly the last 50,000 years (oxygen isotope stages 1 to 3) and, more importantly, the last 20,000 years (stages 1 and 2). In the first half of oxygen isotope stage 3 (ca. 57,000–35,000 years ago (Nelson et al., 1993)), the climate in New Zealand was 2°–3° C cooler than at present. Average annual temperatures then decreased and reached a glacial minimum at 18,000 years ago, during the Kumara-2 glacial advance (Suggate and Moar, 1970; Suggate, 1990), of 4°–5° C cooler than the present (McGlone, 1988; Mildenhall, 1995). There were some minor retreats and advances of glaciers, but full glacial conditions lasted at least until about 14,000 years ago (Suggate, 1965, 1990; Suggate and Moar, 1970), and it has even been suggested that the retreat of glaciers did not begin until 12,500 to 13,000 years ago in some areas (Mabin, 1983). Temperatures approaching those of the present were achieved about 10,000 years ago. An increase in precipitation was associated with warming, whereas the glacial periods were cold and dry.

The coldest periods of the glaciation saw the treeline lowered by an average of 800 m to 830 m below that of the present (Soons, 1979; McGlone, 1985, 1988). Trees and shrubs declined in importance from about 30,000 years ago and by 18,000 years ago were in low percentages, if present at all, in most sites. A corresponding rise in the representation of pollen of Poaceae and various shrub taxa shows that a mosaic of grassland and shrubland dominated the landscapes. In western areas, at lower altitudes, it is probable that some stands of forest survived because it is unlikely that rainfall could have dropped to sufficiently low levels to have prevented the growth of forest, as it did in eastern areas (McGlone, 1988).

In the west-coast study area, the vegetation during the coldest times of the last glacial period (Otiran) was a mosaic of tall shrubland and beech forest, with grassland and shrubland in the river valleys, induced by localized cold air drainage off the mountains. The pollen record indicates that a tall, closed-canopy podocarp forest became established shortly after 12,000 years ago and has been the vegetation ever since (McGlone, 1988; Worthy and Holdaway, 1993).

Around Honeycomb Hill Cave, a tall shrubland, including tree ferns, persisted in the valley floor throughout the glacial period, but shorter, shrubland-grassland mosaics occupied adjacent slopes. The present tall, closed-canopy, mixed podocarp forest became established between 10,000 and 12,000 years ago (Worthy and Mildenhall, 1989).

On Takaka Hill, the sites were well above the depressed treeline of the last glacial period. Although a glacial pollen record for this region is lacking, it seems reasonably certain that there was a mosaic of shrubland and grassland around the fossil sites at this time. With the warming at the end of the glacial period, a tall shrubland became established, which was replaced about 8000 years ago by a beech forest that has persisted to the present day (McGlone, 1988; Worthy and Holdaway, 1994a). A similar history is envisaged for Mt. Cookson, although it is probable that this more eastern area was even drier and that the Otiran vegetation was even more open and sparse and was dominated by grassland (McGlone, 1988; Worthy and Holdaway, 1995).

The vegetational history of the study areas in North and South Canterbury and in North Otago is inferred to have been similar (McGlone, 1988). Shrublands and grasslands were the primary vegetation types throughout the Otiran period. In the late glacial, about 12,000 years ago, a taller shrubland community became established, and areas of grassland were reduced.

Tall shrublands persisted until 5000–6000 years ago, when increased precipitation allowed a tall podocarp forest to develop, at least in valley floors and on lower slopes. Beech forest spread in higher altitudes, but shrubland remained a significant component of regional vegetation. Between 800 and 1000 years ago all forest and tall shrubland was destroyed by anthropogenic fires, and grassland and short shrubland again became widespread.

McGlone et al. (1995) described pollen profiles from central Otago sites that record the vegetation from the late Pleistocene to the late Holocene. Between about 12,000 and 9000 years ago, a low scrub (1–2 m high) of small-leaved and xerophytic species formed a mosaic with *Chionochloa* grassland. Although tall podocarp forest was established in coastal areas of Southland and Otago by 9500 years ago, such forest is unlikely to have existed in other than small isolated stands in the interior before about 7500 years ago. The delay in forest establishment there may be explained by a decrease in available water at that time, either by lower rainfall or by a combination of increased evapotranspiration (resulting from higher temperatures) and decreased rainfall. The absence of, or very slow, peat deposition during this interval seems to support a prevailing water deficit. An abundance of tree-fern spores in the same period, however, suggests water was not limiting, at least in sheltered gullies. Frequent fires enabled the continued presence of tree ferns by stopping the establishment of slower growing, fire-sensitive podocarps, thus maintaining seral conditions.

About 7500 years ago a coniferous forest of *Prumnopitys taxifolia, Dacrycarpus dacrydioides,* and *Podocarpus* abruptly replaced lower altitude grassland communities, whereas *Phyllocladus alpinus* Hook.f. and *Halocarpus bidwilli* (Hook.f. ex Kirk) Quinn formed the upper treeline. The afforestation has been attributed to increased precipitation and a slight decrease in temperature. *Nothofagus menziesii* (Hook.f.) Oerst. became established in the area about 6000 years ago, followed shortly by a *Nothofagus fusca* type and *Dacrydium cupressinum,* although *Phyllocladus* dominated pollen assemblages. Significant percentages of pollen of shrub taxa such as *Coprosma,* Asteraceae, and Poaceae indicate the continued presence of grassland-shrubland communities above the treeline. After 3000 years ago, episodic destruction of podocarp forests by fire resulted in a reduction in the frequency of some tree pollen, especially *Prumnopitys taxifolia,* and an increase in grass pollen. Forests were widely destroyed by anthropogenic fires, resulting in a sudden proliferation of *Pteridium esculentum* (Forster f.) Nakai spores and vastly increased amounts of charcoal about 600 years ago.

Avifaunal Changes

The composition of the Late Quaternary and Holocene avifauna of terrestrial and inland wetland habitats is summarized in Table 1 from data in Millener (1990), with alterations as elucidated in Worthy (1993a, 1997) and Worthy and Holdaway (1993, 1994a, 1996). The following notes support the numbers of species listed herein as inhabiting such inland areas.

Pelecaniformes	Only *Pelecanus, Phalacrocorax carbo,* and *P. melanoleucos* are inland taxa.
Ciconiiformes	Only *Egretta alba, Botaurus stellaris,* and *Ixobrychus novaezelandiae* are inland taxa.
Anseriformes	I do not accept *Anas rhynchotis* or *Oxyura* as part of the prehuman fauna, *Mergus* was coastal, and only *Cnemiornis* had endemic species on each island.
Falconiformes	*Circus approximans* is a recent immigrant, so the prehuman fauna comprised one eagle, one harrier, and one falcon.
Gruiformes	The North and South Island pairs *Aptornis otidiformis/A. defossor* and *P. mantelli/Porphyrio hochstetteri* each consist of separate species (Trewick, 1996); *Porphyrio p. melanotus* is considered a recent immigrant; *Gallirallus philippensis* is recorded from glacial deposits on South Island; and *Porzana tabuensis* and *P. pusilla,* although rare as fossils, are assumed to have been on both islands.
Charadriiformes	Only *Haematopus unicolor, Charadrius bicinctus, Thinornis novaeseelandiae, Anarhynchus frontalis, Coenocorypha aucklandica, Himantopus novaezelandiae, Larus dominicanus, L. bulleri,* and *Sterna albostriata* used inland areas habitually.
Passeriformes	There are seven acanthisittid wrens, among which *Pachyplichas* had discrete species on each island and *Dendroscansor decurvirostris* was endemic to South Island. The three

TABLE 1.—The number of species in each order of birds that inhabited prehuman inland wetlands and/or terrestrial habitats on North and South islands, New Zealand. Data is from Millener (1990), Worthy (1993a, 1997), and Worthy and Holdaway (1993, 1994a, 1996).

Order	North Island	South Island	Total
DINORNITHIFORMES	7	9	11
APTERYGIFORMES	2	3	3
PODICIPEDIFORMES	2	2	2
PELECANIFORMES	3	3	3
CICONIIFORMES	3	3	3
ANSERIFORMES	11	11	12
FALCONIFORMES	3	3	3
GALLIFORMES	1	1	1
GRUIFORMES	9	8	11
CHARADRIIFORMES	9	9	9
COLUMBIFORMES	1	1	1
PSITTACIFORMES	5	5	5
CUCULIFORMES	2	2	2
STRIGIFORMES	2	2	2
CAPRIMULGIFORMES	1	1	1
CORACIFORMES	1	1	1
PASSERIFORMES	20	20	24
Total	82	84	94

species of *Mohoua* are distributed one on North Island and two on South Island. North Island has two endemic monotypic genera, *Notiomystis* and *Heterolocha*. Procellariids are not listed here, although at least 15 species nested on one island or the other.

A total of 94 species lived in inland habitats in mainland areas of New Zealand prior to human colonization: 82 on North Island and 84 on South Island. The birds recorded in fossil faunas from South Island are listed in Table 2.

CHANGES CAUSED BY THE LOWERED TREELINE

Some faunal changes are directly explicable as the result of downslope movement of faunal groups that in the Holocene are associated with the subalpine zone. The recovery of faunas from the numerous fossil sites in the extensive areas of karst in subalpine areas of northwest Nelson has provided considerable data (Worthy, 1989, unpublished data). Fossil avifaunas from caves now above the treeline (>1200 m) are assumed to have accumulated in the last few thousand years of the Holocene because the karst was glaciated in the last glacial period. More-

TABLE 2.—The fossil avifauna of South Island, New Zealand. West coast data is from Worthy and Holdaway (1993), with glacial faunas derived particularly from Babylon Cave, Hermits Cave, and Honeycomb Hill (Worthy, 1993). Takaka faunas are from Worthy and Holdaway (1994a), with sites in Irvines Tomo, the cave in the Golden Bay Cement Co. silica quarry, Hawkes Cave, Kairuru Cave, and Hobsons Tomo, the most important site for the Otiran fauna. Data for North Canterbury is mainly from the Waikari study area (Worthy and Holdaway, 1996), but the last glacial faunas are derived from Merino Cave, Mt. Cookson (Worthy and Holdaway, 1995), fluvial sites at Omihi Stream, Waipara (Worthy and Holdaway, 1996), and from loess sites (Worthy, 1993b). Data for South Canterbury and for Otago is from Worthy (1997, unpublished data, respectively). (Ab=species at least locally abundant, coastal=species present only in coastal sites, rare=species rare, valley=species present only in Takaka Valley, Y=species present in fossil record.)

Taxon	West Coast (Glacial)	West Coast (Holocene)	Takaka (Glacial)	Takaka (Holocene)	North Canterbury (Glacial)	North Canterbury (Holocene)	South Canterbury (Glacial)	South Canterbury (Holocene)	North Otago (Holocene)	Central Otago (Holocene)
Megalapteryx didinus	Y (Ab)	Y	Y		Y			Y (rare)		Y (Ab)
Anomalopteryx didiformis		Y (Ab)		Y (Ab)		Y (rare)		Y (rare)		
Pachyornis elephantopus	Y (Ab)		Y (Ab)		Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)
Pachyornis australis	Y[1]		Y							
Euryapteryx geranoides	Y (Ab)[2]		Y (Ab)		Y (Ab)	Y (Ab)		Y (Ab)	Y (Ab)	Y (Ab)
Emeus crassus					Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)
Dinornis struthoides	Y	Y	Y	Y (Ab)	Y	Y		Y	Y	Y
Dinornis novaezealandiae		Y (Ab)	Y	Y (Ab)	Y			Y (rare)		Y (rare)
Dinornis giganteus			Y (valley)		Y	Y (Ab)	Y	Y	Y	Y
Apteryx australis/haastii	Y	Y (Ab)	Y	Y (Ab)	Y	Y	Y	Y	Y	Y
Apteryx owenii		Y		Y (Ab)		Y		Y	Y	Y
Poliocephalus rufopectus						Y				
Procellaria parkinsoni		Y								
Procellaria westlandica		Y								
Pterodroma inexpectata	Y	Y		Y		Y		Y		
Pterodroma cookii	Y	Y				Y		Y	Y	
Puffinus griseus						Y (coastal)				
Puffinus spelaeus (s) or *gavia/huttoni* (g/h)	Y(s) (Ab)	Y(s) (Ab)	Y(s)	Y(s)		Y(g/h)		Y(g/h)	Y(g/h)	Y
Pelecanoides urinatrix	Y (Ab)[3]	Y				Y		Y	Y	
Oceanites nereis						Y		Y	Y	
Fregetta tropica ssp.	?	?								
Pelagodroma marina									Y	
Pachyptila turtur	Y (Ab)	Y						Y		
Anas chlorotis		Y		Y (Ab)		Y (Ab)		Y	Y	Y
Anas gracilis						Y				
Anas superciliosa					Y	Y		Y	Y	
Aythya novaeseelandiae					Y	Y				
Euryanas finschi	Y (Ab)		Y (Ab)		Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)
Hymenolaimus malacorhynchos	?	Y		Y				Y		Y
Malacorhynchus scarletti						Y			Y	
Biziura delautouri									Y	
Tadorna variegata	Y		Y (valley)		Y	Y (Ab)		Y	Y	Y
Cnemiornis calcitrans	Y (Ab)[4]		Y (valley)		Y	Y	Y (Ab)	Y (Ab)	Y (Ab)	Y (Ab)
Cygnus sumnerensis					Y				Y	

TABLE 2.—Continued.

Taxon	West Coast (Glacial)	West Coast (Holocene)	Takaka (Glacial)	Takaka (Holocene)	North Canterbury (Glacial)	North Canterbury (Holocene)	South Canterbury (Glacial)	South Canterbury (Holocene)	North Otago (Holocene)	Central Otago (Holocene)
Strigops habroptilus		Y (Ab)	Y	Y (Ab)		Y		Y	Y	
Nestor meridionalis		Y (Ab)		Y		Y (Ab)		Y	Y	
Nestor notabilis	Y (Ab)	Y	Y	Y	Y	Y		Y	Y	Y (Ab)
Cyanoramphus spp.	Y	Y		Y (Ab)		Y (Ab)		Y (Ab)	Y (Ab)	Y
Ninox novaeseelandiae	Y		Y	Y		Y		Y	Y	
Sceloglaux albifacies	Y		Y	Y	Y	Y (Ab)		Y (Ab)	Y (Ab)	Y
Aegotheles novaezealandiae	Y	Y (Ab)		Y (Ab)	Y	Y (Ab)		Y	Y	Y
Hemiphaga novaeseelandiae	Y	Y	Y	Y	Y	Y (Ab)		Y (Ab)	Y (Ab)	Y
Eudynamys taitensis		Y							Y	
Falco novaeseelandiae	Y	Y	Y	Y		Y		Y	Y	Y
Circus eylesi	Y		Y	Y	Y	Y		Y	Y	
Harpagornis moorei	Y		Y		Y	Y	Y	Y	Y	Y
Gallinula hodgenorum	Y		?		Y	Y (Ab)		Y (Ab)	Y (Ab)	Y
Gallirallus australis	Y (Ab)	Y (Ab)	Y	Y (Ab)	Y	Y (Ab)	Y	Y	Y	Y
Gallirallus philippensis	Y									
Porphyrio hochstetteri	Y		Y			Y	Y	Y	Y	Y
Fulica prisca	Y		Y		Y	Y (Ab)	Y	Y	Y	
Aptornis defossor	Y (Ab)[5]		Y		Y	Y (Ab)	Y	Y	Y	
Larus dominicanus									Y	
Coenocorypha aucklandica	Y	Y		Y		Y (Ab)		Y	Y	Y
Charadrius bicinctus						Y		Y	Y	
Thinornis novaeseelandiae						Y				
Sterna albostriata						Y				
Himantopus novaezelandiae						Y			Y	
Egretta alba						Y				
Phalacrocorax carbo		Y		Y						
Phalacrocorax varius				Y						
Coturnix novaezelandiae	Y			Y (rare, valley)	Y	Y (Ab)	Y	Y (Ab)	Y (Ab)	Y
Acanthisitta chloris	Y	Y (Ab)		Y (Ab)		Y		Y	Y	Y
Xenicus sp.	Y	Y (Ab)		Y (Ab)		Y		Y	Y	
Traversia lyalli		Y (Ab)		Y (Ab)		Y		Y	Y	
Pachyplichas yaldwyni	Y	Y (Ab)		Y (Ab)		Y		Y		
Dendroscansor decurvirostris	?		Y							
Bowdleria punctata						Y		Y	Y	
Prosthemadera novaeseelandiae		Y		Y		Y (Ab)		Y	Y	
Anthornis melanura		Y		Y (Ab)		Y		Y	Y	Y
Petroica australis	Y	Y (Ab)		Y (Ab)		Y (Ab)		Y (Ab)	Y (Ab)	Y
Petroica macrocephala	Y	Y (Ab)		Y		Y		Y	Y	
Mohoua ochrocephala	Y	Y		Y (Ab)		Y		Y	Y	
Mohoua novaeseelandiae		Y		Y		Y		Y	Y	
Gerygone igata		Y		Y		Y		Y		
Corvus moriorum	Y		Y			Y		Y (rare)	Y	
Rhipidura fuliginosa		Y		Y		Y		Y (Ab)	Y	
Anthus novaeseelandiae	Y			Y rare		Y		Y (Ab)	Y (Ab)	Y
Callaeas cinerea	Y	Y (Ab)	Y	Y		Y (Ab)	Y	Y (Ab)	Y (Ab)	Y
Philesturnus carunculatus	Y	Y (Ab)		Y (Ab)		Y		Y	Y	
Turnagra capensis	Y	Y		Y rare		Y (Ab)		Y (Ab)	Y (Ab)	
TOTAL[6]	42–45	42	27–28	40	25	64	13	59	58	16

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[1] *Pachyornis australis* was abundant in Honeycomb Hill (300 m above sea level (a.s.l.)) Otiran faunas.

[2] *Euryapteryx geranoides* was common at low levels on the west coast but was rare at Honeycomb Hill.

[3] *Pelecanoides urinatrix* was abundant in some coastal sites in the Otiran, e.g., Road Cave (Worthy, unpublished data).

[4] *Cnemiornis* was abundant at low levels on the west coast but was rare at Honeycomb Hill in the Otiran.

[5] *Aptornis* was abundant at Honeycomb Hill (300 m a.s.l.) but was rare at low levels on the west coast in the Otiran.

[6] This total species diversity does not include recent self-introduced species, listed below, or any of the European introductions that are incorporated in the youngest faunas. The following species are not found in any deposits demonstrably older than 1000 years and so are assumed to have colonized New Zealand following the habitat disruptions caused by Polynesians: shoveler (*Anas rhynchotis*), pukeko (*Porphyrio p. melanotus*), and Australasian Harrier (*Circus approximans*).

over, they did so in much the same environment as is now there (Worthy, 1989).

The dominant moa in subalpine sites is the Upland Moa (*Megalapteryx didinus*), with the Crested Moa (*Pachyornis australis*) the only other emeid. The dinornithids are most commonly represented by the Slender Moa (*Dinornis struthoides*) and the Large Bush Moa (*D. novaezealandiae*); the Giant Moa (*D. giganteus*) has never been found at these altitudes. Associated birds included Finsch's Duck (*Euryanas finschi*), Great-spotted Kiwi (*Apteryx haastii*), Little-spotted Kiwi (*Apteryx owenii*), New Zealand Coot (*Fulica prisca*), South Island Takahe (*Porphyrio hochstetteri*), Weka (*Gallirallus australis*), Eyles's Harrier (*Circus eylesi*), Haast's Eagle (*Harpagornis moorei*), New Zealand Falcon (*Falco novaeseelandiae*), Kakapo (*Strigops habroptilus*), Kea (*Nestor notabilis*), New Zealand Pipit (*Anthus novaeseelandiae*), Rock Wren (*Xenicus gilviventris*), and Stephens Island Wren (*Traversia lyalli*) (Worthy, 1989; unpublished data).

Downslope from the subalpine zone there is a gradual change in the species composition of moa faunas. For example, in sites of Holocene age in northwest Nelson near Mt. Arthur, *Megalapteryx didinus* dominates assemblages between 700 m and 900 m, but *Anomalopteryx didiformis* also is present. Below 700 m, *A. didiformis* is the only emeid present. Similar altitudinal changes in species composition are known for Fiordland (Worthy, 1989).

On Takaka Hill, the Holocene moa fauna is dominated by *A. didiformis,* whereas *M. didinus* is unknown (Worthy and Holdaway, 1994a). In deposits of the last glacial age, however, *M. didinus* is present, and *A. didiformis* is absent, a difference best explained as the result of altitudinal depression of the subalpine ecosystems. The deposits in Honeycomb Hill Cave, to the west, record a similar pattern: *M. didinus* and *Pachyornis australis* dominate deposits 14,000–20,000 years old.

REGIONAL CHANGES IN AVIFAUNAS

The most significant result of the recent studies of the South Island Quaternary avifaunas is that faunas from sites separated by as little as a few meters may differ markedly in species composition because of different ages. As a result, where in the past such associations were used as evidence for the coexistence of various species (e.g., Atkinson and Millener, 1991), they are now known to be the result of deposition at different times with markedly different environments. Graham and Lundelius (1984) expressed the opinion that most individual stratigraphic units are deposited over too short a time period for them to have accumulated through periods of environmental change. In New Zealand, unconformities separating deposits of glacial, late glacial, and Holocene age are the exception rather than the rule, and many sites have faunal remains essentially on the cave floor that range in age from modern to 20,000–30,000 years old, such as Hawkes Cave (Worthy and Holdaway, 1994a). Articulated skeletons of all ages indicate continuous deposition throughout this time. In the caves where many dates on individual bones are available, such as Madonna Cave (Worthy and Holdaway, 1993), Hawkes Cave, Kairuru Cave, Irvines Cave (Worthy and Holdaway, 1994a), and Honeycomb Hill Cave (Worthy, 1993a), the association of the moas *Pachyornis elephantopus* and *Euryapteryx geranoides* with *Anomalopteryx didiformis* is shown to be the result of deposition at different time periods. Many other undated talus accumulations beneath cave entrances have essentially unstratified deposits, with these same species found together, indicating that the deposits were accumulated and mixed over a significant time period, for example, Ngarua Cave and Commentary Cave (Worthy and Holdaway, 1994a). Graham (1993) described deposits such as these as time-averaged sequences and detailed numerous methods, with examples, whereby disharmonious associations could form by various time-averaging processes. In New Zealand, the factors that promote time-averaged sequences are constant humidity (deposits are always wet), low temperatures (most sites average <10° C, so weathering is slow, bones last longer, and weathering of cave surfaces provides little sediment), and low rates of alluvial sedimentation.

The fossil faunas from New Zealand caves in the regions now characterized by wetter climates all record major changes in the living faunas between the Otiran glacial period and the Holocene, especially the late Holocene (<6000 years ago). Thus, there are two distinct faunas in the fossil deposits, as the data in Tables 2 and 3 show.

THE WESTERN OTIRAN FAUNA.—The Otiran (last glacial) lowland fauna of western regions is characterized by the presence of the Stout-legged Moa (*Euryapteryx geranoides*), the Heavy-footed Moa (*Pachyornis elephantopus*), and a large morph of *Megalapteryx didinus.* Associated carinates include the South Island Goose (*Cnemiornis calcitrans*), South Island Adzebill (*Aptornis defossor*), *Fulica prisca,* New Zealand Gallinule (*Gallinula hodgenorum*), *Harpagornis moorei,* and *Euryanas finschi.* The members of this group, hereafter termed the *Euryapteryx* assemblage (Table 3), are all unknown from, or are very rare in, Holocene deposits in these areas.

There are differences in the relative frequency of species between the study areas within this western region. For example, the Otiran fauna at Honeycomb Hill differs from those in the lower-altitude west coast area in that *Pachyornis australis* is abundant, *P. elephantopus* is rare, *Cnemiornis* is rare, and *Aptornis* is common. In the Punakaiki karst, *P. australis* is rare, and *Cnemiornis* is more common than *Aptornis.*

THE WESTERN HOLOCENE FAUNA.—In contrast to Otiran faunas, Holocene deposits have a distinctive suite of species termed the *Anomalopteryx* assemblage (Table 3). The small emeid *Anomalopteryx didiformis* dominates this fauna and is usually associated with *Dinornis struthoides* and *D. novaezealandiae.* If *Megalapteryx didinus* is present, it is only as small morphs. Kakapo (*Strigops habroptilus*), Weka (*Gallirallus australis*), and kiwis (*Apteryx* spp.) are common, and the Brown Teal (*Anas chlorotis*) is the duck most often encoun-

TABLE 3.—Lists of characteristic species of the *Anomalopteryx* and *Euryapteryx* assemblages that respectively characterize the closed-canopy wetter forests typical of western areas in the Holocene and the forest-shrubland-grassland mosaics of the drier eastern areas, when these species occur together in abundance.

Anomalopteryx assemblage	*Euryapteryx* assemblage
Anomalopteryx didiformis	*Euryapteryx geranoides*
Dinornis novaezealandiae	*Euryapteryx curtus*
Apteryx australis	*Emeus crassus*
Strigops habroptilus	*Dinornis giganteus*
Anas chlorotis	*Pachyornis mappini/elephantopus*
Gallirallus australis	*Pachyornis australis* (uplands only)
Callaeas cinerea	*Megalapteryx didinus* (uplands only)
Philesturnus carunculatus	*Cnemiornis gracilis/calcitrans*
Pachyplichas jagmi/yaldwyni	*Euryanas finschi*
Xenicus longipes	*Aptornis otidiformis/defossor*
Petroica australis	*Gallinula hodgenorum*
	Fulica prisca
	Harpagornis moorei
	Coturnix novaezelandiae

tered. Acanthisittid wrens of several species are abundant in deposits (when conditions of preservation permit), and the New Zealand Robin (*Petroica australis*) and Saddleback (*Philesturnus carunculatus*) are abundant. It is important to note that these species are found in faunas deposited under vegetational mosaics but are relatively rare and infrequent, in contrast to their numerical abundance and dominance of faunas from areas where the vegetation was a closed-canopy forest. It is therefore not presence or absence so much as relative frequency that is important in the definition of this assemblage. In contrast, the mere presence of species listed in the *Euryapteryx* assemblage indicates the presence of open habitat.

NORTH CANTERBURY.—The Mt. Cookson study area occupies an intermediate zone between the wetter west and the drier east and, as expected, does not exhibit the same degree of faunal turnover. The drier climate of eastern areas is probably responsible for the delay of the establishment of closed-canopy forest until about 6000 years ago, much later than in the west. During the latter stages of oxygen isotope stage 3 and the early part of stage 2, *Pachyornis elephantopus* dominated moa faunas on Mt. Cookson but was associated with rare remains of *Dinornis giganteus, D. struthoides, Megalapteryx didinus, Emeus crassus,* and *Euryapteryx geranoides.* During the coldest period of the last glacial, however, *P. elephantopus* was virtually the only moa living in these and other eastern landscapes, where loess was being deposited. But, as in the west, with warming temperatures and forest establishment in the late Holocene, *Anomalopteryx didiformis* and *Dinornis novaezealandiae* came to dominate the faunas. Unlike in the west, however, *Euryanas finschi* and *Aptornis defossor* remained common in the late Holocene fauna, perhaps because the forests remained much drier.

THE TYPICAL EASTERN FAUNAS.—In contrast to the above faunas, those of the lowlands in North and South Canterbury and North Otago provide no evidence for any faunal turnover in the period spanning the last glacial to the late Holocene. The greatest change detected is a reversal of dominance roles within the same suite of species: whereas *Emeus crassus, Euryapteryx geranoides,* and *P. elephantopus* were the main emeids throughout this time, *Pachyornis elephantopus* dominated glacial faunas, but *Emeus crassus* was the most common during the Holocene. *Dinornis giganteus* and *D. struthoides* were the dominant dinornithids during the glacial and the Holocene.

In these eastern lowlands, there is no evidence of local extirpation of taxa at the end of the glacial period, as there is for western regions. The lack of glacial faunas containing smaller birds limits comparisons of faunal turnover to moas. Because there are no drastic changes in the moa faunas, however, and because *Cnemiornis, Harpagornis,* and *Aptornis* are known to have frequented the Otiran landscapes, and continued to do so in the Holocene, we can speculate on the composition of the associated fauna. These larger birds are part of the *Euryapteryx* assemblage that frequented Otiran western landscapes. So, as in the west, *Euryanas finschi, Gallirallus australis, Nestor notabilis,* New Zealand Crow (*Corvus moriorum*), New Zealand Pipit (*Anthus novaeseelandiae*), New Zealand Quail (*Coturnix novaezelandiae*), Piopio (*Turnagra capensis*), *Fulica prisca,* and *Gallinula hodgenorum* were probable associates of *Cnemiornis, Harpagornis,* and *Aptornis* in Canterbury.

The relative abundance of species in late Holocene faunas of the east differs from that of western areas. This partly results from eastern areas having a much greater diversity resulting from the continued presence of all the presumed Otiran species during the Holocene, when other species typical of forest habitats became established. Such species include Kakapo (*Strigops habroptilus*), *Philesturnus carunculatus,* and *Petroica australis.* These species, however, are all relatively rare compared to their abundance in western faunas. Differences in the frequency of a species can usually be explained by the availability of the preferred habitat of that species. For example, the grassland inhabiting quail, *Coturnix novaezelandiae,* had little or no habitat in the west during the Holocene and is rare there, but in the east it is common. The most common passerine in late Holocene deposits in eastern areas was *Turnagra capensis,* which suggests that the preferred habitat of this extinct bird was the shrubland mosaics of drier areas. This is supported by the observation that *Turnagra* is present in fossil deposits of western areas only in Otiran deposits, when shrubland habitats were widely available.

THE CENTRAL OTAGO FAUNAS.—The few data available for the Otiran fauna of central Otago indicate *Pachyornis elephantopus* and *Dinornis giganteus* were the most common moas, with *Cnemiornis calcitrans* being the only known carinate. The abundance of the last species in these deposits and in Otiran loess deposits in Canterbury illustrates its preference for the open, short shrubland/grassland habitats prevailing at that time.

The Holocene moa fauna of central Otago is most similar to eastern ones, but it is influenced by altitude. In the broad valleys, *Emeus crassus* is common, and *E. geranoides* and *P. ele-*

phantopus are common associates. *Megalapteryx didinus,* however, also is common, especially in hill sites, which reflects the presence of upland shrubland habitats, as this species dominates subalpine Holocene deposits. In central Otago, the smaller carinates are better represented in late-Holocene deposits than in older deposits, but, even so, they are not easily compared with those of other eastern areas because they do not include faunas accumulated by predators. As in Eastern faunas, *Euryanas finschi* is abundant, *Sceloglaux albifacies,* parakeets (*Cyanoramphus* spp.), New Zealand Snipe (*Coenocorypha aucklandica*), *Gallinula hodgenorum,* New Zealand Pigeon (*Hemiphaga novaeseelandiae*), and *Coturnix novaezelandiae* are common, *Cnemiornis calcitrans* is present, and *Gallirallus australis* and *Apteryx* spp. are relatively rare. *Nestor notabilis* is more abundant than in other regions, which also reflects the presence of substantial areas of upland habitat.

The *Anomalopteryx* assemblage characterized rimu-dominated podocarp forests of the west coast and central North Island and the beech forests of Takaka Hill and Mt. Cookson during the Holocene. This observation supports the contention of Graham (1992) that vegetation structure may be more important to some animals than the species composition of the vegetation. Although these areas differed markedly floristically, they presented a common structure of a continuous closed canopy that excluded significant areas of grassland and shrubland.

THE QUESTION OF PLEISTOCENE EXTINCTIONS OF MEGAFAUNA

The faunal turnover at the end of the glacial period in New Zealand has considerable international relevance to the worldwide debate on the cause or causes of Pleistocene extinctions of megafauna, whether climate-induced or attributable to overkill by humans (Martin and Klein, 1984; Graham, 1986). The term megafauna has been defined in various ways, although most definitions encompass the larger species (Martin and Klein, 1984). In Australia, megafauna is often used for all species that went extinct in the late Pleistocene, regardless of size (Murray, 1991). In New Zealand, as elsewhere in the world, larger species were more susceptible to extinction, with all terrestrial birds greater than two kilograms becoming extinct (Cassels, 1984). The faunal changes documented for western areas of the South Island (Worthy, 1993a; Worthy and Holdaway, 1993) demonstrate that in New Zealand there were extinctions at the end of the Pleistocene, but they were only regional in extent. These are equivalent to the faunal shifts commonly related to past climatic changes in Quaternary faunas of Australia (Lundelius, 1983) and North America (Graham, 1987, 1992; Graham and Grimm, 1990).

The warming climate in New Zealand produced habitats characterized by continuous tracts of closed-canopy forest for which the members of the *Euryapteryx* assemblage were not adapted, and so they were displaced by the *Anomalopteryx* assemblage. Such faunal shifts support the environmental change/habitat destruction hypothesis advocated as causal for North American Pleistocene extinctions (Graham, 1986). In New Zealand, however, all known species survived into the last millenium, with local adjustments in range. The *Euryapteryx* assemblage was restricted to the areas of grassland, shrubland, and forest mosaics that persisted east of the Southern Alps. Their continued survival in these areas could be considered an accident of geography because the Alps create a rainshadow, hence the dry conditions necessary to maintain this vegetational mosaic. But this is not the only reason because in the North Island and along the Southland coast, the ecotonal dunelands present a fundamentally similar vegetation structure, albeit in very small areas, sufficient for the survival of the dominant Otiran species alongside members of the *Anomalopteryx* assemblage. Also, the past survival of these species through several glacial-interglacial cycles suggests that they were not at risk of extinction in this last cycle. All moas, indeed all of New Zealand's Late Quaternary terrestrial species that eventually became extinct, did so only after humans arrived, about 800 to 1000 years ago (Anderson, 1991).

In North America, greater habitat heterogeneity during the glacial and late glacial is associated with faunas of higher species diversity than those of the Holocene, so the loss of this habitat variety may have contributed to megafaunal extinctions (Graham, 1985, 1986). In New Zealand, although the members of the *Euryapteryx* assemblage lived in the areas of most heterogenous habitat, the greatest species diversity was achieved not in glacial times but rather during the late Holocene, when the warm-temperate forest element populated the forest segments of this mosaic. It may be equally valid to argue that, in a landscape that was otherwise forested, the species with requirements for grassland and shrubland habitats found refuge in these mosaics. That all members of the *Euryapteryx* assemblage became extinct seems to support the concept that the loss of habitat heterogeneity was important in the extinction event. Countering this, however, is the fact that many members of the *Anomalopteryx* assemblage also became extinct.

The presence of heterogenous habitats are not implicitly a glacial/late glacial phenomenon, as inferred for North America by Graham (1992), but are rather a function of water availability and ecotonal habitats. That species with preferences for open areas, such as grassland, closed forests, or forest margins, can all find available habitat in such areas contributes to high species diversity. In New Zealand, forest remnants in the vegetational mosaics probably provided the source from which the members of the *Anomalopteryx* assemblage spread to dominate the faunas of the new closed-canopy forests of the Holocene. Conversely, at an earlier stage of the glacial-interglacial cycle, the *Euryapteryx* assemblage spread from remnant mosaic habitats existing in the last interglacial to dominate the open glacial landscapes.

It therefore seems unlikely that the last of many phases of alternate constriction and expansion of areas of particular vegetation physiognomies caused by climatic shifts contributed to megafaunal extinction in New Zealand. New Zealand differs fundamentally from North America or Australia in that humans were not present 10,000 years ago. The New Zealand data, demonstrating a combination of regional extirpations at the end of the Pleistocene and total extinction when humans arrived, suggest that neither overkill nor changing environments are wholly explanatory hypotheses. Both are contributing factors in a complex interaction. Murray (1991) reviewed the evidence on megafaunal extinction in Australia and concluded that although many factors were involved, the megafauna would have survived until European arrival without the influence of aboriginal humans. The New Zealand data fit with Murray's conclusion.

In summary, climatic change at the end of the Pleistocene led to widespread habitat change in continental Australia and North America, vastly reducing the available habitat for the megafauna and their associates inhabiting Pleistocene vegetational mosaics. These species were thus compressed into small areas, where, in the absence of humans, they are likely to have survived as they did in New Zealand. Humans entered both North America and Australia several thousand years before the end of the last ice age and its associated climatic and vegetational changes. It seems probable that the continued exploitation of megafaunal species as food resources, after environmental changes had severely constricted the ranges of these species, then led to their extinction.

The concept of the community in the evolving biota can be examined by studying the pattern of changes in the range of species. The individualistic model suggests communities are an amalgam of species that respond to changes in their environment in accordance with individual tolerances. As a result, communities are continually evolving, and modern associations do not necessarily represent analogs for previous time periods (Graham, 1985, 1992; Graham and Grimm, 1990). North American fossil faunas provide much support for this concept (Graham, 1992). An alternative hypothesis is that individuals are constrained by their ecological requirements and form recognizable associations that move across the landscape following available habitat. Alroy (MS) reanalyzes the North American data and finds much support for this concept of ecological tracking. The homogeneity of the *Euryapteryx* assemblage throughout Pleistocene and Holocene landscapes of South Island suggests that this suite of species was inextricably linked by habitat requirements; hence, it supports the ecological tracking model. The presence of *Euryanas* and *Aptornis* in Holocene forests of Mt. Cookson is an apparent contradiction of the discreteness of the *Anomalopteryx* and *Euryapteryx* assemblages, but it is explained by this area being an ecotonal zone between dry and wet areas and thus supporting a mix of species.

COMPARISON OF CLIMATIC VERSUS HUMAN EFFECTS.—The small, relatively unmodified area of Takaka Hill invites comparison of the relative importance of climatic and human effects on the fauna. At the end of the last glacial period, the moas *Megalapteryx didinus, Pachyornis elephantopus, P. australis,* and *Euryapteryx geranoides* were displaced from Takaka Hill. With them went their main predator, *Harpagornis moorei,* and at least the associated species *Euryanas finschi, Aptornis defossor, Fulica prisca,* and *Gallinula hodgenorum. Dendroscansor decurvirostris* was probably lost from the area at the same time. During the Holocene, the faunal composition remained constant from the time of forest reestablishment, about 9000 to 10,000 years ago, until humans arrived in New Zealand. Major changes in the composition of the fauna resulted from various human activities and from predation by newly introduced mammals (Cassels, 1984; Anderson, 1989; Holdaway, 1989; Bell, 1991). Initially, only humans and the Pacific Rat (*Rattus exulans* (Peale)) preyed on the native fauna, but with the coming of Europeans another wave of predators swept through the forest (King, 1984), and much of the land was cleared for farming.

The result has been that in the last 1000 years, 10 species on Takaka Hill have become locally extinct: *Apteryx owenii, A. haastii, A. australis, Anas chlorotis, Strigops habroptilus, Porphyrio hochstetteri, Xenicus gilviventris, Mohoua ochrocephala, Callaeas cinerea,* and *Philesturnus carunculatus.* A further 11 species became globally extinct: *Anomalopteryx didiformis, Dinornis struthoides, D. novaezealandiae, Sceloglaux albifacies, Aegotheles novaezealandiae, Circus eylesi, Coturnix novaezelandiae, Xenicus longipes, Traversia lyalli, Pachyplichas yaldwyni,* and *Turnagra capensis.* Therefore, at least 21 bird species living on Takaka Hill about 1000 years ago have been extirpated by the activities of humans and various introduced mammals, with most losses being among the terrestrial browser and nocturnal guilds (Holdaway and Worthy, 1996). Of the remaining birds, *Nestor meridionalis* and *Cyanoramphus* spp. are in serious decline in the area. In the first wave of extinctions associated with Polynesian arrival, the species that became extinct were large and flightless (moas, *Aptornis, Cnemiornis*), and thus susceptible to human hunting, or were very small and flightless or ground nesting (e.g., flightless acanthisittid wrens and procellariids), and thus subject to predation by the Pacific Rat. With the arrival of mustelids, other rats, and cats, other mainly flightless or weak-flying species became extinct or endangered (*Sceloglaux, Strigops, Nestor*). The impact of humans caused the regional or total extinction of more than double the number of birds that were only displaced from Takaka Hill at the Otiran/Holocene transition and so was considerably worse than the effect of major climate change.

Note Added In Press: In 1998, the Weka *Gallirallus australis* went extinct on Takaka Hill. The losses continue.

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The Middle Pleistocene Avifauna of Spinagallo Cave (Sicily, Italy): Preliminary Report

Marco Pavia

ABSTRACT

A preliminary study of the middle Pleistocene birds from Spinagallo Cave (Siracusa, Sicily) shows an avifauna composed of 61 species (28 Passeriformes and 33 non-Passeriformes), including Anseriformes, Falconiformes, Gruiformes, Charadriformes, and Strigiformes. Three extinct taxa, probably new to science, include a large *Tyto*, a long-legged *Athene*, and a small species of Corvidae to be described later. Paleoenvironmental reconstruction of the site indicates a temperate climate, like the present or slightly colder.

Introduction

In 1959 and 1960, many fossil bones were collected from Pleistocene cave deposits in Spinagallo Cave, near Siracusa, southeastern Sicily, Italy (Accordi et al., 1959; Accordi and Colacicchi, 1962) (Figure 1). The fossil association contains bones of mammals, especially dwarf elephants, reptiles, amphibians, and birds. The age, determined by Bada et al. (1991) from amino-acid racemization analysis of mammal bones, is about 500,000 years, or middle Pleistocene. There are no signs of human activities on the bones or in the cave, so the accumulation is not artificial. The specimens have been stored in the Museum of the Dipartimento di Scienze della Terra (Università "La Sapienza") di Roma.

The Pleistocene vertebrate fauna of mammals, reptiles, and amphibians from Spinagallo has been described by various authors (Accordi, 1962; Ambrosetti, 1968, 1969; Petronio, 1970; Kotsakis, 1977, 1984; Kotsakis and Petronio, 1980). The eastern part of Sicily, during the middle Pleistocene, was inhabited by two species of dwarf elephants (Ambrosetti, 1968), a giant species of Gliridae (Ambrosetti, 1969; Petronio 1970), and an exctinct lizard (Kotsakis, 1977, 1984; Delfino, pers. comm., 1995). The mammal and reptile faunas seem to indicate that Sicily was isolated during most of the Pleistocene and was colonized by a typically mainland fauna only in the late Pleistocene.

The fossil avifauna consists of almost 1000 bones that have been identified by comparison with recent skeletons in the Museo Regionale di Scienze Naturali di Torino, the Regalia Collection stored in the Institut de Paléontologie Humaine de Paris, and the collections of the Département des Sciences de la Terre de l'Université de Lyon.

Systematic List

The avifauna of Spinagallo is composed of 61 taxa, which are listed according to the nomenclature of Voous (1973, 1977).

Non-passeriformes

Geronticus eremita
Anser erythropus
Branta sp.
Anas penelope
Anas querquedula
Marmaronetta angustirostris
Accipiter gentilis
Accipter nisus
Falco tinnunculus
Falco columbarius
Falco subbuteo
Falco eleonorae
Coturnix coturnix
Rallus aquaticus
Grus sp.
Recurvirostra avosetta
Scolopax rusticola
Larus minutus
Larus ridibundus
Columba livia
Columba livia/oenas
Columba palumbus
Streptopelia turtur
Cuculus canorus
Tyto, species undescribed[†]
Otus scops
cf. *Surnia ulula*
Athene, species undescribed[†]
Asio otus
Caprimulgus cf. *europaeus*
Apus apus/pallidus
Apus melba
Picus viridis
Dendrocopos leucotos

Passeriformes

Calandrella brachydactyla
Lullula arborea
Hirundo sp.
Anthus sp.
Prunella modularis
Erithacus rubecula
Oenanthe cf. *hispanica*
Monticola solitarius
Turdus sp. 1
Turdus sp. 2
Sylvia sp.
Phylloscopus sibilatrix/collybita
Lanius senator
Pica pica
Pyrrhocorax graculus
Corvidae genus and species indet.[†]
Sturnus sp.
Petronia petronia
Fringilla coelebs/montifringilla
Serinus sp.
Carduelis chloris
Carduelis sp.
Pyrrhula pyrrhula
Coccothraustes coccothraustes
Emberiza sp. 1
Emberiza sp. 2
Emberiza sp. 3
Passeriformes indet.

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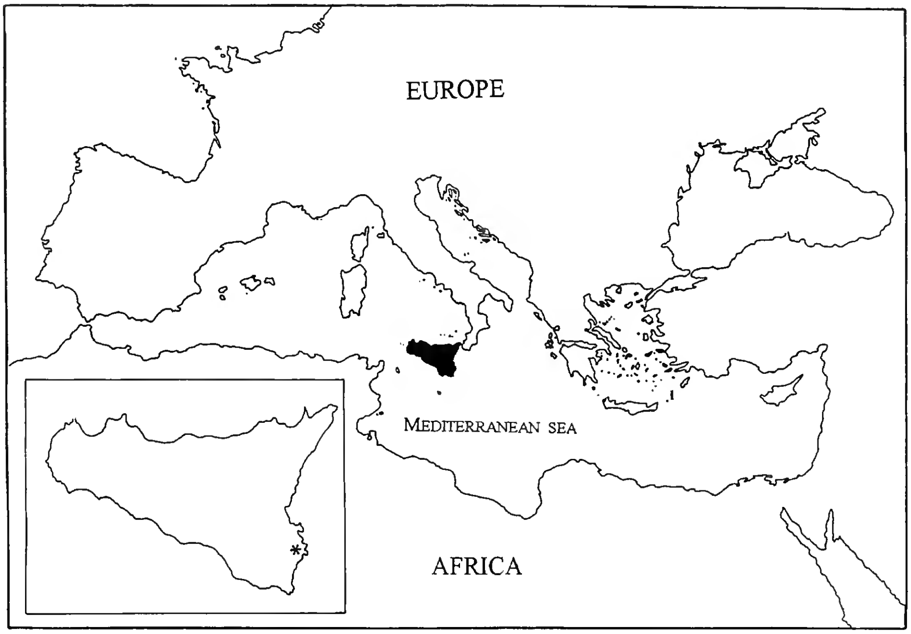

FIGURE 1.—Map of Sicily (shaded); inset shows the position of Spinagallo cave (*).

Remarks

The Pleistocene avifauna contains two new extinct species that are probably endemic to Sicily: a giant *Tyto,* similar in size to *Tyto robusta* (Ballmann, 1973), and a new species of *Athene,* characterized by having the legs longer than in *Athene noctua* but shorter than in *Athene cretensis* (Weesie, 1982). Descriptions of both are in preparation. Another extinct species, an undetermined Corvidae, probably the same as found in the Balearic Islands (Alcover et al., 1992), was found in Spinagallo and in another cave in Sicily of the same age (Alcover, pers. comm., 1995). Bones of a large crane, similar in size to the living *Grus antigone,* also were found.

The presence of apparently endemic forms, combined with other typical features of insular avifaunas (Alcover et al., 1992), seems to confirm the isolation of Sicily during the middle Pleistocene, as previously suggested by the mammalian fauna. One of the most evident characteristics of fossil island avifaunas is the absence of Galliformes, with the exception of *Coturnix coturnix* (Alcover et al, 1992), which is true of Spinagallo. This is in contrast to mainland cave avifaunas, which are dominated by members of this order. On the Mediterranean islands, remains of *C. coturnix* are common, doubtless because of the migratory habits of the species. The absence of partridges of the genus *Alectoris* also is typical, although they are now present on Mediterranean islands, probably due to human introduction, and are very common. The presence of Laridae differs from the normal composition of insular avifaunas (Alcover et al., 1992) but can be explained by the short distance between Sicily and the mainland, where fossil and recent gulls are both recorded.

The composition of the avifauna suggests a coastal environment with a cliff close to the sea; the same Miocene cliff in which the cave was formed. This physiographic feature supported many species, such as *Geronticus eremita, Falco eleonorae, F. tinnunculus, Tyto* (species undescribed), *Columba livia,* Apodidae, and *Pyrrhocorax graculus.* Inland, on top of the cliff, it is supposed that there was an extension of Mediterranean forest with large trees and dense undergrowth, appropriate habitat for *Accipiter gentilis, A. nisus, Falco subbuteo, Scolopax rusticola,* Strigidae (except the probable vagrant *Surnia ulula*), *Columba palumbus, Streptopelia turtur, Caprimulgus europaeus,* all the Picidae, and many Passeriformes. Along the sea, wetland is indicated by the Anseriformes and other waterbirds such as Laridae. The records of *Falco columbarius, Caprimulgus europaeus,* and many Passeriformes, such as Alaudidae, *Anthus* sp., *Lanius senator, Oenanthe hispanica, Carduelis* sp., and the Emberizidae, suggest that open, dry country with scattered bushes also was present. The number of birds of prey in the Spinagallo fauna is high, possibly because many raptors lived in or near the cave.

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Birds in the Economy and Culture of Early Iron Age Inhabitants of Ust' Poluisk, Lower Ob' River, Northwestern Siberia

Olga R. Potapova and Andrei V. Panteleyev

ABSTRACT

The archaeological settlement of Ust' Poluisk, located in the lower Ob' River basin in northwestern Siberia (66°33′N, 66°35′E), yielded a rich vertebrate fauna with a high ratio of bird remains (1996 bones). Cultural remains were deposited over several centuries and were dated by association with archaeological artifacts to 400–100 BC. Thirty-nine species were identified in the bird assemblage. Among these species, 10 are represented by rare breeding and rare vagrant birds, indicating a somewhat warmer climate at the Ob' River mouth than at present. The remains of Golden Eagles and White-tailed Eagles excavated from sacrificial areas of the settlement are of special interest. These findings indicate special cultural attention to and attitude toward eagles, which may have been kept in captivity. Based on bird remains, the site has provided the earliest evidence of eagle worship in Siberia.

Introduction

Humans have been dependent upon nature throughout their history. The economic lifeways of ancient peoples were mainly determined by natural conditions. The best evidence of this is found in the north, where agriculture was absent, the possibilities of plant gathering were limited, and subsistence activities were based primarily on hunting and fishing. In northern latitudes, fowling was an important means of survival. Besides being a source of sustenance and of feathers (for fletching arrows and myriad other uses), birds played a significant role in the cultures of many peoples. Cultural roles included cult ceremonies, decorations, and subjects in tales, legends, and traditions. The abundant remains of birds from Ust' Poluisk settlement in northwestern Asia (Figure 1) provides data on the economic, subsistence, and cultural systems of its early Iron Age human inhabitants.

MATERIALS AND METHODS.—The Ust' Poluisk archaeological site was discovered in 1932. Bones examined in this study were collected during excavations conducted in 1935 and 1936 by V.S. Adrianov (Museum of Anthropology and Ethnography (MAE)), St. Petersburg, Russia. The size of the settlement was estimated to be about 4000 m^2. It was surrounded by a kremlin wall and a trench. About 10% of the site (410 m^2) was excavated. Thirty-six thousand artifacts and bones were recovered (Adrianov, MSa). For unknown reasons, the excavations were not completed, and almost all documents from the 1936 excavations were lost.

The cultural layer of the site is generally 20–30 cm thick, but it widens to 40–50 cm thick in hollows, indicating its homogeneity and the long duration of site occupation (Moshinskaya, 1953). Artifacts were dated to 400–100 BC based on artifacts and tools of the Anan'inskaya and Tagarskaya cultures (Chernetsov, 1953). Discovery of metal knives at the site indicate an early Iron Age settlement (T.A. Popova, pers. comm., 1997). Bird bones were apparently excavated from trench number 5, where remains of two or three dwellings and a sacrifice area were found. Also located were a hearth with a pile of dog skulls, reindeer bone fragments, isolated human bones, and numerous ceramic, bone, and some bronze artifacts (Moshinskaya, 1953). Other faunal remains included squirrel, beaver, hare, fox, arctic fox, sable, moose, pinnipeds, and some large fish (Adrianov, MSc). Among nonavian, partly identified bone remains, reindeer were predominant at the site (Kosintsev, 1997). Beavers were represented by 23 specimens, among which were 20 young animals and one juvenile (O.R. Potapova, pers. obs., 1997).

Descriptions of excavation methods are lacking in Adrianov's 1935 report (MSa, MSb, MSc). The authors believe the deposits were excavated using shovels and knives but were not screened. The deposits were, however, most likely subjected to

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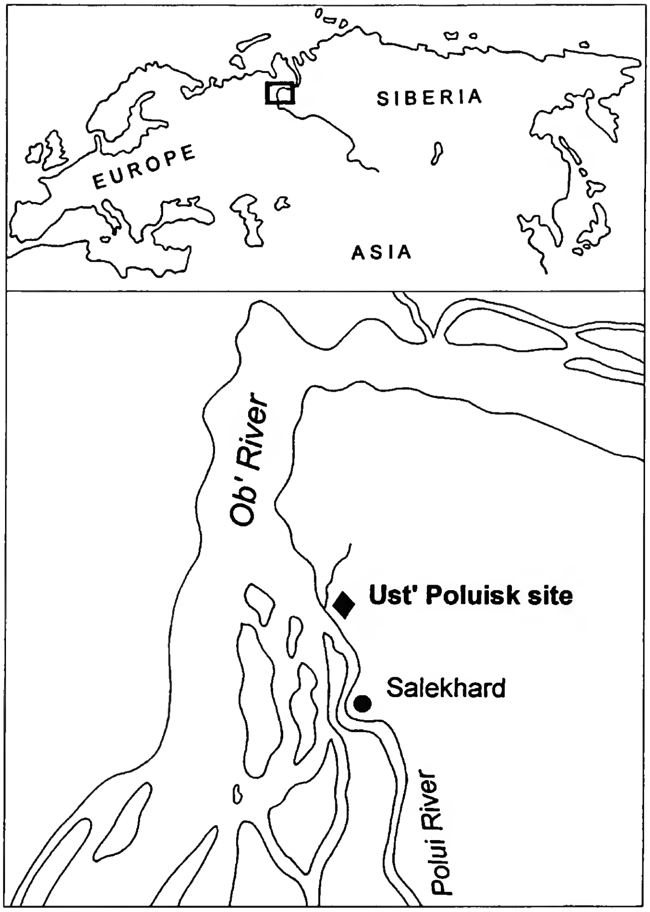

FIGURE 1.—Map showing location of Salekhard and Ust' Poluisk settlement (diamond).

thorough visual examination after removal from the excavation units. This excavation methodology was in general use by Russian archaeologists in the 1930s (D.N. Praslov, Institute of Material Culture, St. Petersburg, pers. comm., 1996). The authors believe excavation methods were quite thorough, judging from the small size of many of the artifacts collected and of some bird bones (quadratum, premaxilla, and others).

The lack of small passerine birds at the site may be due to taphonomic conditions, similar to the other open-air sites on the Russian Plain (i.e., Kostenki) (D.N. Praslov, pers. comm., 1996) and North Caucasus (i.e., Ilskaya 2) (O.R. Potapova, pers. obs., 1997). The deposits from these sites were screened but yielded no small passerine bird remains and only extremely rare fossilized rodents. The hunting preferences of aboriginal humans, oriented to prey larger than passerine birds, could be another reason. There is, however, the possibility that some of the smallest bone material was not located or was lost.

All bird-bone collections from the site are deposited in the Zoological Institute, Ornithological Section, St. Petersburg, Russia. Bird-bone artifacts are deposited in the MAE.

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Discussion

Thirty-nine bird species were indentified from excavations at Ust' Poluisk settlement (Table 1). Many of these species are now restricted to more southern regions and only occasionally visit the lower Ob' River as vagrants or, rarely, as breeders, this being the northern boundary of their current range. It is possible that 2000 years ago the breeding ranges of these birds extended farther to the north, because the paleobotanical record suggests that at that time northwestern Siberia had a warmer climate than at present (Volkova et al., 1989). Two thousand years ago the timber line was north of Salekhard, and there were pine forests at the mouth of the Polui River (Moshinskaya, 1953). The presence of a forest ecosystem during the time the site was occupied is supported by relatively numerous archaeological findings of birch bark and of remains of forest-dwelling animals, such as squirrels, beavers, sable, and moose (Kosinstsev, 1997), at the site.

The bird-species assemblage includes individuals from seven groups. More than 92% are grouse and waterfowl. Diurnal birds of prey and owls represent 6.1% (Table 2). Birds from these groups were probably hunted for food or may have played a role in the cultural traditions of the population. Passerine birds are represented by corvids, which might have been attracted to the settlement by garbage.

At Ust' Poluisk, grouse account for 51.4% of all bones, with most of these belonging to Willow Ptarmigans (*Lagopus lagopus* (Linnaeus)). This species is numerous in Paleolithic-age sites of the northern and middle Urals (Potapova, 1990, 1991) and in forest and forest-steppe zone sites on the Russian Plain, such as Kostenki, Novgorod-Severskii, Mezin (Zubareva, 1950), and Afontova Gora-3 in southern Siberia (Tugarinov, 1932).

In Holocene archaeological sites, the remains of Willow Ptarmigans are rare. At Mayak 2, an early Bronze Age site on the Kola Peninsula, the remains of Willow Ptarmigans com-

TABLE 1.—Bird species from Ust' Poluisk (NISP=number of bones; MNI=minimum number of individuals; *=rare vagrant or rare breeding species at the Ob' River mouth).

Taxon	Common name	NISP	MNI
Gavia stellata	Red-throated Loon	25	7
Gavia arctica	Arctic Loon	48	10
Podiceps cristatus	* Great Crested Grebe	8	2
Cygnus cygnus	Whooper Swan	28	5
Cygnus bewickii	Bewick's Swan	10	2
Anser cf. *albifrons*	Greater White-fronted Goose	132	41
Anser cf. *fabalis*	Bean Goose	88	10
Branta spp.	small geese	3	1
Anas platyrhynchos	Mallard	12	5
Anas crecca	Green-winged Teal	50	23
Anas penelope	Eurasian Wigeon	40	10
Anas acuta	Northern Pintail	24	4
Anas querquedula	Garganey	6	2
Anas clypeata	Northern Shoveler	12	3
Anas spp.	teal	6	2
Aythya fuligula	Tufted Duck	4	4
Aythya marila	Scaup	1	1
Melanitta fusca	White-winged Scoter	1	1
Melanitta nigra	Black Scoter	2	1
Clangula hyemalis	Oldsquaw	14	5
Bucephala clangula	Common Goldeneye	7	2
Mergus albellus	* Smew	1	1
Mergus merganser	* Common Merganser	1	1
Anatidae indeterminate	ducks	46	18
Haliaeetus albicilla	White-tailed Eagle	143	10
Accipiter gentilis	Northern Goshawk	4	1
Buteo lagopus	* Rough-legged Hawk	1	1
Aquila chrysaetos	* Golden Eagle	28	7
Circus cyaneus	Northern Harrier	2	1
Accipitridae indeterminate	kites, hawks, eagles	1	1
Falco peregrinus	* Peregrine Falcon	2	1
Lagopus mutus	Rock Ptarmigan	134	36
Lagopus lagopus	Willow Ptarmigan	653	144
Lagopus indeterminate	ptarmigan	318	30
Tetrao urogallus	Capercaillie	16	6
Lyrurus tetrix	Black Grouse	1	1
Grus grus	* Common Crane	1	1
Grus leucogeranus	Siberian White Crane	6	1
Larus argentatus	Herring Gull	65	10
Charadriiformes indeterminate	shorebirds	1	1
Bubo bubo	* Eagle Owl	4	1
Nyctea scandiaca	Snowy Owl	12	2
Strix nebuloza	* Great Gray Owl	1	1
Corvus cornix	Hooded Crow	11	3
Corvus corax	* Common Raven	11	2
Aves indeterminate	birds	12	
TOTAL		1996	422

TABLE 2.—Bird remains analyzed by groups from Ust' Poluisk (MNI=minimum number of individuals).

Groups	Number of species	MNI	MNI%
Loons, grebes, shorebirds, gulls	5	30	7.1
Ducks, geese, swans	19	142	33.7
Diurnal raptors	6	22	5.2
Grouse	4	217	51.4
Cranes	2	2	0.5
Owls	3	4	0.9
Crows	2	5	1.2
TOTAL	41	422	100

prise only 1% of all bird bones (Potapova and Sablin, 1994; O.R. Potapova, pers. obs., 1997). In the northern Urals, Willow Ptarmigan bones were reported only from the Kaninskaya cave Bronze-Iron Age site on the upper Pechora River (Kuzmina, 1971).

All skeletal elements of Willow Ptarmigans and Rock Ptarmigans (*Lagopus mutus* (Montin)) were found at Ust' Poluisk, with humeri and femora being the most common (see Figure 2A). The relative abundance of skeletal elements is similar to that of skeletal elements found at Abri Fontalès, Ebbou, and La Colombiére archaeological sites in France (Mourer-Chauvire, 1983). The numbers of skulls, sterna, and pelvises found at the Ust' Poluisk site suggest that the birds were delivered to the site intact, with processing occurring at the site. All the bones are very well preserved, with unbroken bones constituting almost 88% of the total. The majority of bones belong to adults, with only 1.5% belonging to young individuals, based on spongy tissue at the ends of the long bones. Many tibiae and femora have distinct tooth marks (13% of all *Lagopus* bones) that appear as small holes and dents on their ends (these fall into three size classes: 1.6 × 3.0 mm; 2.0 × 3.7 mm; 2.7 × 2.9 mm). Some of the bones (0.4%) have signs of cuts on the shafts (femora) and have cuts through the entire articular ends (humeri).

Willow Ptarmigans probably attracted prehistoric hunters because their seasonal abundance and behavior patterns made them relatively easy to obtain. The hunting process required no special equipment, such as bows or arrows, because nooses, traps, or nets could be used successfully (Silantyev, 1898; Kolosov and Shibanov, 1957). Not long ago these methods were still widely used in the Russian north. In the nineteenth century Silantyev (1898:367) wrote: "Local hunters get grouse without guns." Catching grouse with nets in the spring was used in the tundra of the Lena-Khatanga depression (Romanov, 1934), and net hunting is still widely applied in the Lower Kolyma throughout the year (E.R. Potapov, pers. comm., 1997). In North America, it is still possible to catch large numbers of grouse in the Great Plains using nets or clubs; nets were used by nineteenth century Shoshone Indians during rabbit drives, and fiber nets dating from thousands of years ago have been located in archaeological sites in the Great Plains and Great Basin (L.W. Rom, pers. comm., 1997). The technology of producing nets from nettles or willow bast was known to all fishing peoples from the Neolithic-Bronze Age (Kosarev, 1987a, 1991; Krushanov, 1989). It is possible that the same nets were employed for fishing and catching molting geese in summer and for hunting grouse in other seasons. Although not required, it also is possible that some special equipment was used for hunting grouse. Besides the more productive hunting in the fall, winter, and spring, inhabitants could catch grouse during other seasons by beating or by catching birds by hand in remote areas, where birds were not afraid of humans (Potapov, 1985).

Except during the breeding period, Willow Ptarmigans live in flocks. On the Lower Ob' River, the young form small flocks in August, and flocks of up to 100 birds have been observed in

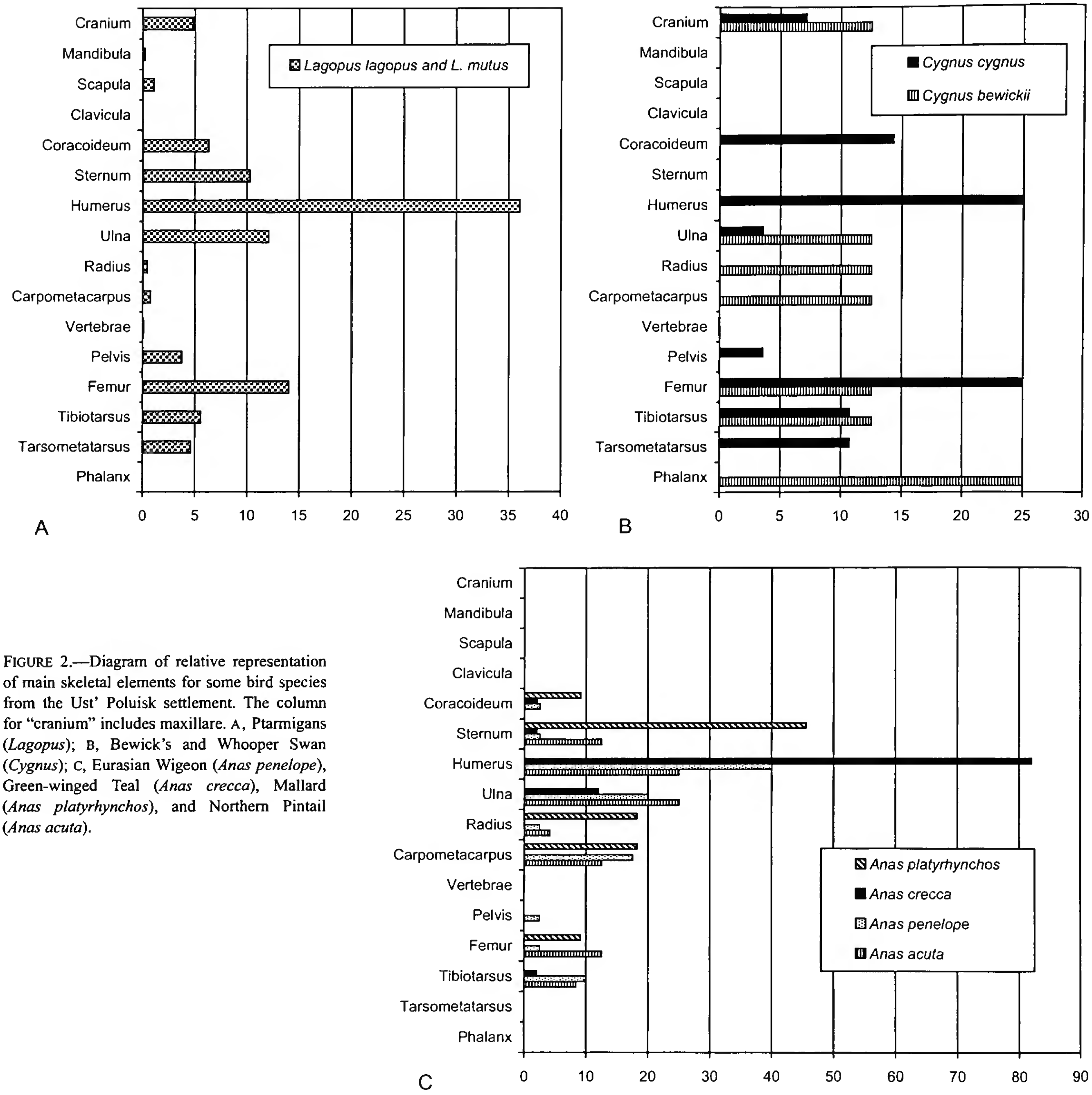

FIGURE 2.—Diagram of relative representation of main skeletal elements for some bird species from the Ust' Poluisk settlement. The column for "cranium" includes maxillare. A, Ptarmigans (*Lagopus*); B, Bewick's and Whooper Swan (*Cygnus*); C, Eurasian Wigeon (*Anas penelope*), Green-winged Teal (*Anas crecca*), Mallard (*Anas platyrhynchos*), and Northern Pintail (*Anas acuta*).

October (Boikov, 1965). In late autumn Willow Ptarmigans start to migrate toward the timberline, at times reaching such a high density that they are commercially hunted (Potapov, 1985). Thus, late autumn through spring might have been the main ptarmigan-hunting period for the ancient Polui dwellers.

The bones of Capercaillie (*Tetrao urogallus* Linnaeus) and Black Grouse (*Lyrurus tetrix* (Linnaeus)) found at the Ust' Poluisk site are from adults of both sexes. As in many archaeological sites on the northern Russian Plain, their remains are much less numerous than those of *Lagopus*.

Geese and ducks also were important groups at the Ust' Poluisk site, where their remains can be easily explained by the presence of the Polui River. Waterfowl could have been hunted during both the breeding and the migration seasons.

Of the waterfowl, it appears that the hunters from ancient Ust' Poluisk preferred teals (*Anas* spp.), Greater White-fronted

(*Anser albifrons* (Scopoli)) and Bean geese (*Anser fabalis* (Latham)), and Eurasian Wigeons (*Anas penelope* Linnaeus). These species each make up 8% to 34% of all individuals. Geese and swans were presumably hunted during the very short molting season (mid-July) or during migration. Hunting molting geese was a common practice for local tribes at the Lena River mouth (Kosarev, 1987b) and the Kolyma River (Wrangel, 1848) in the eighteenth century.

The relative numbers of each of the skeletal elements of waterfowl are similar to those for Willow Ptarmigans (Figure 2B,C), although few or no sterna of swans or of Greater White-fronted or Bean Geese were found. The sternum, as would be the case for other inedible parts of the skeleton, was presumably used for a variety of purposes. The 17 spoons examined from the site were made of bird sterna belonging to loons (*Gavia* sp., 11 spoons), a goose (1) a Greater White-fronted Goose (1), eagles (*Aquila chrysaetos* (Linnaeus) or *Haliaeetus albicilla* (Linnaeus)) (2), a Mallard (*Anas platyrhynchos* Linnaeus) (1), and an Oldsquaw (*Clangula hyemalis* (Linnaeus)) (1). Moshinskaya (1953) considered the spoons made of large-waterfowl sterna to be the most archaic elements among the spoon-like tools that might have been used by inhabitants in rituals at the site. Production of various types of spoons from bird sterna has been well documented in recent times. The Mansi used bone spoons during sacrificial and burial rituals, and in Nenets folklore, the main hero Pornene, half woman and half bear, used the sternum of a swan as a spoon (Moshinskaya, 1953).

Northern Pintails (*Anas acuta* Linnaeus) and Green-winged Teal (*Anas crecca* Linnaeus) are represented primarily by wings. Northern Pintails are rare in the bone remains from this site, although they have been very numerous in the lower Ob' region in recent times. People of northern Russia still use duck wings with brightly colored feathers as a decoration for clothing and housewares. Today, bird wings are used for applying cooking oil when preparing pancakes or other foods in rural houses and in Russia's urban areas. The people of the lower Kolyma region commonly use wings of geese as rubbish brushes (brooms) in their cabins (E.R. Potapov, pers. comm., 1997). In the past, wings of Northern Shovelers (*Anas clypeata* Linnaeus), Northern Pintails, and Green-winged Teals were probably used for similar purposes.

Loons and gulls, which are migratory species, can be obtained in the lower Ob' River region between May and August (Flint, 1988; Yudin and Firsova, 1988). The relatively few remains of loons and Herring Gulls (*Larus argentatus* Pontoppidan) at Ust'Polusik, species common in the lakes and rivers of the tundra-forest zone today, could suggest that these species were rarely hunted and were less desirable. It also could indicate that they were less common 2000 years ago. The skeletal-element representation of these species is similar to that of the Willow Ptarmigan and suggests full utilization by ancient hunters (Figure 3A). The skins of loons and Great Crested Grebes (*Podiceps cristatus* (Linnaeus)) now are greatly valued for their use in clothing (Kolosov et al., 1975), and these species might have been hunted in the site area for the same purpose. Loons could have been used for fat, which generally is of great value for northern peoples. Between 1000 BC and medieval times, inhabitants of the Udal and Buckquoy sites, in the Outer Hebrides and Orkney Islands, respectively, hunted loons exclusively for fat (Serjeantson, 1988); however, gull remains at Mesolithic and early medieval sites in northern Scandinavia and Scotland are rare (A.K. Hufthammer, pers. comm., 1991; Serjeantson, 1988). Therefore, it is probable that rather than being less desirable species, loons and gulls were less common in the Ust' Poluisk area when the site was occupied.

The remains of owls at Ust' Poluisk belong to three large species: the Snowy Owl (*Nyctea scandiaca* (Linnaeus)), which is the most abundant; the Eagle Owl (*Bubo bubo* (Linnaeus)); and the Great Gray Owl (*Strix nebulosa* Forster). Among the bird images on tools and kitchenware found at the site, there was one bronze, stylized owl (Adrianov, MSc). Because of the frequency of their remains, it appears that owls were specifically hunted. Derugin (1898) reported that the local people hunted owls in autumn and winter, when owls accumulated large quantities of fat and were considered a delicacy. Their wings were subsequently used as fans against mosquitoes. The Samoeds (Nentsy), of the Yamal Peninsula, Russia, hunted owls using nooses fixed on high poles (Shukhov, 1915) and using traps at nests (Zhitkov, 1912). Indians of the North American Great Plains treated owls as a superstitious power and sometimes even as a medicine. They kept owls in captivity for soothsaying and used their feathers (especially those of the Great Horned Owl, *Bubo virginianus* (Gmelin)) for ceremonies and dances. Some tribes utilized certain species of owls for food, and there is evidence that the Arikara Indians ate Great Horned Owls (Parmalee, 1977a).

At the sacrificial area of the Ust' Poluisk site, a number of bones of Golden and White-tailed Eagles were found. Golden Eagles (*Aquila chrysaetos*) were represented by disproportionately high numbers of skulls, one of which has had the upper part completely cut off (Figure 4C,D). White-tailed Eagles (*Haliaeetus albicilla*) were represented by full sets of bones (Figures 3B,C), and, unlike Golden Eagles, they were buried intact. The different proportions of skeletal elements suggest different uses for these species.

Among the bones of White-tailed Eagles, one tibia and one ulna (out of a minimum of 10 individuals found at the site) had been broken and had grown back together (Figure 4A,B). Birds with healed broken bones are rare in the wild. In the remains from the Ust' Poluisk site there were only two other cases of knitted fractures found: one femur of a Willow Ptarmigan (0.5% of individuals) and one fibula of a Greater White-fronted Goose (2.0% of individuals). Among several thousand Pleistocene bones from the Binagady asphalts (eastern Caucasus), only two were found with knitted fractures: one mallard and one Steppe Eagle (*Aquila rapax* Temminck) (Burchak-Abramovich, 1949, 1968). In ducks, healed fractures may be found

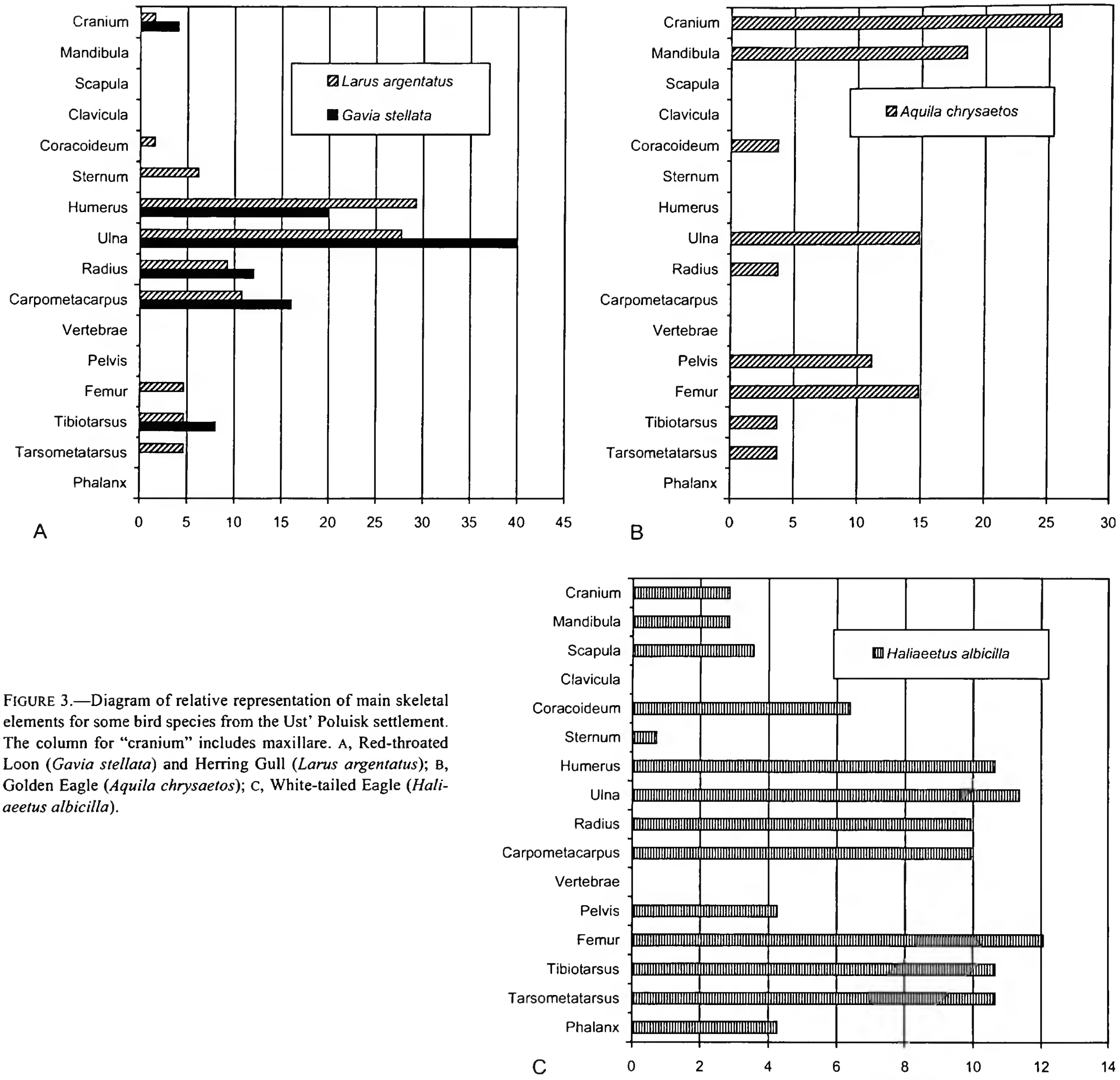

FIGURE 3.—Diagram of relative representation of main skeletal elements for some bird species from the Ust' Poluisk settlement. The column for "cranium" includes maxillare. A, Red-throated Loon (*Gavia stellata*) and Herring Gull (*Larus argentatus*); B, Golden Eagle (*Aquila chrysaetos*); C, White-tailed Eagle (*Haliaeetus albicilla*).

more often (13% of 256 wild duck skeletons examined by Tiemier, 1941). A bird of prey with a broken leg or wing has very little chance of survival in the wild. It is possible that eagles, at least White-tailed Eagles, were kept captive at the settlement. Brothwell (1993:37) noted that "excluding injury received in the wild, birds are most likely to display evidence of trauma as a result of hunting, catching, keeping, or handling." Interestingly, among 145 skeletons of captive macaws (*Ara* spp.), birds of ritual and trade value for Pueblo Indians found in archaeological sites in Arizona and New Mexico, 13% have healed bones (Brothwell, 1993). Furthermore, one ulna from a Mexican macaw found at an archaeological site in Arizona (Brothwell, 1993, fig. 2B) has a similar pattern of trauma as the eagle ulna from the Ust' Poluisk site.

Keeping captive birds, including birds of prey, was widespread in various groups of people. Eagles taken from nests were kept by the Ayny, Selkups, and Kets (Sokolova, 1972; Kosarev, 1981, 1991). The Ayny kept eagles in cages for sacrifices (Sokolova, 1972). Mikhail Litvin, traveling in southwestern Russia during the second half of the sixteenth century,

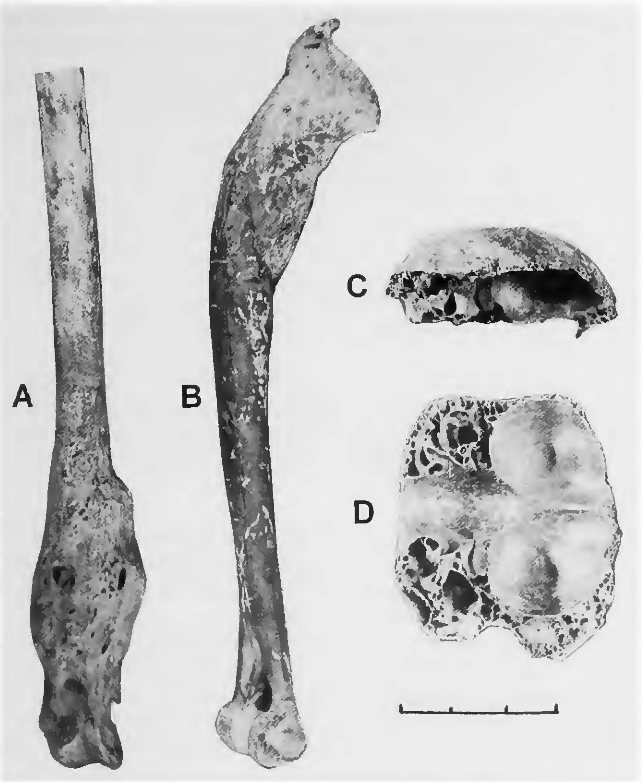

FIGURE 4.—Bones of the White-tailed Eagle (*Haliaeetus albicilla*). *a*, broken and healed distal part of ulna, *b*, broken and healed tibiotarsus, *c*, lateral and *d*, ventral views of the upper part of a cranium showing clear evidence of having been cut. (Scale=3 cm.)

noted that eagles were kept to provide feathers for arrows (Aristov, 1866). In some California Indian tribes, birds of prey were used as decoys for hunting eagles; this also was a ritual event among the Great Plains Indians (Parmalee, 1977b). Remains of Golden and Bald Eagles (*Haliaeetus leucocephalus* (Linnaeus)) were discovered in 60% of 51 Arikara tribe sites in South Dakota and constituted 9% of the bone remains from these sites (Parmalee, 1977b).

Golden and Bald Eagles, along with other birds of prey, still play important roles in Great Plains Indian material and spiritual culture, as they have in the past. They were, and are, represented in rock art, ledger art, and all types of decoration. They form integral components of legends and visions. Archaeological sites specifically devoted to capturing eagles are known throughout the North American Great Plains (L.W. Rom, pers. comm., 1997).

Many Siberian people worshipped eagles, and some of them call March the month of the Eagle. Eagles were associated with the sun god, were equated with the sun god, or were the sun's owner, or creator. The eagle was the supreme god, the benefactor of individuals, peoples, or clans, or a bird of fortune (Sternberg, 1925:718). In the Urges tribe of the Ob' River, the totemic cult of the eagle was linked to the image of the soul-bird (the fourth soul of a person), which dwelled in the hair (Chernetsov, 1959; Kosarev, 1981). Sculptural images of eagles are very common on kitchenware and cult weapons from the Ust' Poluisk site. They are engraved on combs, buckles, suspenders, spoons, *klevtsy* (ritual axes), and knives (Moshinskaya, 1953; Chernetsov, 1953). Among 12 bone carvings of birds found at the site in 1935–1936, nine were eagles. Six of the carved eagles, on combs and bone tools, are depicted sitting on and pecking either a moose head or the head of another stylized bird having a heavy beak. Two other artifacts have stylized pecking eagles, and one has a stylized eagle with outstretched wings (Adrianov, MSb, figs. 2, 3, 18, 51, 70, 176, 177, 190, 260). Chernetsov (1953) believed that forest hunters of the Ob' River basin, who practiced the cult of moose or bear, later adapted the eagle cult from the south-steppe Skiph-Sarmatian tribes who inhabited the steppe zone north to the Kama River basin.

The bird from the sun, "Kars" (eagle), was the most important part of worship dedicated to the "Upper" world. This worship is very ancient and is believed to have originated in India or southern Iran (Sternberg, 1925; Chernetsov, 1947). Kars, from heaven, was believed to be seated in a sacred tree, where the sun and the moon grew. In Siberia this tree was either a birch or a larch (Sternberg, 1925).

Chernetsov (1959) observed the initiation procedure in the clan of the Winged Old Man (Eagle) of the Urges in the Ob' River region. According to his account, young men that had reached the age of initiation walked to a special, sacred place where they climbed a sacred tree, home of the clan's "winged" ancestor. In the twentieth century the Urges from Ob' perform a similar ritual, but without a real bird in the tree; however, perhaps in their shamanistic past there was a live eagle in the tree.

The eagle, as a totem bird, was considered untouchable by many Siberian peoples. Yakuts buried dead eagles, and a community member who killed an eagle by mistake was expected to roast it on a fire and eat all but its head (Sternberg, 1925:723). This possibly explains why there were so many skulls of eagles at the Ust' Poluisk site.

Conclusions

The species composition of the bird-fauna remains collected at the Ust' Poluisk settlement indicates more favorable environmental conditions in that area and a warmer climate at the time of deposition, ca. 400–100 BC, than at present. This conclusion is supported by findings at the site of remains of forest-animal species with ranges that now stop at the timberline, which is south of the site. Avifaunal remains indicate that settlement inhabitants hunted fatty and/or meaty birds that could have been obtained easily, like grouse and waterfowl, as well as birds of ritual importance. The latter included eagles, which were hunted or which might have been kept alive at the settlement, as evidenced by healed, broken eagle bones. Additional evidence of an eagle cult at the site comes from the numerous bone artifacts with engravings or carvings of eagles. Interestingly, at the place of sacrifice there also were found about 40 broken skulls of dogs that were killed for a ceremonial purpose (Adrianov, 1936; Moshinskaya, 1953). The eagle cult still exists and is practiced by local tribes today (Sternberg, 1925), and the bone remains of eagles reported herein provide the earliest evidence of eagle worship in the Siberian region.

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Seabirds and Late Pleistocene Marine Environments in the Northeast Atlantic and the Mediterranean

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ABSTRACT

The technique of reconstructing Pleistocene environments by finding present-day areas of sympatry for the taxa occurring in paleofaunas has been extensively used with micromammals in North America. For a number of reasons the method is not generally applicable to birds; however, most of these objections do not apply to obligate seabirds. This paper treats 31 West Palearctic late Pleistocene faunas from 22 sites containing two or more species of obligate seabirds. The analysis suggests that the waters around the British Isles during the last (Eemian) interglacial were slightly warmer than during the present interglacial, that conditions in the western Mediterranean during much of the last glaciation were similar to those found in the Bay of Biscay and around the British Isles at the present time, and that conditions in the Norwegian Sea during the warmest part of the mid-Weichselian interstadial were similar to those found off the west coast of Spitzbergen today. The stratigraphic position of a number of undated avifaunas containing seabirds is discussed based on the species composition of the seabirds.

Intoduction

Reconstructing Pleistocene environments by identifying present-day areas of sympatry for the taxa occurring in paleofaunas is a method that has been extensively used in North America, particularly as applied to micromammals on the Great Plains (e.g., Graham et al., 1987). The theory and procedures used are summarized by Graham and Semken (1987). The same method of analysis was independently applied by Olson and Rasmussen (1986) to the Oligocene avifauna of Fayum in Egypt, but otherwise this technique does not seem to have been applied to birds.

The method has been little used in Europe for several reasons. The concept works best in large blocks of relatively homogenous territory without dispersal barriers, where taxa can migrate freely in response to climatic changes. This applies to central North America but not to large parts of Europe, where mountain ranges and marine barriers strongly affect the distribution of terrestrial animals. Most European Pleistocene faunas also are "disharmonious," that is, they contain taxa that are allopatric at the present time, either because there are no good modern analogs of the relevant Pleistocene habitats, or because the modern ranges of taxa have been affected by humans. European Pleistocene mammalian faunas also frequently contain a fairly large proportion of extinct taxa, the habitat requirements of which cannot be determined with certainty.

These and similar factors also affect avifaunas. Although the proportion of extinct taxa is quite low in late Pleistocene European avifaunas, and dispersal barriers affect birds less than mammals, a large proportion of the European avifauna consists of long-distance migrants with total annual ranges so large that their occurrence provides very little constraint on environmental conditions. The high vagility of birds also means that there is always a risk that a fossil record may be from a vagrant and is outside the species' normal range.

There is, however, one group of birds to which most of these problems do not apply, namely, strictly marine seabirds. These birds use a continuous habitat (the sea), without any dispersal barriers. Although their modern range has certainly been influenced by humans, this would be more likely to result in the decimation or extirpation of breeding colonies than in changes in the total annual range of species.

Late Pleistocene European avifaunas contain two extinct species of seabirds (*Puffinus holei* Walker et al. (the incorrect original spelling "*holei*" used herein was emended to "*holeae*" by Michaux et al., 1991) and *Pinguinus impennis*), but this does not seriously compromise the usefulness of the sympatry method, particularly because it is possible to reconstruct the "present-day" range of *Pinguinus impennis* with fair precision from historical data and subfossil records (Figure 1). The range of *Puffinus holei* cannot be reconstructed, although it is known to have bred on Fuerteventura, Canary Islands (Walker et al., 1990). The composition of a local fauna of obligate seabirds should therefore be a reasonably good indicator of the condition of the nearshore waters off the site.

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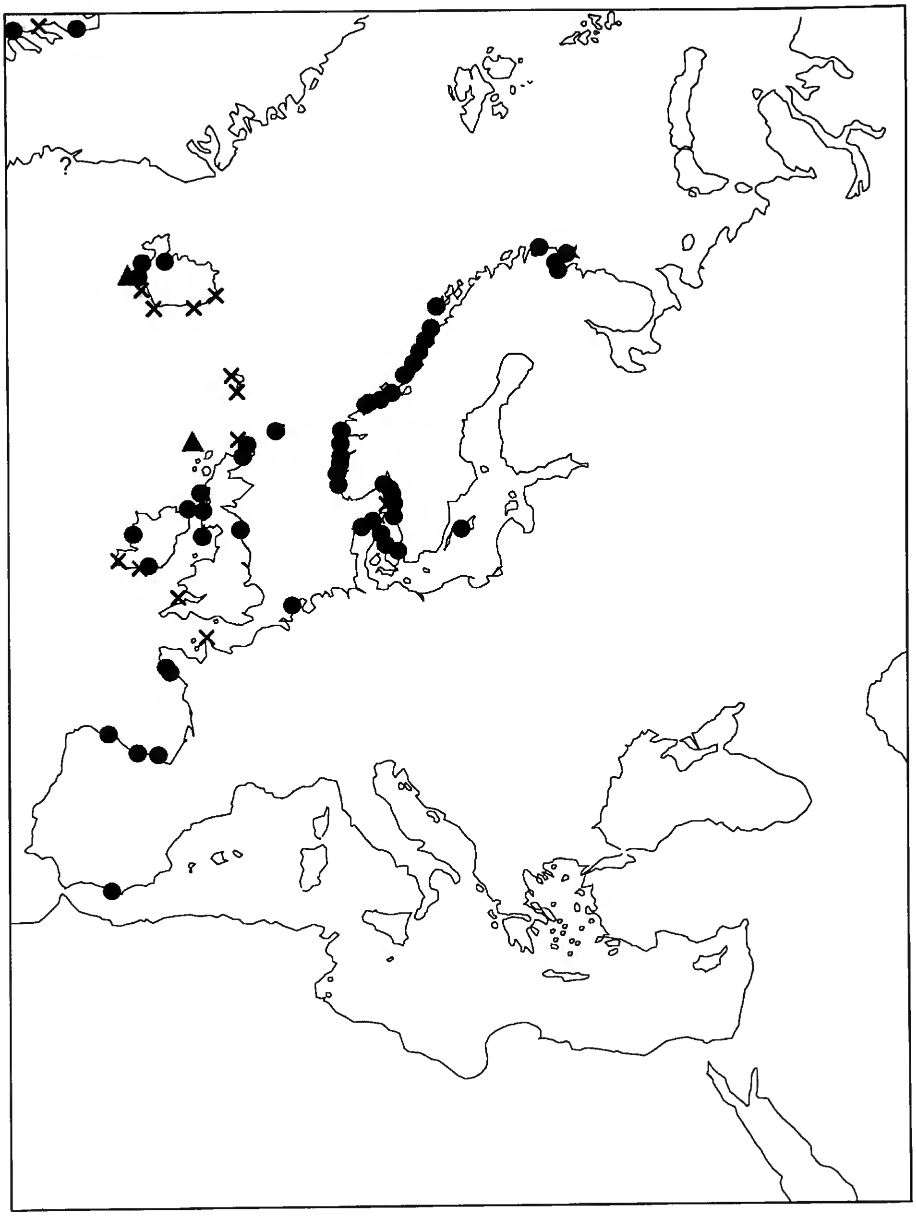

FIGURE 1.—The reconstructed "modern range" of *Pinguinus impennis* in the East Atlantic used to determine areas of sympatry. (● =Holocene subfossil record, ▲=historical breeding site, ×=historical nonbreeding record, ?=occurrence uncertain.)

Unfortunately, despite the fact that well over 1000 sites with late Pleistocene avifaunas are known from the West Palearctic, obligate seabirds occur in only a very small proportion of these sites. The main reason for this is the eustatic lowering of sea levels during glacial periods, which means that coastal sites of glacial age are now mostly submerged. Exceptions to this rule are mostly found on steep Mediterranean coasts and in northern Europe (e.g., Norway), where the isostatic rebound of formerly glaciated areas have kept pace with the eustatic rise of the sea level. In one case (Archi, in Calabria, Italy), a glacial coastal site has been preserved through tectonic movements (Ascenzi and Segre, 1971a, 1971b). In principle, interglacial coastal sites should be accessible, but avifaunas of interglacial age are unfortunately extremely rare. The reasons for this are not well understood, but extensive erosion and weathering (near the end of interglacials?), which have destroyed most interglacial cave deposits, are presumably at least a partial explanation.

METHODS

Only strictly marine species are considered in this study to ensure that the occurrence of the birds truly reflects marine conditions. For birds that regularly frequent freshwater or land habitats, occurrence at a site might indicate that suitable freshwater or terrestrial, rather than marine, habitat existed in the vicinity.

The species used herein are all Procellariidae, all Hydrobatidae, *Morus bassanus, Phalacrocorax aristotelis, Somateria mollissima, Catharacta skua, Larus audouinii, Rissa tridactyla, Pagophila eburnea,* and all Alcidae (including *Pinguinus*). Nomenclature for species' binomials and English names of modern birds follows Sibley and Monroe (1990). With two exceptions, these species are never found inland except as rare vagrants. The exceptions are *Somateria mollissima* and *Rissa tridactyla,* which regularly fly over land on migration but rarely stop at inland sites. *Xema sabini* also might have been included, but it has not yet been recorded from the Pleistocene. *Larus hyperboreus* has not been included because it can probably not be reliably separated from *Larus marinus* on osteological criteria. *Puffinus puffinus* and *P. yelkouan* have been treated as one species because they were not considered separate species at the time when most of the determinations were made.

Only late Pleistocene sites where at least two marine species were reported are included in this study. Data on relevant avifaunas and their dates were obtained through an extensive search of the literature. This yielded a total of 22 sites and 31 faunas that fulfill these criteria (Tables 1, 2). At stratified sites, each layer has been considered as a separate fauna. Only late Pleistocene records have been considered, both because dating of older records is usually quite uncertain and because the ecology of the birds may have changed over a longer time interval.

For modern distributions, the maps in Cramp (1977, 1983, 1985) were used. These are admittedly only approximate in offshore areas, but because the fossil record necessarily samples the coastal fauna, the nearshore distribution, which is better known, is more significant. It should be noted that the ranges used are the total ranges of the species in question, breeding ranges usually being considerably more restricted. It is, however, only rarely possible to determine whether a fossil is from a breeding bird or not. It should be noted that the ranges in Cramp only define the main area of distribution and that most species are found more or less regularly in small numbers well outside the indicated range. This, of course, introduces a margin of error, but the probability of a rare or vagrant species being preserved as a fossil is certainly very low. For the recently extinct *Pinguinus impennis,* a "modern" distribution map was compiled from literary and subfossil data (Figure 1).

Faunas

The faunas (Table 1) are treated in approximately chronological order below.

TABLE 1.—Sites with late Pleistocene seabird faunas.

Site	Sources
Cyprus	
Akrotiri Aetokremnos	Mourer-Chauviré, in litt., 1996
Italy	
Archi	Ascenzi and Segre, 1971a, 1971b; Cassoli and Segre, 1985
Arene Candide	Cassoli, 1980
Buca del Bersaglieri	Lambrecht, 1933; Wolf 1938
Cala Genovesi a Levanzo	Cassoli and Tagliacozzo, 1982
Grotta dei Fanciulli	Del Campana, 1946
Grotta Pietro Tampoia	Lambrecht, 1933; Mayaud and Schaub, 1950; Newton, 1922; Wolf, 1938
Grotta Romanelli	Cassoli et al., 1979
Norway	
Blomvåg	Lie, 1986; Undås, 1942
Skjonghelleren	Larsen, 1984; Larsen et al., 1987
Portugal	
Grotte de Furninha	Lambrecht, 1933; Roche, 1972; Villalta, 1964
Gruta de Figueira Brava	Mourer-Chauviré and Antunes, 1991; Mourer Chauviré, in litt., 1995
Spain	
Cova den Jaume Orat	McMinn et al., 1993
Cova Nova	Florit and Alcover, 1987; McMinn and Alcover, 1992
Cueva de Nerja	Boessneck and von den Driesch, 1980; Eastham, 1986, 1988, 1989; Hernandez, 1993, 1994, 1995, and in litt.
Devil's Tower	Garrod et al., 1928; Villalta, 1964
Es Pouàs	Alcover et al., 1981, 1992; Florit et al., 1989
Gorham's Cave	Eastham, 1968, 1989; Vega Toscano, 1990 (dating only)
Great Britain	
Bacon Hole	Harrison, 1977, 1987; Stringer et al., 1986
Creag nan Uamh	Newton, 1917; Lambrecht, 1933; Wolf, 1938; Stuart, 1983 (dating only)
Paviland Cave	Bell, 1922; Bowen, 1970 (dating only)
Potter's Cave	David, 1991

TABLE 2.—Composition of late Pleistocene seabird faunas. 1=*Fulmarus glacialis*, 2=*Puffinus puffinus*, 3=*Puffinus holei*, 4=*Puffinus gravis*, 5=*Puffinus griseus*, 6=*Puffinus* spp., 7=*Calonectris diomedea*, 8=*Hydrobates pelagicus*, 9=*Phalacrocorax aristotelis*, 10=*Morus bassanus*, 11=*Somateria mollissima*, 12=*Catharacta skua*, 13=*Rissa tridactyla*, 14=*Pagophila eburnea*, 15=*Alle alle*, 16=*Uria aalge*, 17=*Uria lomvia*, 18=*Uria* sp., 19=*Cepphus grylle*, 20=*Alca torda*, 21=*Pinguinus impennis*, 22=*Fratercula arctica*.

Site	Layer	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Cyprus																							
Akrotiri Aetokremnos			×							×													
Italy																							
Archi											×											×	
Arene Candide	P9									×							×				×		×
	P7							×									×						
	P5		×														×						×
	P4																×				×		
Buca del Bersaglieri			×							×													
Cala Genovesi a Levanzo	l. 2 t. 4		×					×															
	l. 2 t. 3		×					×															
Grotta Pietro Tampoia			×					×	×														
Grotta Romanelli	C						×			×				×								×	
Grotta dei Fanciulli	A6									×				×									
Norway																							
Blomvåg		×	×									×		×			×	×		×	×	×	
Skjonghelleren	B											×				×			×	×			×
	G	×												×	×	×	×	×		×			×
Portugal																							
Grotte de Furninha								×		×													
Gruta de Figueira Brava				×							×											×	
Spain																							
Cova den Jaume Orat				×				×	×														
Cova Nova								×		×											×		
Cueva de Nerja	EP					×		×		×	×		×				×					×	
	UP		×		×	×		×		×	×						×				×	×	
	UP/EP				×			×			×										×		
Devil's Tower			×					×		×							×					×	
Es Pouàs			×					×		×													
Gorham's Cave	A2									×													×
	B1		×																				×
	K									×						×						×	
Great Britain																							
Bacon Hole	D–F							×													×		
Creag Nan Uamh	5											×				×							
Paviland Cave											×						×						
Potter's Cave			×																				×

DATED FAUNAS

EEMIAN INTERGLACIAL.—Only one site can be confidently assigned to the last interglacial (Eemian/Ipswichian sensu stricto, i.e., oxygen isotope stage (IS) 5e), Bacon Hole on the Gower Peninsula in Southwest Wales. Layers D–F at this site, which have been U/Th dated to 122±9 kilo annum (Ka) BP (Stringer et al., 1986), contain a temperate avifauna, including *Calonectris diomedea* and *Alca torda* (Harrison, 1977, 1987). The current area of sympatry of these two species is situated in an area stretching from the waters southwest of the British Isles to the western Mediterranean (Figure 2). There is no sympatric breeding of these two species today, but this might be due to the absence of suitable breeding sites for seabirds between Bretagne and Northwest Spain. The occurrence of these two species in Wales supports evidence from other sources (e.g., McIntyre et al., 1972; Ruddiman and McIntyre, 1976) that the Northeast Atlantic was somewhat warmer during the Eemian than during the present interglacial.

THE EARLY WEICHSELIAN.—This is a climatically complex interval comprising two moderately cold stadials (IS 5b and IS 5d) and two interstadials of nearly interglacial magnitude (ISs 5a and 5c). The character of these interstadials was different in southern and northern Europe. In the south, IS 5a was, if anything, warmer than the earlier IS 5c, whereas in Scandinavia the opposite was the case (e.g., Mangerud, 1991). The extent of glaciation during the stadials is uncertain, but in Scandinavia it seems to have been mainly restricted to the mountains except in the far north. No fauna can be definitely assigned to this period, but it is possible that the fauna from Grotte de Furninha, Portugal (Tables 1, 2), for example, belongs here.

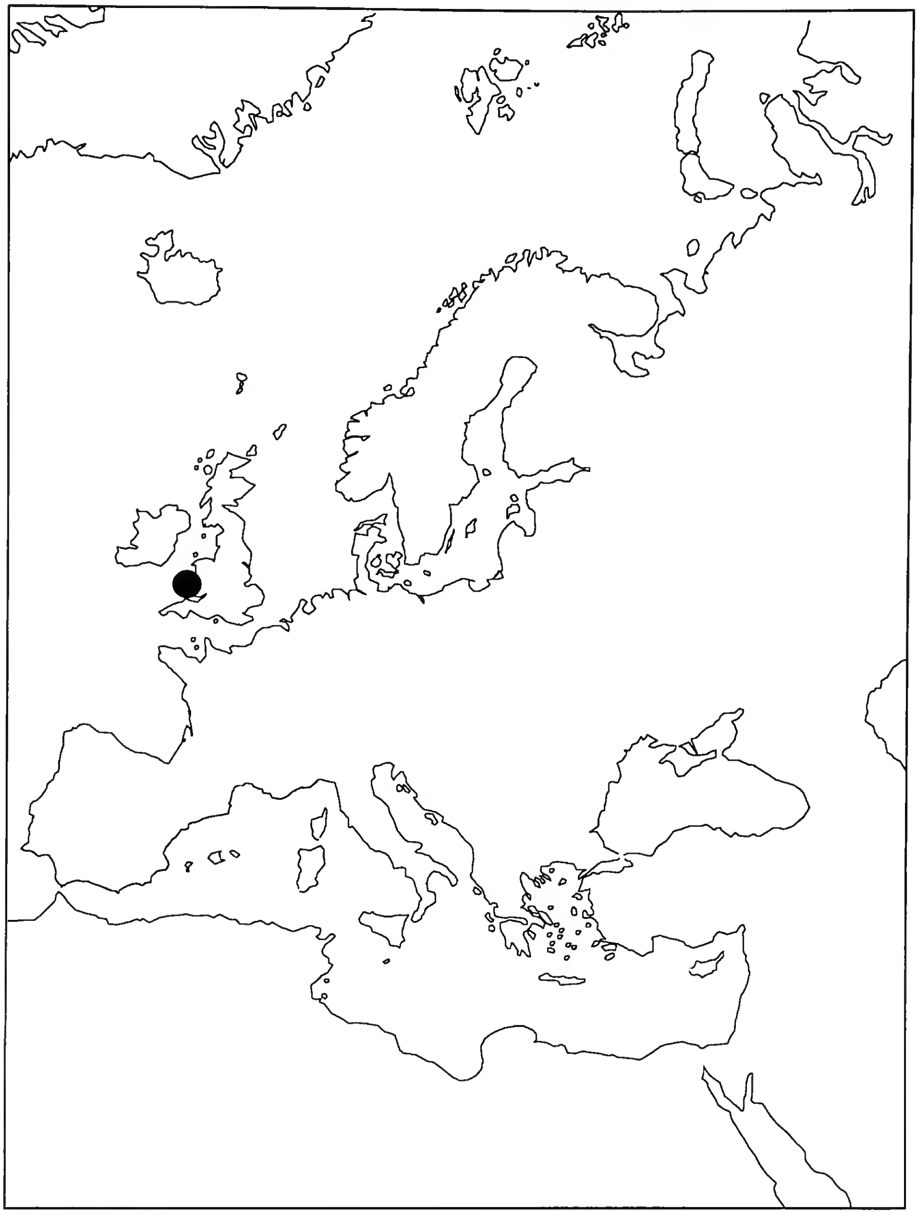

FIGURE 2.—Area of sympatry of seabirds from Bacon Hole, Great Britain (*Calonectris diomedea, Alca torda*). (● = fossil site.)

THE EARLY WEICHSELIAN PLENIGLACIAL.—This fairly short stadial (ca. 75–60 Ka BP) was quite cold, and the Scandinavian icecap expanded as far as eastern Denmark and northern Poland. The only fauna that might be assigned to this interval is layer K at Gorham's Cave (Gibraltar), which has been dated to "Würm I" (Hernández Carrasquilla, 1993). This is a rather "cold" fauna (*Phalacrocorax aristotelis, Alle alle, Pinguinus impennis*) (Figure 3), and the presence of at least *Alle alle* would certainly seem to indicate pleniglacial conditions, although layer K also has been dated (Vega Toscano, 1990) to the somewhat milder mid-Weichselian (ca. 45 Ka BP).

THE MID-WEICHSELIAN INTERSTADIAL COMPLEX.—This spans the period ca. 65–25 Ka BP, during which the climate was strongly cyclic. In very general terms, it consisted of two milder interstadials, ca. 60 Ka BP and ca. 30 Ka BP, separated by a colder stadial. For most of this interval, southern Scandinavia and at least parts of the Norwegian coast were ice-free.

The most interesting site from this interval is Skjonghelleren (layer G) in Norway, dated to the Ålesund interstadial

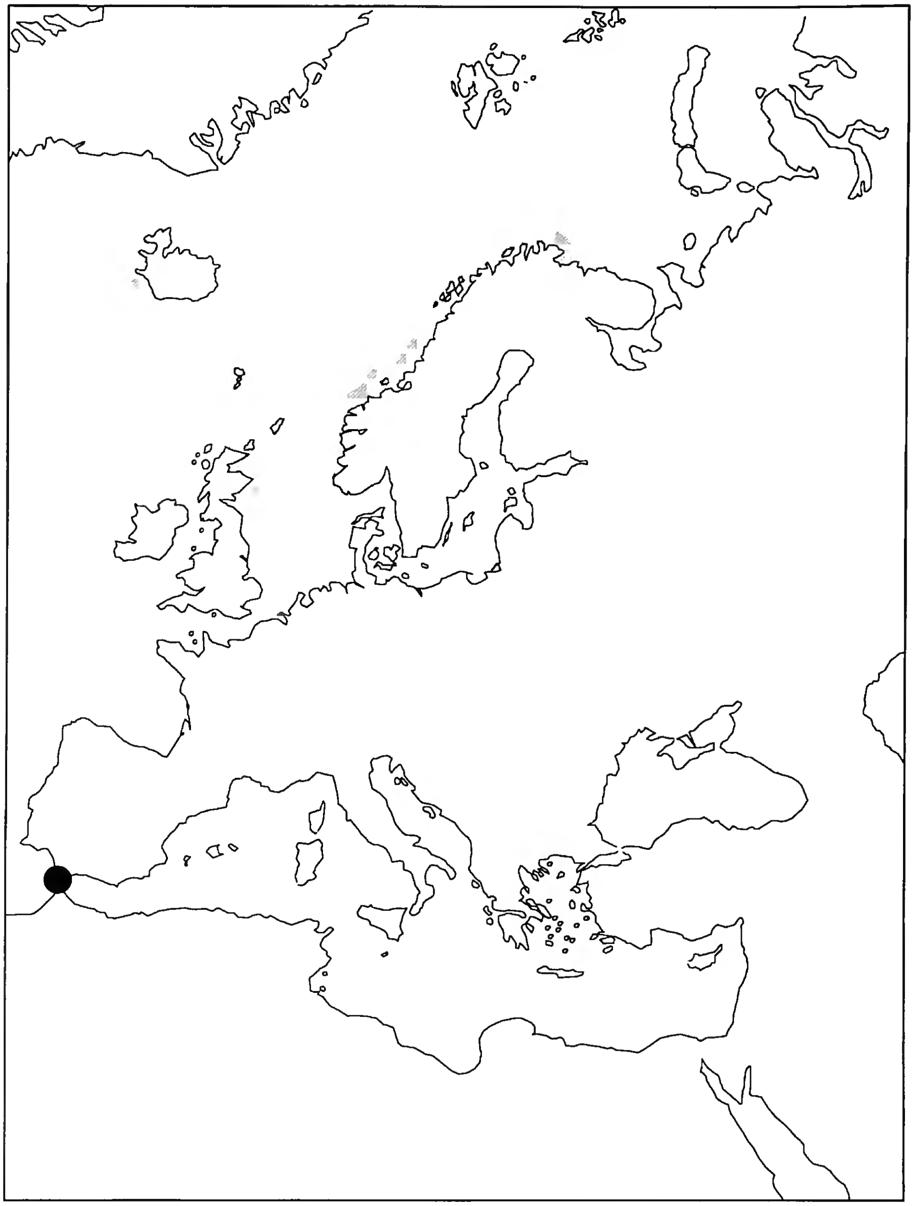

FIGURE 3.—Area of sympatry of seabirds from Gorham's Cave, Spain, layer K (*Phalacrocorax aristotelis, Alle alle, Pinguinus impennis*). (● = fossil site.)

30,000 yrs. BP) (Larsen, 1984; Larsen et al., 1987). This has a rich seabird fauna including *Fulmarus glacialis, Rissa tridactyla, Pagophila eburnea, Alle alle, Uria aalge, Uria lomvia, Cepphus grylle,* and *Fratercula arctica.* The site is a sea cave without any trace of human presence, and the fauna likely samples mostly species breeding in the vicinity. This is the only fauna containing truly arctic taxa, and the area of sympatry is a rather narrow area stretching from the seas north of Iceland to the west coast of Spitzbergen plus the waters off Northwest Novaya Zemlya (Figure 4). The areas of "best fit" with regard to breeding birds are Jan Mayen, Bear Island, Prince Charles' Foreland (all three with all species except *Pagophila eburnea*), and southern Spitzbergen (all species except *Uria aalge*). The presence of *Fratercula arctica* and *Uria aalge* as well as some non-avian taxa (e.g., *Lutra lutra* (Linnaeus), *Pollachius virens* (Linnaeus), *Brosmius brosme* (Ascanius)), however, indicates that water from the North Atlantic Current must have penetrated the Norwegian Sea for at least part of the Ålesund interstadial.

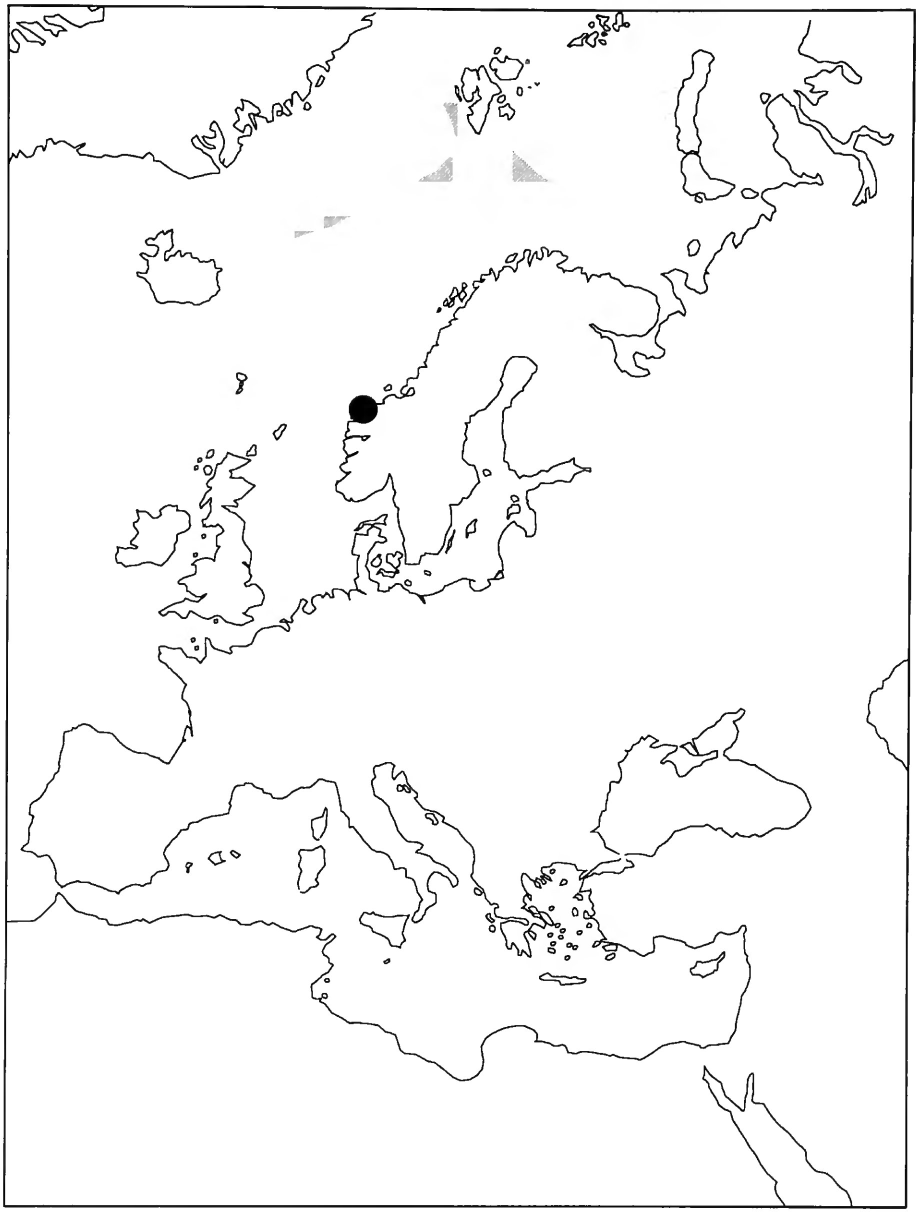

FIGURE 4.—Area of sympatry of seabirds from Skjonghelleren, Norway, layer G (*Fulmarus glacialis, Rissa tridactyla, Pagophila eburnea, Alle alle, Uria aalge, Uria lomvia, Cepphus grylle, Fratercula arctica*). (● = fossil site.)

Within the rather wide margins of C14-dating, another fauna coeval with the Skjonghelleren fauna is that from the Gruta de Figueira Brava in Portugal. This is one of the youngest Mousterian sites known and has been C14-dated to 30,930±700 yrs. BP (Mourer-Chauviré and Antunes, 1991). The fauna includes *Puffinus holei, Morus bassanus,* and *Pinguinus impennis.* The distribution of *Puffinus holei* outside the breeding season is unknown, but the area of sympatry of the other two species are shown in Figure 5. Clearly this is a boreal fauna and suggests conditions approximating those found around the British Isles today. This is supported by the other seabirds found at the site (*Gavia stellata, Melanitta nigra, Melanitta fusca, Clangula hyemalis*).

A third site from this time interval is Archi in Calabria, Italy. This can probably be dated to ca. 40,000 yrs. BP (Cassoli and Segre, 1985). The fauna includes *Morus bassanus* and *Pingui-*

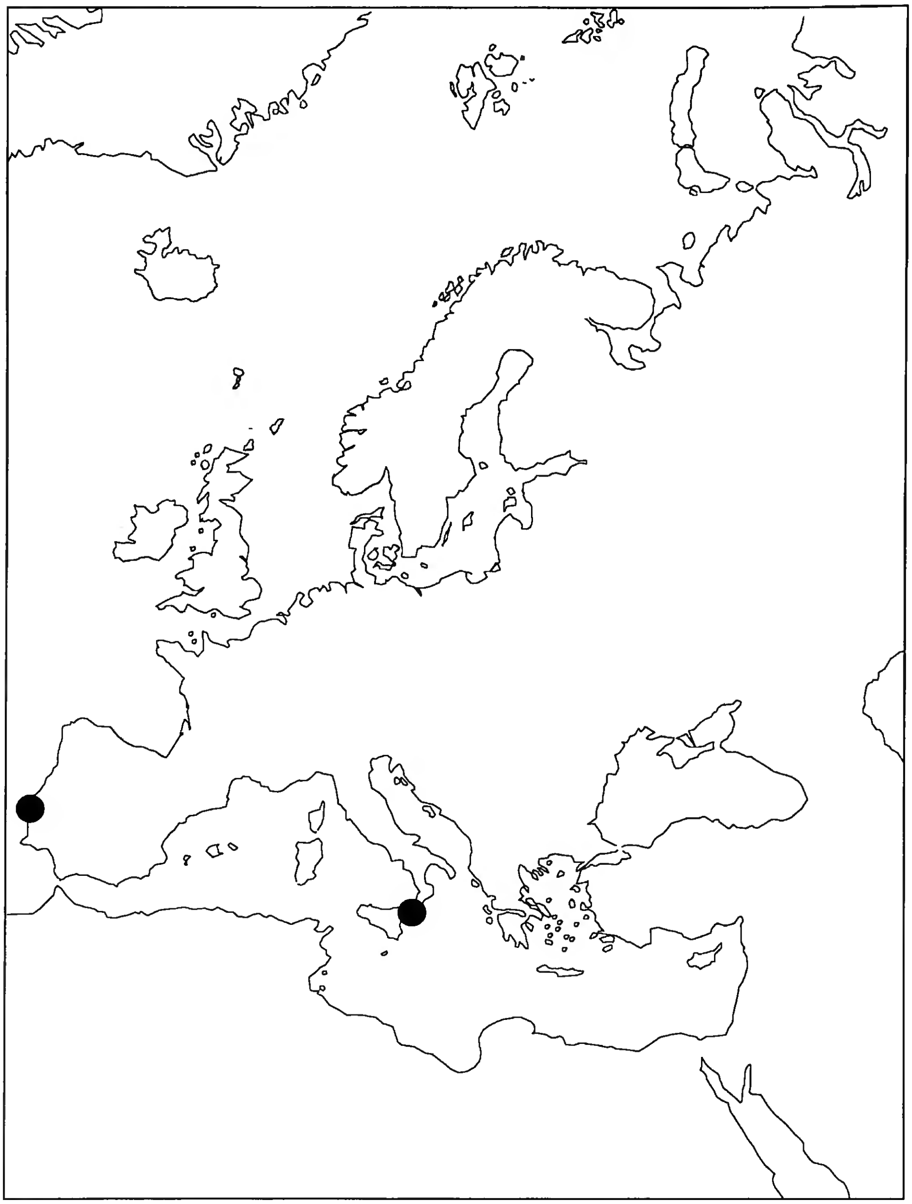

FIGURE 5.—Area of sympatry of seabirds from Figueira Brava, Portugal, and Archi, Italy (*Morus bassanus, Pinguinus impennis*). (● = fossil sites.)

nus impennis, which yields the same area of sympatry as Gruta de Figueira Brava (Figure 5). This similarity in a fauna from the central Mediterranean is probably due to a somewhat colder climate at the time when the Archi fauna was deposited.

THE LATE WEICHSELIAN PLENIGLACIAL.—Unfortunately, there are few sites that can be assigned to the glacial maximum, ca. 25,000–15,000 yrs. BP, probably both because this was the period of maximum eustatic lowering of the sea and because deposition of organic material virtually ceased over large areas during the coldest intervals. The only site that definitely falls within this interval is Arene Candide on the Italian Riviera. This site is very close to the sea today, and because the coast is quite steep, the sea was only ~3 km distant even during the glacial maximum. The layers P4, P5, P7, and P9 at this site (the only ones to contain two or more species of seabirds) are all older than 18,500 yrs. BP but are probably younger than 25,000 yrs. BP (Bietti, 1987). The seabirds in these layers include *Calonectris diomedea* (P7), *Puffinus puffinus* (P5), *Pha-*

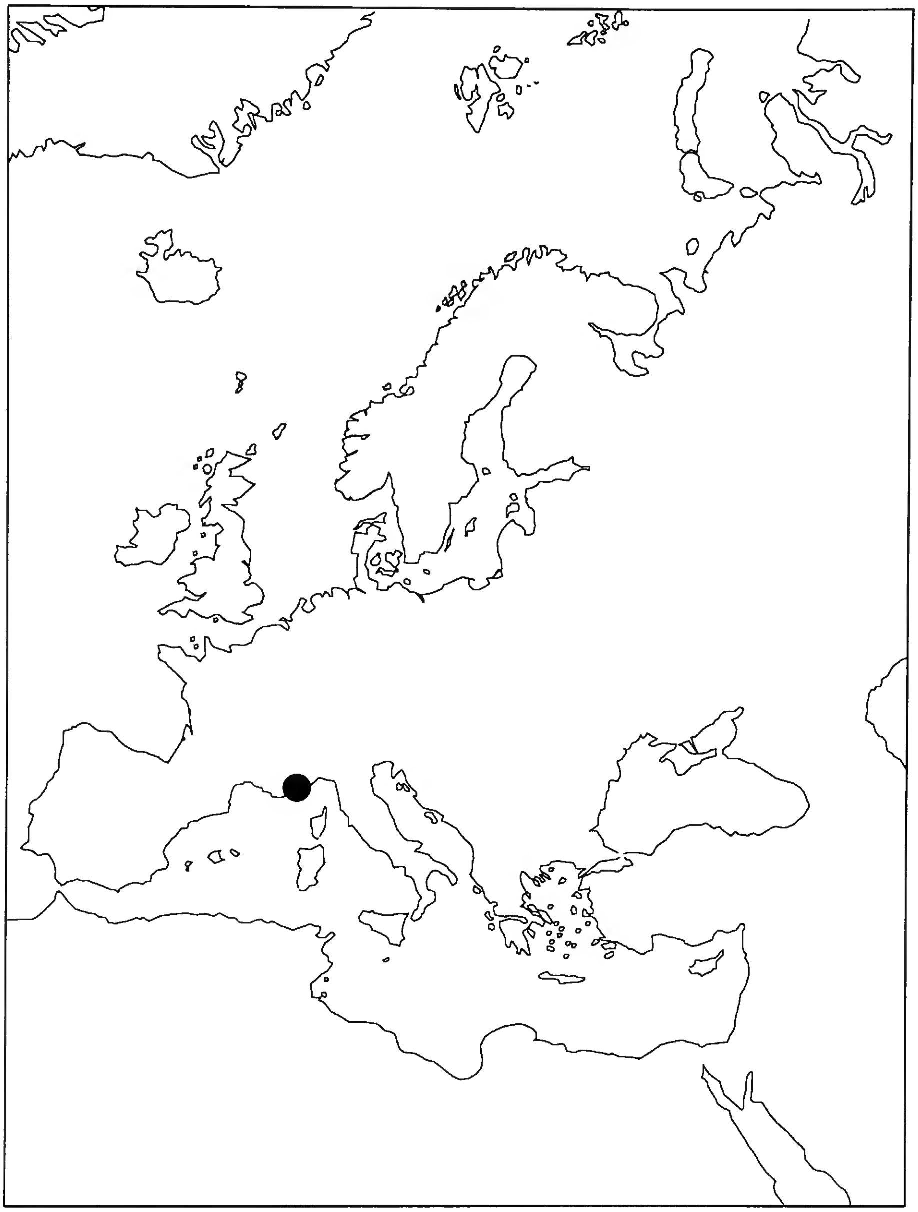

FIGURE 6.—Area of sympatry of seabirds from Arene Candide, Italy, layer P9 (*Phalacrocorax aristotelis, Uria aalge, Alca torda, Fratercula arctica*). (● = fossil site.)

lacrocorax aristotelis (P9), *Uria aalge* (P4,5,7,9), *Alca torda* (P4,9), and *Fratercula arctica* (P5,9). The areas of sympatry for the faunas in layers P4, P5, and P9 are rather similar and suggest that conditions approximating those around the British Isles at the present time prevailed off the Ligurian coast during the glacial. The area of sympatry for layer P9, which has the largest number of seabird species (4), is shown in Figure 6. Conditions may have been slightly milder when layer P7 was deposited (Figure 7).

The Upper Paleolithic fauna from Cueva de Nerja (UP layers) near Malaga, Spain (Figure 8), is dated to the interval 16,520–13,350 yrs. BP (Hernandez, 1995) and falls within the later part of the pleniglacial, including the Lascaux interstadial and the Dryas 1 stadial. The unusually rich seabird fauna consists of *Calonectris diomedea, Puffinus puffinus, P. gravis, P. griseus, Phalacrocorax aristotelis, Morus bassanus, Uria aalge, Alca torda,* and *Pinguinus impennis*. This fauna has only a very small area of sympatry off Southwest Ireland. Such a

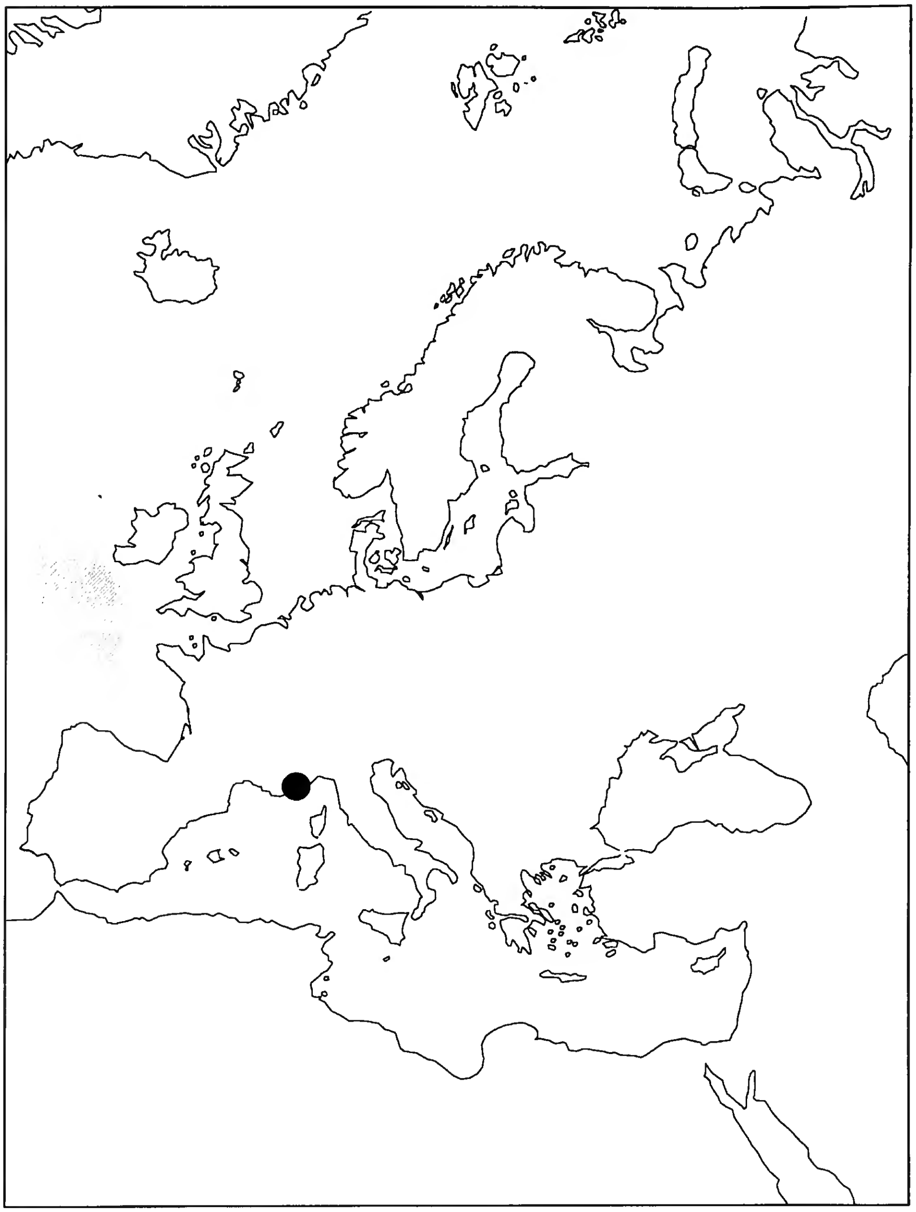

FIGURE 7.—Area of sympatry of seabirds from Arene Candide, Italy, layer P7 (*Calonectris diomedea, Uria aalge*). (● = fossil site.)

small overlap in the elements of the fauna may indicate a considerable degree of climatic change during the period of deposition. In any case, the rich seabird avifauna indicates that the sea off Granada must have been cool and biologically rich at the time.

THE LATE GLACIAL.—Sites with avifaunas from this interval (ca. 13,000–10,000 yrs. BP) are more common than for earlier intervals. Dating of the sites also is more exact, which makes it possible to divide late glacial records into three climatically distinct phases, the Bölling and Alleröd interstadials and the Dryas 3 (Younger Dryas) stadial. The Bölling interstadial (ca. 13,000–12,000 yrs. BP) was a quite mild interval, when at least summer temperatures may have approached present values in some areas. Climatic conditions during the Alleröd interstadial (ca. 11,800–10,800 yrs. BP) are somewhat controversial. The traditional view is that it was an interstadial comparable to, or even warmer than, Bölling and separated from it by a short but cold stadial (Dryas 2) ca. 12,000 yrs. BP. More recently the re-

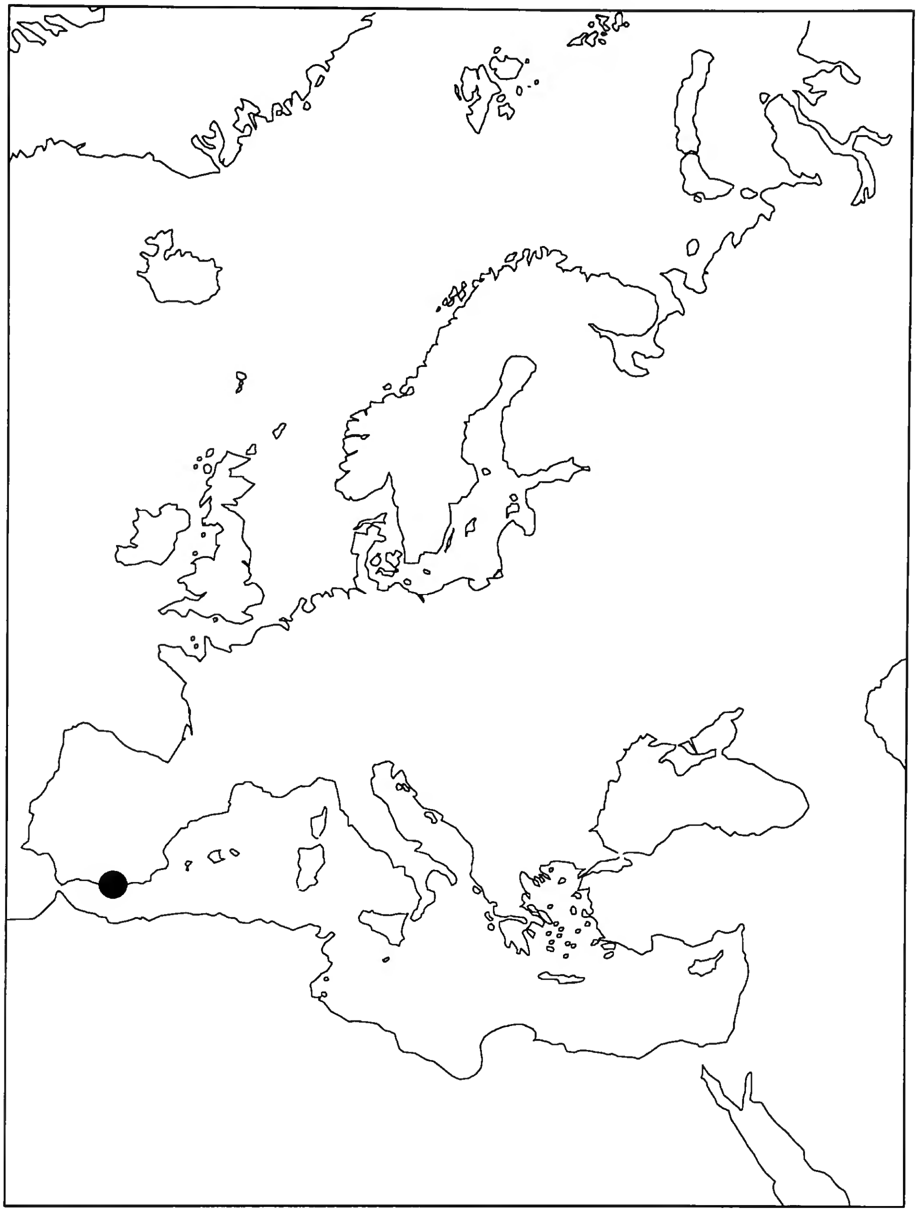

FIGURE 8.—Area of sympatry of seabirds from Cueva de Nerja, Spain (upper Paleolithic layer) (*Puffinus puffinus, Puffinus gravis, Puffinus griseus, Calonectris diomedea, Morus bassanus, Phalacrocorax aristotelis, Uria aalge, Alca torda, Pinguinus impennis*). (● = fossil site.)

ality of the Dryas 2 stadial has been questioned, and it has been argued that Alleröd was actually colder than Bölling (Nilssom, 1983). There is, however, no doubt that during the Dryas 3 stadial (ca. 10,800–10,100 yrs. BP), the last "cold snap" of the Würmian glacial cycle, there was a return to fully glacial climatic conditions lasting several centuries.

The Blomvåg site near Bergen in Norway is securely C14-dated to the Bölling interstadial (12,700–12,200 yrs. BP) (Lie, 1986). The seabird fauna consists of nine species (*Fulmarus glacialis, Puffinus puffinus, Somateria mollissima, Rissa tridactyla, Alca torda, Uria aalge, U. lomvia, Cepphus grylle, Pinguinus impennis*). The area of sympatry of these species (Figure 9) indicates conditions only slightly colder than at present. This implies a considerable contrast between conditions in the Norwegian Sea and on land because most of Scandinavia was still ice-covered at this time, and the ice-edge must

FIGURE 9.—Area of sympatry of seabirds from Blomvåg, Norway (*Fulmarus glacialis, Puffinus puffinus, Somateria mollissima, Rissa tridactyla, Alca torda, Uria aalge, U. lomvia, Cepphus grylle, Pinguinus impennis*). (● =fossil site.)

have been quite close to Blomvåg. Indeed, the site was temporarily overrun by the ice at some time after deposition of the fauna but before the Dryas 3 stadial.

The fauna in layer B at Skjonghelleren in Sunnmöre, Norway, is C14-dated to either the end of the Alleröd interstadial or the Dryas 3 stadial (11,510±190–10,360±170 yrs. BP) (Larsen, 1984; Larsen et al., 1987). The fauna consists of *Somateria mollissima, Alle alle, Uria* sp., *Cepphus grylle,* and *Fratercula arctica.* Unfortunately, this is not a very informative set of taxa and only indicates boreal or low arctic conditions, which might fit either a cool late phase of Alleröd or the early part of the Dryas 3 stadial.

There also is a fauna from Scotland that cannot be dated with any precision but is most likely from the late glacial. This is the fauna from layer 5 in Creag Nan Uamh cave, which has been considered to be either very late Pleistocene or earliest Ho-

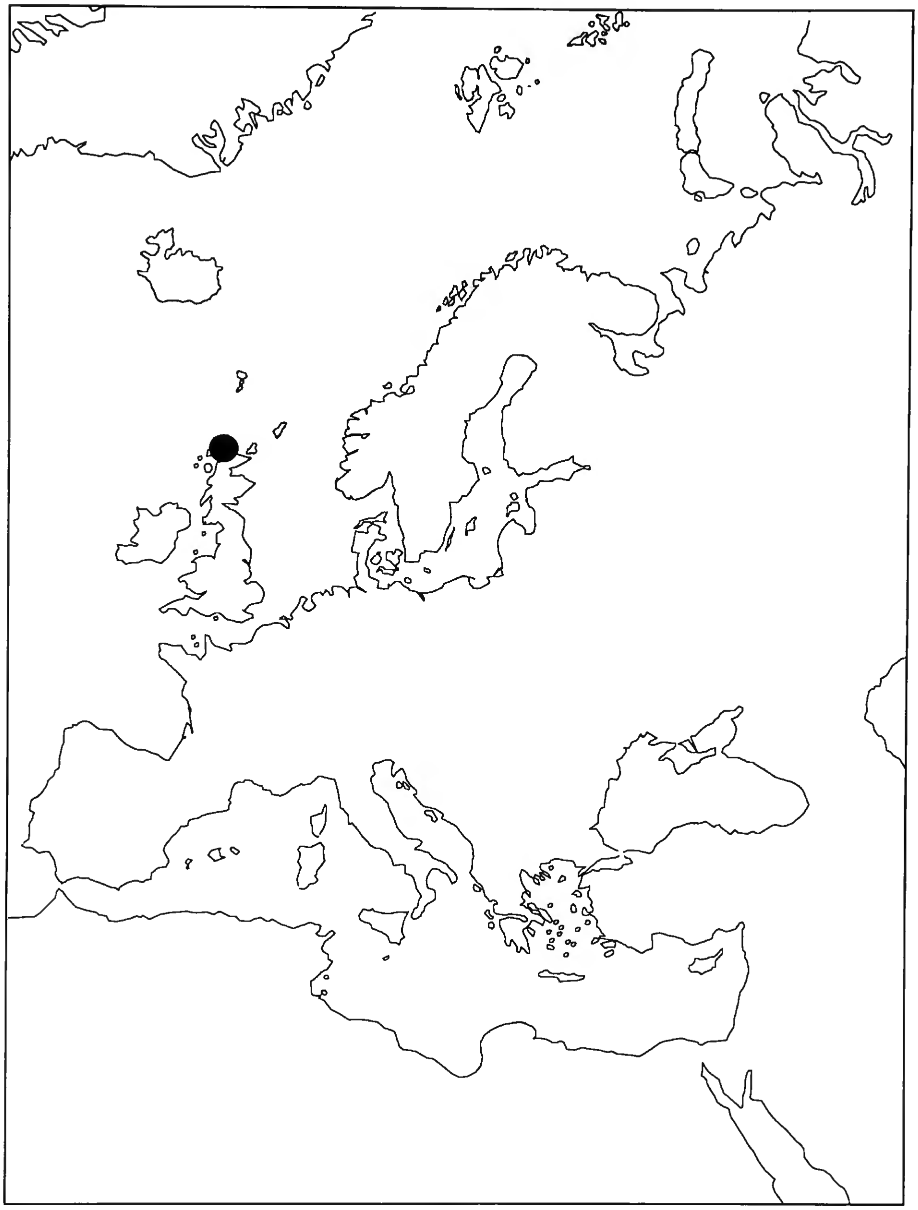

FIGURE 10.—Area of sympatry of seabirds from Creag Nan Uamh, Scotland (*Somateria mollissima, Alle alle*). (● = fossil site.)

locene (Stuart, 1983). It contains *Somateria mollissima* and *Alle alle* and indicates conditions similar to or slightly colder than at present (Figure 10). Other faunal elements from the site, such as *Rangifer tarandus* (Linnaeus), support this conclusion.

The fauna from layer C in Grotta Romanelli in Apulia, Italy (*Puffinus* spp., *Phalacrocorax aristotelis, Rissa tridactyla, Pinguinus impennis*), which is securely dated to the middle part of Dryas 3, has been published only in part (Cassoli et al., 1979), but it indicates that cool "Atlantic" conditions prevailed in the central Mediterranean even during this final cold snap of the Pleistocene (Figure 11).

There are a few more Mediterranean faunas that are either late glacial or early Holocene: Gorham's Cave, Gibraltar, layers A2 (*Phalacrocorax aristotelis, Fratercula arctica*) and B1 (*Puffinus puffinus, Fratercula arctica*); Cueva de Nerja, Spain, epipaleolithic (EP) layers (*Calonectris diomedea, Puffinus griseus, Phalacrocorax aristotelis, Morus bassanus, Catharacta skua, Uria aalge, Pinguinus impennis*) dated to 13,350–8770

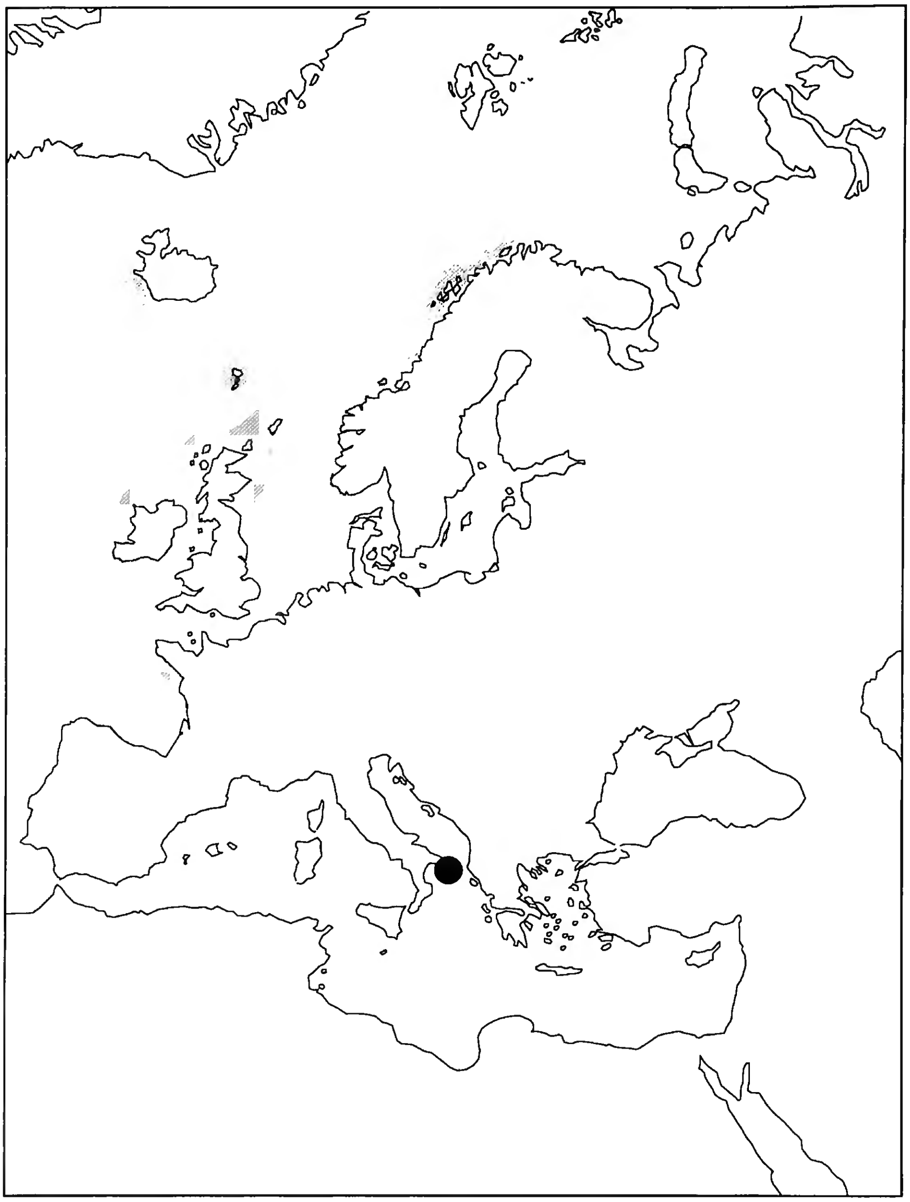

FIGURE 11.—Area of sympatry of seabirds from Grotta Romanelli, Italy (*Puffinus* spp., *Phalacrocorax aristotelis, Rissa tridactyla, Pinguinus impennis*). (● = fossil site.)

yrs. BP (Hernandez, 1995); Cala Genovesi on Levanzo Island off Sicily (*Puffinus puffinus, Calonectris diomedea*), which is younger than 11,180 yrs. BP (Cassoli and Tagliacozzo, 1982); and Akrotiri Aetokremnos on Cyprus (*Puffinus puffinus, Phalacrocorax aristotelis*), which is dated to 11,700–9000 yrs. BP (Simmons, 1991; Mourer-Chauviré, in litt.). These faunas mostly indicate conditions more or less similar to the present day, which may indicate early Holocene age. The exception is the Cueva de Nerja epipaleolithic layer (Figure 12), which indicates cool Atlantic conditions and may date largely to the cold Dryas 1 and/or Dryas 3 stadials. The fauna from Akrotiri Aetokremnos (Figure 13) also may indicate a slightly colder and more eutrophic sea around Cyprus than at present, perhaps because the fossils were deposited during the Dryas 3 stadial.

UNDATED FAUNAS

There are a number of faunas containing seabirds that are not at present satisfactorily dated. In these cases, consideration of the environmental information given by the seabirds may help

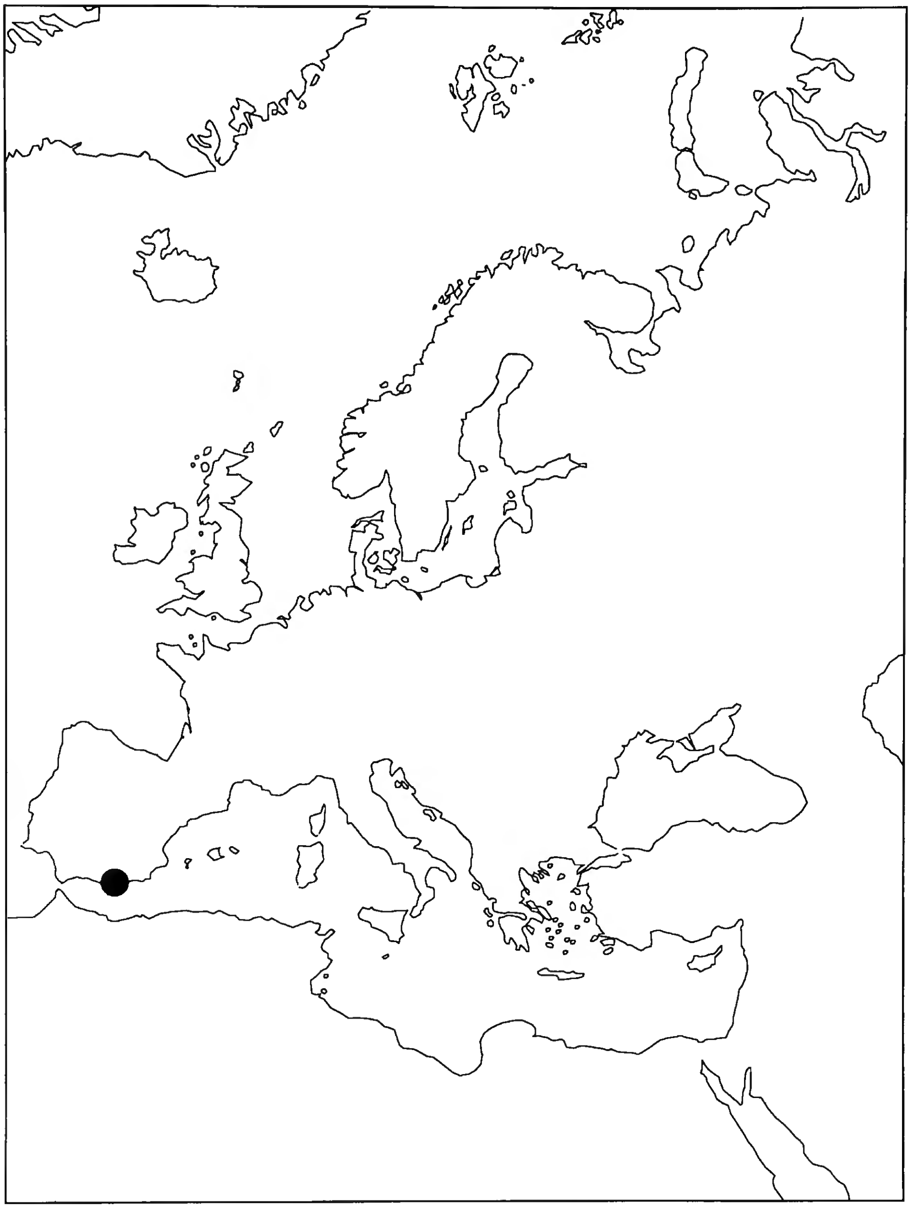

FIGURE 12.—Area of sympatry of seabirds from Cueva de Nerja, Spain (epipalaeolithic layer) (*Puffinus griseus, Calonectris diomedea, Morus bassanus, Phalacrocorax aristotelis, Catharacta skua, Uria aalge, Pinguinus impennis*). (● =fossil site.)

in defining the age of these faunas. These faunas can be divided into two groups: faunas that indicate significantly colder conditions than at present and faunas that indicate conditions approximately similar to the present day.

GROTTA PIETRO TAMPOIA, ITALY.—This is a "warm" fauna (*Puffinus puffinus, Calonectris diomedea, Hydrobates pelagicus*), indicating conditions similar to today, which supports Mayaud and Schaub's (1950) view that the fossils from this site are largely or wholly of Holocene age.

BUCA DEL BERSAGLIERI, ITALY.—This also is a warm fauna (*Puffinus puffinus, Phalacrocorax aristotelis*) (Figure 13), particularly because at least some of the shearwater fossils are from the warm-water species *Puffinus* (*puffinus*) *yelkouan*. Very little information on the date of the deposits is available, but it seems likely that the fauna is at least partly Holocene, a hypothesis that is supported by the composition of the avifauna in general and by the presence of *Rattus rattus* Linnaeus (Wolf, 1938).

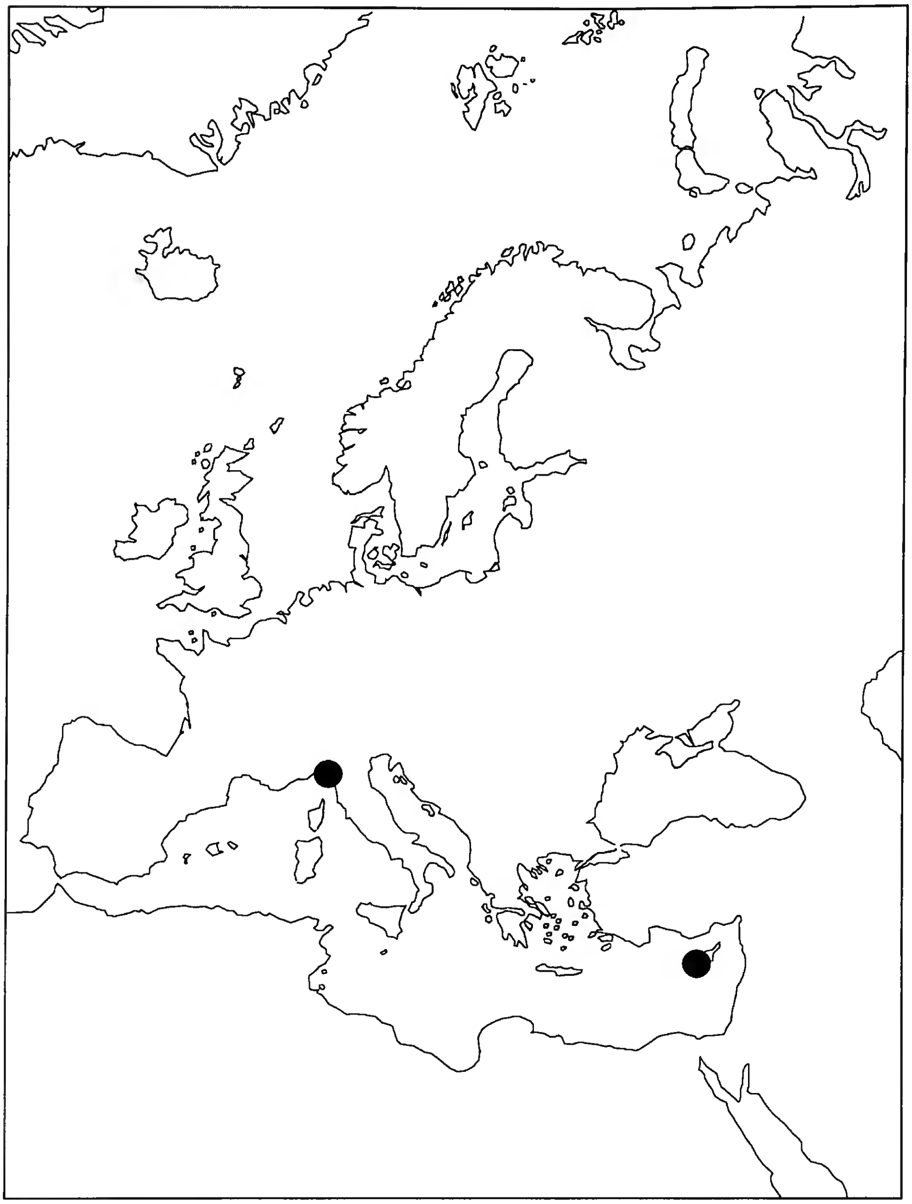

FIGURE 13.—Area of sympatry of seabirds from Akrotiri Aetokremnos, Cyprus, and Buca del Bersaglieri, Italy (*Puffinus puffinus, Phalacrocorax aristotelis*). (● =fossil sites.)

PAVILAND CAVE, GREAT BRITAIN.—The seabirds from this site (*Morus bassanus, Uria aalge*) indicate temperate conditions similar to the present, and the remains are therefore very unlikely to be contemporary with the famous Upper Paleolithic "red lady of Paviland," which has been C14-dated to 18,460±340 yrs. BP (Bowen, 1970), the coldest part of the pleniglacial. During the Pleniglacial, Paviland Cave would in any case have been situated a very considerable distance from the seashore. The seabird remains may well be Holocene.

POTTER'S CAVE, GREAT BRITAIN.—It has been surmised that the seabirds from this site are younger than the other bird remains and are actually Holocene (David, 1991). The sympatric area of the species (*Puffinus puffinus, Fratercula arctica*) indicates temperate conditions and supports a Holocene date.

Discussion

Reconstructions of past conditions based on the composition of fossil faunas are based on the premise that the ecological requirements of the species used has remained constant during the period studied. This is probably a safe assumption for most of the seabirds in this study. It should be noted that none of the 31 faunas contains seabird species with allopatric ranges (although this might have been the case if *Puffinus yelkouan* had been treated as a distinct species). This absence of allopatric species is in marked contrast to late Pleistocene nonmarine avifaunas, where species that are today widely allopatric (e.g., *Nyctea scandiaca* and *Alectoris* spp.) frequently occur together. This similarity with modern seabird faunas also is an argument that the ecology of the species concerned has remained fairly constant over the period studied.

Most of the reasonably well-dated faunas described above are either from the western Mediterranean or from Norway. The western Mediterranean faunas mostly suggest cool, biologically productive seas, and the western Mediterranean together with the waters around the Macaronesian islands may have been an important refugium for boreal seabirds during the coldest parts of the glaciation. Unfortunately, there is a dearth of sites from the mildest parts of the glaciation and from the eastern Mediterranean basin, although an isolated record shows that *Morus bassanus* occurred as far east as Crete during some part of the last glaciation (Suriano, 1980).

The Norwegian faunas, of course, date only from the milder parts of the glaciation and are perhaps most interesting as illustrations of violent climatic and environmental shifts during the late Pleistocene. This is particularly striking when comparing the Blomvåg fauna (Figure 9) from the mild Bölling interstadial with the 2000 years younger Grotta Romanelli fauna (Figure 11) from the cold Dryas 3 stadial. The occurrence of *Pinguinus impennis* in both these faunas is particularly noteworthy and suggests that even this nonvolant species was capable of changing its distribution quite rapidly in response to changing conditions. This contradicts Bengtson's (1984) theory that the extinction of *Pinguinus impennis* was at least partly due to an inability to adapt to environmental changes and supports the traditional view that the species' extinction was directly caused by human action.

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Intraspecific Variation in Modern and Quaternary European *Lagopus*

John R. Stewart

ABSTRACT

Skeletal proportions of modern European populations of *Lagopus lagopus* (Linnaeus) and *L. mutus* (Montin) from Britain, Iceland, Scandinavia, northern Russia, and the Alps are compared with their Quaternary fossil counterparts from Britain, Poland, France, and Belgium. *Lagopus lagopus* and *L. mutus* from most pre-Holocene deposits are found to differ allometrically from modern samples. This difference is best seen in the tarsometatarsus, which often is more robust in both species in the Pleistocene and in turn may reflect greater body weight. Possible correlations between this phenomenon and the climatic and ecological conditions of the past, as well as the possibility that these birds were less sedentary, are discussed.

Introduction

Previous workers, such as Newton (1924), Mourer-Chauviré (1975a, 1975b), Jánossy (1974, 1976), Bocheński (1974, 1985, 1991), Harrison (1980), Potapova (1986), and Bocheński and Tomek (1994) have described differently sized and proportioned postcranial bones of both *Lagopus mutus* (Montin) and *Lagopus lagopus* (Linnaeus) from the fossil record of Europe. Specifically, samples of both species from the Pleistocene were seen to differ in size and allometry from skeletons of their recent counterparts. These allometric differences were seen in the relative proportions of their tarsometatarsi, carpometacarpi, phalanx 1 digit III pedis, and phalanx 1 digit II alae, as well as in cranial elements.

Newton, who was probably the first to note the occurrence of anomalously proportioned *Lagopus* fossils of Pleistocene age, believed that a third species had existed (Newton, 1924). He referred to this species, found at Merlin's Cave, a late Pleistocene site in Britain, as a "small ptarmigan" and never named it as a distinct form, which is how many authors have dealt with these anomalies since. Exceptions are the species *Lagopus atavus* Jánossy (1974) from the late Pliocene of Poland (Jánossy, 1976; Bocheński, 1991) and the subspecies *L. lagopus noaillensis* Mourer-Chauviré (1975a) and *L. mutus correzensis* Mourer-Chauviré (1975a) from La Fage, a Rissian (middle Pleistocene) site in France.

Lagopus lagopus noaillensis and *L. mutus correzensis* were described by Mourer-Chauviré as being distinguished by the robustness of their tarsometatarsi as compared to modern populations. She also plotted the mean lengths and shaft widths of tarsometatarsi of both species from La Colombière and Gigny, two assemblages of different ages from the last glacial of France, together with the two named subspecies from La Fage. This showed that they, too, had relatively robust tarsometatarsi, although their lengths varied, producing allometric-shape variation.

The most detailed study of *Lagopus* fossils to date was that by Bocheński (1974). In his book he compared a number of Polish fossil populations of both species from the last glaciation with samples from much of their modern European distribution. He concluded that the fossil birds possessed longer carpometacarpi and humeri but shorter tarsometatarsi than their modern counterparts, and that the articular ends of the humeri, tarsometatarsi, and coracoids were more massive. Bocheński interpreted the differences in the wing-bone lengths as indicating that the primary feathers of both species had become shorter, thus reducing wing-surface area over time. This, together with the change in bone robustness, especially that of the coracoid, indicated to him that the two species had maintained, or had only slightly reduced, their body size over time. Later, Bocheński (1985) showed that Pleistocene *L. lagopus* in Poland had longer distal-wing bones (carpometacarpi and phalanx 1 digit II alae) and shorter distal-leg elements (tarsometatarsi and phalanx 1 digit III pedis) when compared to modern birds. Subsequently, Bocheński and Tomek (1994) focused on the relative lengths of postcranial bones of Pleistocene *L. mutus* in Austria and showed that they differed from modern alpine birds in having shorter tarsometatarsi but longer carpometacarpi.

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Recent investigations by neontologists into intraspecific variation in size and allometry, seen across both space and recent time, emphasize the need for a broader-based approach to variation seen in fossils. Zink and Remsen's (1986) review of the relevance of geographic variation to evolution, and case studies such as those by Johnston and Selander (1964), Grant (1971, 1986), Fleischer and Johnson (1982), James (1983), and Dennison and Barker (1991), demonstrate that within-species morphological differences in birds are frequently observed across space, and that these differences may evolve over relatively short spans of time. Analyses of present-day intraspecific geographic variation therefore give an insight into the spectrum of variation that may have occurred over recent geological time in species.

A notable exception to the lack of application of these neontological studies to fossils or subfossils is the study by Ericson (1987), wherein subfossil Common Eider (*Somateria mollissima* Linnaeus) from Scandinavia were compared to a variety of different extant subspecies and were shown to differ significantly. In this instance various environmental criteria were considered causal, including climatic change and anthropogenic effects; the author preferred the latter as an explanation.

MATERIALS AND METHODS

The present study has attempted to bring together a widely distributed body of data on both species of *Lagopus* from the present-day western Palearctic. These data were used for biometric comparison with a broader range of geographically and temporally separated fossils than has been previously achieved. All but the British and Belgian fossil samples have been metrically studied by others, although no one has examined all these samples together. Those that are newly analyzed herein are from Pin Hole Cave (Manchester City Museum), Merlin's Cave (University of Bristol Speleological Society Museum), Westbury-sub-Mendip (Paleontology Department, Natural History Museum, London), and Remouchamps (Musée Royaux d'Art d'Histoire, Bruxelle).

The tarsometatarsus is invariably the most frequently occurring skeletal element of medium-sized Galliformes in European cave assemblages (Mourer-Chauviré, 1983) and is thus the main element dealt with herein. The relative abundance of this bone is fortunate because it is one of the elements most easily identified as either *Lagopus lagopus* or *L. mutus* (Kraft, 1972; Mourer-Chauviré, 1975a; Bocheński, 1985). There appear to be no details of morphology that can aid determination, and the two species are identified simply on the basis of size: *L. lagopus* is consistently larger than *L. mutus* (see Figure 2). Many other postcranial bones present greater problems because they overlap considerably in size and therefore make analysis more complicated.

Table 1 lists all the modern skeletal samples of both species, including two populations of *L. lagopus scoticus* (Latham), one from Scotland and one from Derbyshire, England; samples of *L. lagopus lagopus* from Scandinavia and Russia; and an individual skeleton of *L. lagopus major* Lorenz. *Lagopus mutus* is represented by skeletons from Scotland (*L. m. millaisi* Hartert), Iceland (*L. m. islandorum* Faber), Scandinavia (*L. m. mutus*),

TABLE 1.—Mensural data for the tarsometatarsus of modern and fossil samples of both *Lagopus lagopus* and *L. mutus*. See Table 2 for fossil site locations. Sites that have no mean and have question marks instead of a minimum value for *L. lagopus* and a maximum value for *L. mutus* are such because insufficient tarsometatarsal length difference was present between specimens to define the respective upper limits of *L. lagopus* and the lower limits of *L. mutus* (see Figure 2). (GL=greatest length; KB=shaft width; *n*=number of specimens.)

Samples	Minimum–Maximum (*n*)	Mean
MODERN		
Lagopus lagopus lagopus (Scandinavia)	GL 37.04–42.1 (*n*=11)	38.95
	KB 2.96–3.34 (*n*=11)	3.18
Lagopus lagopus lagopus (Russia)	GL 38.1–42.88 (*n*=6)	40.61
	KB 2.84–3.44 (*n*=5)	3.19
Lagopus lagopus scoticus (Derbyshire, England)	GL 38.6–43.58 (*n*=19)	41.1
	KB 2.94–3.98 (*n*=19)	3.24
Lagopus lagopus scoticus (Scotland)	GL 38.38–44.06 (*n*=9)	41.1
	KB 3.1–3.6 (*n*=9)	3.36
Lagopus lagopus major (Kazakhstan)	GL 45.32 (*n*=1)	–
	KB 3.64 (*n*=1)	–
Lagopus mutus mutus (Scandinavia)	GL 29.44–34.08 (*n*=2)	31.76
	KB 2.66–2.74 (*n*=2)	2.7
Lagopus mutus millaisi (Scotland)	GL 33.22–35.9 (*n*=5)	34.69
	KB 2.88–3.12 (*n*=5)	3
Lagopus mutus helveticus (French Alps)	GL 31.8–35.7 (*n*=16)	33.06
	KB 2.46–2.94 (*n*=16)	2.71
Lagopus mutus islandorum (Iceland)	GL 30.18–34.82 (*n*=2)	32.5
FOSSIL	KB 2.58–2.86 (*n*=2)	2.72
Mamutowa Cave, *Lagopus lagopus*	GL ?–39.84	–
	KB ?	–
Mamutowa Cave, *Lagopus mutus*	GL 32.1–?	–
	KB ?	–
Remouchamps, *Lagopus lagopus*	GL 39.44–41.64 (*n*=3)	40.19
	KB 3.24–3.4 (*n*=3)	3.3
Merlin's Cave, *Lagopus lagopus*	GL ?–40.28	–
	KB ?	–
Merlin's Cave, *Lagopus mutus*	GL 29.94–?	–
	KB ?	–
La Balme-les-Grottes, *Lagopus lagopus*	GL 36.36–38.8 (*n*=10)	37.75
	KB 3–3.48 (*n*=10)	3.22
La Balme-les-Grottes, *Lagopus mutus*	GL 32.24–32.3 (*n*=2)	32.27
	KB 3.2 (*n*=2)	3.2
La Colombière, *Lagopus lagopus*	GL 35.2–40.6 (*n*=30)	38.21
	KB 3.04–4.08 (*n*=30)	3.4
La Colombière, *Lagopus mutus*	GL 29.26–33.72 (*n*=30)	31.39
	KB 2.6–3.36 (*n*=30)	3
Pin Hole Cave, *Lagopus lagopus*	GL 36.46–41.32 (*n*=22)	38.66
	KB 3.06–3.88 (*n*=22)	3.41
Pin Hole Cave, *Lagopus mutus*	GL 30.54–32.98 (*n*=27)	31.85
	KB 2.74–3.48 (*n*=27)	3.01
La Fage, *Lagopus lagopus noaillensis*	GL 36.52–39.3 (*n*=7)	38.07
	KB 3.22–3.44 (*n*=7)	3.33
La Fage, *Lagopus mutus correzensis*	GL 31.7–34.8 (*n*=9)	33.38
	KB 2.74–3.42 (*n*=9)	3.09
Westbury-sub-Mendip, *Lagopus* sp.	GL –	–
	KB 3.43 (*n*=2)	–
Rebielice Krolewskie, *Lagopus atavus*	GL –	–
	KB 3.96 (*n*=1)	–

and the French Alps (*L. m. helveticus* Thienemann). Fossil samples are from similarly scattered locations. Figure 1 gives the geographical position within Europe of the various fossil localities. An attempt also has been made to examine the species through time, and the approximate ages of the samples are detailed in Table 2.

A brief comment about the chronological framework is worth making because there are problems with correlating Pleistocene fossiliferous deposits across Europe that are too old for C-14 dating. The "Rissian" age quoted for the La Fage site (Chaline, 1975) is best interpreted as middle Pleistocene (oxygen isotope stage 6 or 8) because there is no general agreement as to the correlation of the Alpine stages with the detailed oxygen-isotope chronology derived from deep-sea cores (Shackleton and Opdyke, 1973). This more recently developed chronology has shown the Alpine scheme to be oversimplified, and more interglacial and glacial phases are now recognized, implying that sites described as Rissian, for example, include ones from different cold stages (Bridgland, 1994). Within the northern European scheme, the Westbury-sub-Mendip sample, from the rodent stratum (Andrews, 1990), is regarded as referable to the early Anglian/Elsterian and probably equivalent to oxygen isotope stage 12 (A.P. Currant, The Natural History Museum, London, pers. comm., 1996). The Rebielice Krolewskie material is late Pliocene in age according to the Mammal Neogene (MN) chronology (Mein, 1990; Bocheński, 1991).

The method of measurement for all skeletal elements of *Lagopus* are as detailed in Kraft (1972) and were taken to the nearest 0.02 mm with slide calipers.

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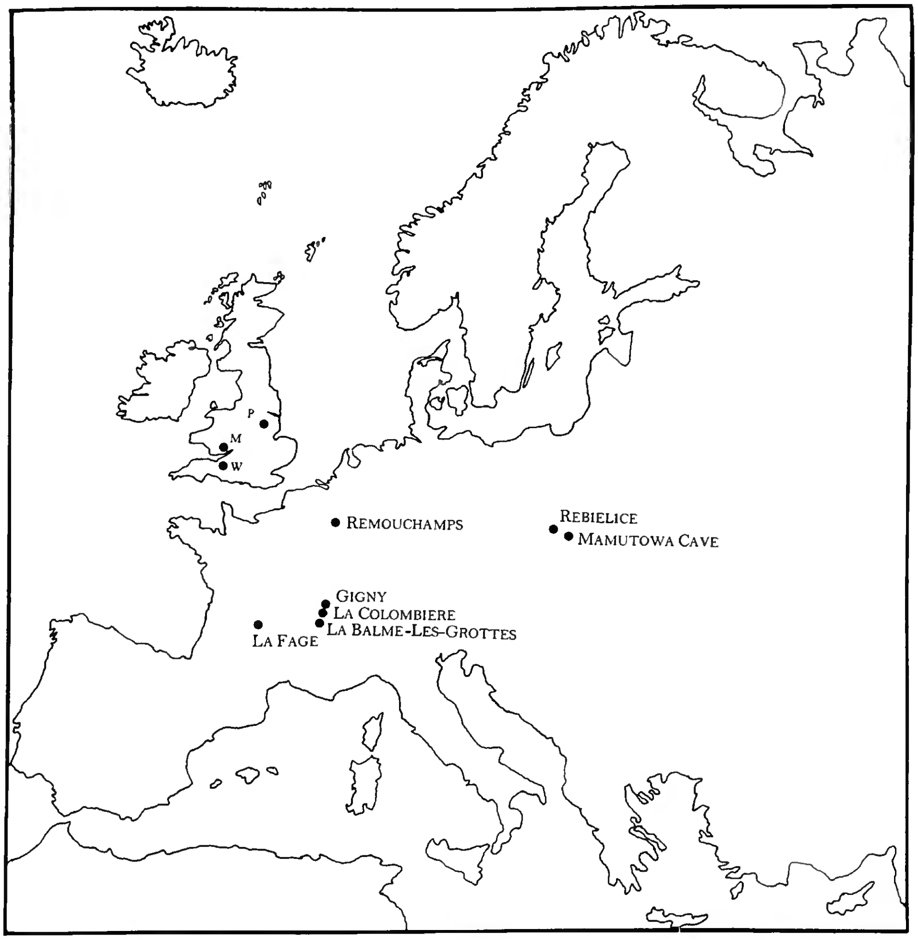

FIGURE 1.—Distribution of sites containing important faunas of *Lagopus* mentioned in the text. (P=Pin Hole Cave; M=Merlin's Cave; W=Westbury-sub-Mendip.)

TABLE 2.—Chronology and location of fossils samples (including ones discussed from literature).

Site	Stratigraphic Position	Reference	Age
Remouchamps, Belgium	late glacial	Hedges et al., 1994	10,330±110 yrs. BP and 10,800±1110 yrs. BP
Merlin's Cave, England	late glacial	Housley, 1991	10,020±120 yrs. BP
Mamutowa Cave, Poland	Vistulian (Upper pleniglacial)	Bocheński, 1974	ca. 30–15 Ka
Pin Hole Cave, England	Devensian	Jacobi, pers. comm., 1996	ca. 100–10 Ka
La Balme-les-Grottes, France	"Würm IV" (late glacial)	Mourer-Chauviré, 1975a	ca. 15–10 Ka
La Colombière, France	"Würm IV" (late glacial)	Mourer-Chauviré, 1975a	13,390±300 yrs. BP
Gigny, France	"Würm II"	Mourer-Chauviré, 1975a	ca. 30–20 Ka
La Fage, France	"Rissian"	Chaline, 1975	ca. 300–150 Ka
Westbury-sub-Mendip, England	Early Anglian (oxygen isotope stage 12)	Currant, pers. comm., 1996	ca. 500–450 Ka
Rebielice Krolewskie, Poland	Biozone MN16	Bocheński, 1991	ca. 3.6–2.4 Ma

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Results

In *Lagopus mutus,* there is a noticeable difference in the mean size of the tarsometatarsi among modern subspecies in Europe (see Table 1). The Scottish subspecies (*L. mutus millaisi*) is larger than populations from Scandinavia (*L. m. mutus*) or the Alps (*L. m. helveticus*). This difference is perhaps best seen in the length, although the bones appear to be isometric. This confirms the findings of Bocheński (1974), although differences in the means calculated in our two studies exist. Kraft (1972) alleged differences between nominate *L. m. mutus* from Scandinavia and *L. m. helveticus* from the Alps, but this could not be confirmed in the present study due to small sample size.

With *Lagopus lagopus* there appears to be greater overlap between the samples, although *L. l. scoticus* is slightly larger than nominate *L. l. lagopus.* The single specimen of *L. l. major* is very much larger, although sample size prevents reliable consideration of this subspecies, which is, however, regarded as larger by ornithologists (Dement'ev and Gladkov, 1967).

The most apparent difference between modern and fossil samples of both species of *Lagopus* is the difference in their tarsometatarsal-shaft widths (Figure 2). This is almost ubiquitous, which is important because the modern samples are geographically widely spaced, and the fossils come from sites of significantly different ages as well as being widely spaced geographically. In addition, there is a tendency for fossils of both taxa from the last glaciation to have shorter tarsometatarsi, thus making these bones very robust (Figure 2). An exception to this pattern is provided by the study made by Mourer-Chauviré (1975a) on a sample from Gigny in France, which, although from the last (Würm) glaciation, had relatively long tarsometatarsi. Tarsometatarsi from La Fage (Rissian) also show this tendency (Mourer-Chauviré, 1975a; Figure 2). Therefore, length is probably more variable among fossil populations than is shaft width.

Given the consistency of greater robustness in Pleistocene tarsometatarsi of *Lagopus,* an explanation should be sought. Although it is conceivable that the species may have changed through evolution or replacement, both *L. lagopus* and *L. mutus* can be traced from the Pleistocene, suggesting intraspecific adaptational changes. Research into bovid limbs and the variables affecting their morphology has shown that shaft width is closely correlated with body mass (Scott, 1985) because of weight-bearing constraints, so the greater robustness of the fossil tarsometatarsi of *Lagopus* may reflect greater mean body weight. To test this hypothesis an attempt was made to assess the degree to which tarsometatarsal dimensions are correlated with body weight in modern *Lagopus.*

Both species of *Lagopus* are included in this analysis to augment the size and range of samples. This approach is considered valid because the relationship should be strictly mechanical and thus comparable between closely related taxa; it would seem unlikely that bones of *L. lagopus* and *L. mutus* possess significantly different mechanical properties. Figure 3 shows that there is a close, positive correlation between bird weights and their tarsometatarsal-shaft widths (correlation coefficient

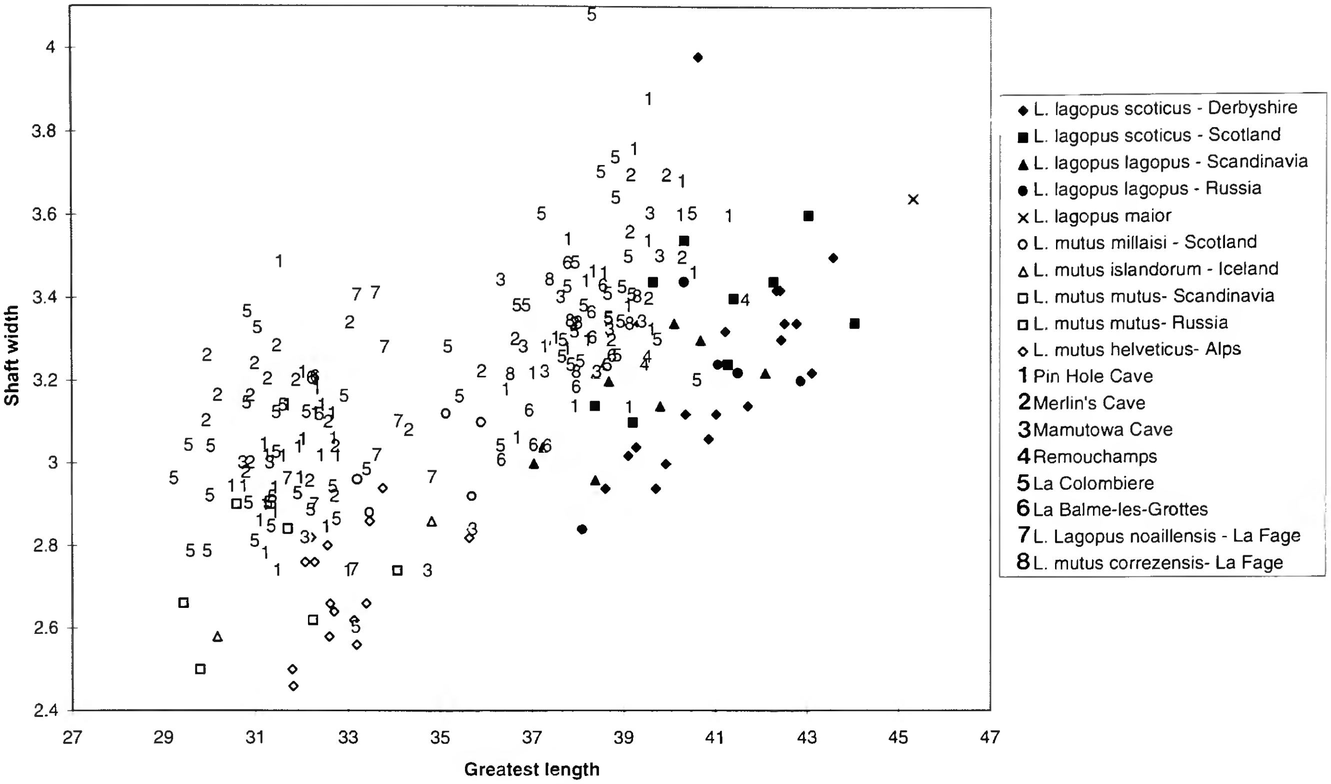

FIGURE 2.—Scattergram of tarsometatarsal-shaft width versus length in *Lagopus lagopus* and *Lagopus mutus*. Includes both modern and fossil populations. Numbered symbols indicate fossil localities detailed in Table 2.

(r)=0.951). Due to the positive correlation between the shaft widths and lengths, a regression also was performed for the tarsometatarsal lengths against bird weights. In this instance (see Figure 4), a positive correlation also is present (r=0.914). It may be significant that although high, the r value is lower than that produced for the tarsometatarsal-shaft width. This is not completely unexpected because similar trends were observed by Scott (1985) for bovids.

Both tarsometatarsal width and length are positively correlated with body weight, which makes the interpretation of the more robust Pleistocene tarsometatarsi as representing larger birds less certain. Therefore, to test further the hypothesis that the Pleistocene birds were larger, various skeletal elements (coracoids, ulnae, carpometacarpi) were considered from a similar perspective. These additional elements were not found to differ from the modern samples. Only when the humerus was subjected to metrical analysis did a difference become apparent. Humeri from La Colombière and Pin Hole Cave were used for this purpose. A plot of humeral length versus humeral-shaft width merely showed that the Pleistocene birds conformed in these dimensions with the modern birds of the two species. When greatest length was plotted against proximal width, however, the fossil humeri proved to have wider proximal extremities than their modern counterparts (Figure 5). It was found that despite the great overlap between the two species of *Lagopus* today, the fossils plot as distinct clusters indicating the presence of *L. lagopus* and *L. mutus* for the larger and smaller humeri, respectively. The wider proximal extremities of the fossils are likely to be due to a need for larger areas of muscle attachment because this measurement takes in the degree of development of both the crista pectoralis and the crista bicipitalis. This in turn implies that there may have been a greater development of the pectoral and bicipital muscles that are needed for flight, supporting the hypothesis of their greater body weight.

Discussion

The hypothesis that both *Lagopus lagopus* and *L. mutus* were birds of greater body weight during the Pleistocene is supported when compared with all modern populations and subspecies examined, except perhaps for *L. lagopus major*. Unfortunately, the exact timing of this change in mean body weight cannot be ascertained due to the lack of Holocene fossils available. If body size declined at the Pleistocene/Holocene boundary, a number of possible causes may be suggested, such as climatic change, vegetational changes, or interspecific competition.

Interspecific competition in the form of character displacement can be invoked as an explanation of size variation within

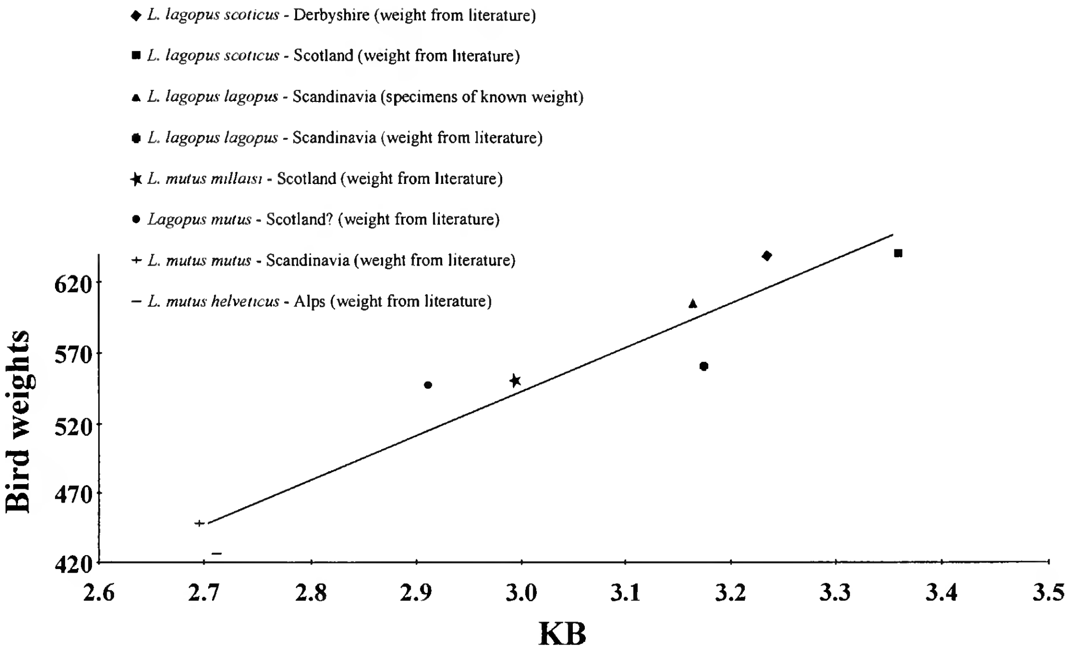

FIGURE 3.—Linear regression of mean weights of *Lagopus* versus mean shaft width (KB) of tarsometatarsi. The data plotted are based on mean weights of subspecies, taken from Cramp (1980), against mean tarsometatarsal-shaft widths and lengths of the corresponding subspecies measured in the present study. Mean weights were taken from the literature in all but one instance because in most cases skeletons in collections had no such data recorded for individual birds. The one exception was a sample of *Lagopus lagopus* from Scandinavia, where weights were recorded.

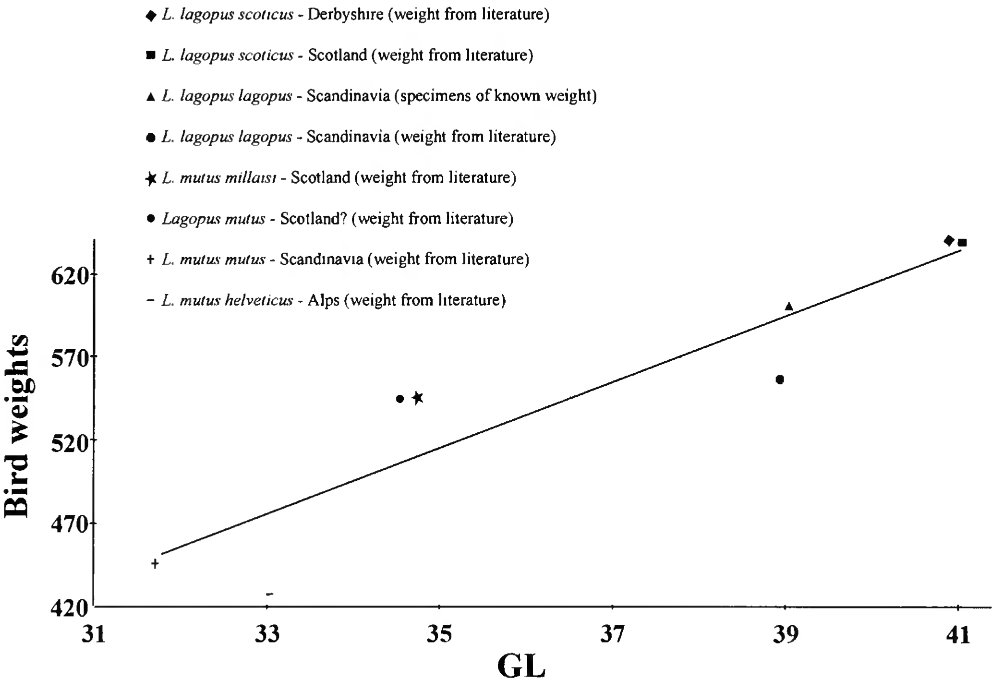

FIGURE 4.—Linear regression of mean weights of *Lagopus* versus their tarsometatarsal length. See legend to Figure 3 for source of data.

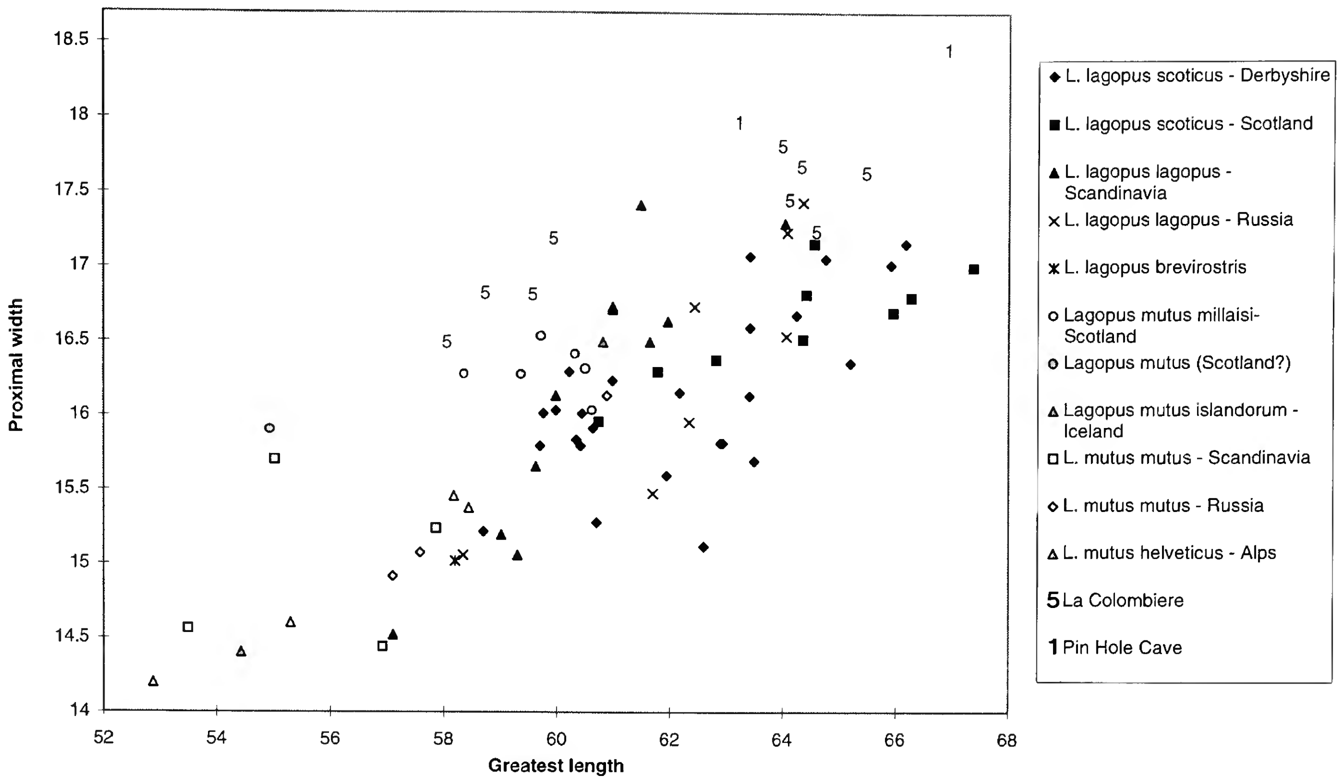

FIGURE 5.—Scattergram of humerus length of *Lagopus lagopus* and *Lagopus mutus* versus proximal width.

certain species. Studies such as that on the pygmy shrew *Sorex minutus* Linnaeus in northern Europe have shown that where two ecologically similar taxa occur in sympatry their sizes will be more divergent than when in allopatry (Malmquist, 1985). This does not appear to affect *Lagopus* today, and it could not affect the change in size seen through time because these changes are independent of sympatry or allopatry. *Lagopus lagopus* and *L. mutus* are presumably not ecologically similar enough for character displacement to take place.

The most often-quoted hypothesis to account for change in body size during the Quaternary is that of climate and, in particular, temperature, which is the mechanism often invoked to account for Bergmann's Rule. Many Pleistocene mammals from glacial episodes were larger than today, and certain authors have suggested that thermoregulation is the causal mechanism (Davis, 1981).

Other paleontologists and biologists, however, have agreed that this mechanism has been applied where it may not be appropriate, and that the subject is a much more complex one (Lister, 1992). A counterargument proposed by Guthrie (1984, 1990) and Geist (1986) is that it is not the climate that directly affects an animal's size but the consequences of the length and quality of the plant growing season, which in turn are affected by climate. The vegetational environment, called steppe-tundra or mammoth-steppe, has been described as very productive on the basis of the large herbivores it supported (Guthrie, 1990). The vegetation was a mosaic of high diversity, although predominated by grassland. It should be noted, however, that some palynologists have disagreed with the concept of the mammoth-steppe. They believe the vegetation was poor, a polar desert, based on the apparently low pollen influx at the time. The idea that the vegetational environment was a rich steppe-tundra has recently been expanded by Lister and Sher (1995), who have suggested that the steppe-tundra vegetation relied on a climatic regime that has vanished. They pointed out that detailed climatic records, such as studies of the Greenland ice cores, have shown that the Holocene is distinct from the late Pleistocene in having unusually stable conditions. Pleistocene climatic instability may have allowed the mosaic vegetation of the steppe-tundra to persist. Once this climatic regime ceased to exist, the megafauna, which relied so heavily on the vegetation type the climate supported, changed along with it. Some animals became extinct, like the giant deer *Megaloceros giganteus* (Blumenbach) and the woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach), or locally extinct, like the lion *Panthera leo* Linnaeus and spotted hyena *Crocuta crocuta* Erxleben (Stuart, 1991). Others underwent a reduction in body size, such as the fox *Vulpes vulpes* Linnaeus and wild boar *Sus scrofa* Linnaeus (Davis, 1981). It is, therefore, an attractive hypothesis that certain birds, such as the two species of *Lagopus,* which abounded in the steppe-tundra environment, also underwent changes upon its demise, such as reduced geographic ranges and body size. Interestingly, the largest subspecies of the genus, *L. l. major,* lives today on the steppes of Kazakhstan.

In support of this idea is the fact that all the fossil populations examined, except that from Rebielice Krolewskie (the late Pliocene site), come from deposits considered to belong to cold phases of the Pleistocene. The oldest members of the genus *Lagopus* examined after those from Rebielice come from a cold horizon above the interglacial at Westbury-sub-Mendip in England, which is early middle Pleistocene (oxygen isotope stage 12). Unfortunately, the fossils are few in number and are fragmentary, which makes it difficult to assess to which species they belong. They do, however, possess relatively robust tarsometatarsi, so it may be that *Lagopus* was already adapted to the steppe-tundra and was larger in relation to today's birds. The next youngest assemblage examined in this survey is that from La Fage, which is late middle Pleistocene. Both species are definitely present, although it may be significant that they appear to be less divergent from each other in their tarsometatarsal lengths than are modern birds (Figure 2). This may be support for Mourer-Chauviré's (1993) suggestion that the species had diverged not long before.

The greater areas of the crista pectoralis and crista bicipitalis may indicate that both *L. lagopus* and *L. mutus* were larger in the Pleistocene. If there were a primary selective force for large body size, so that birds were heavier, they would require greater muscle bulk to fly, which in turn adds further to body weight. Alternatively, the birds may have become larger because of selection for better-developed flight muscles under a different climatic regime when the birds may have been less sedentary. This hypothesis would be bolstered by the findings of Bocheński (1974, 1985) and Bocheński and Tomek (1994), who demonstrated that the distal-wing elements of *Lagopus lagopus* and *L. mutus* during the Pleistocene of Poland and Austria were relatively longer than in present-day birds, and that their legs were relatively shorter. This conclusion, however, was not confirmed by the samples analyzed in the present study.

Bocheński (1974) claimed that there was a clear, positive correlation between temperature and tarsometatarsus length, although he pointed out that local vegetation type also was influential. The nature of the variability seen in tarsometatarsal length over both time and space implies that, unlike the shaft widths, local factors may have had an influence. This seems more likely than the variation being a reflection of the other thermoregulatory biogeographic rule (Allen's Rule), which would produce more uniform clines across the birds' former geographic ranges. Therefore, it may be that influences such as the local terrain are more important than the influence of temperature because locomotion is generally regarded as important in determining leg length in mammals (Scott, 1985). Due to the small magnitude of the differences involved and the small size of the birds in relation to the ground relief, however, this conjecture is difficult to test.

Conclusion

Lagopus lagopus and *L. mutus* differ allometrically between the Pleistocene and the present, a consistent finding even when fossils from widely distributed areas and times are compared with greatly dispersed modern samples from across Europe. This difference is most readily identified in the tarsometatarsal-shaft width and implies a change that was due to a general or widespread effect, not a local adaptation similar to that proposed for the Holocene evolution of the red grouse (*L. l. scoticus*) in the British Isles (Voous, 1960; Tyrberg 1991). The changes in tarsometatarsal length appear to be reactions to variations in local conditions that remain unknown. The uniformity of change in tarsometatarsal width across Europe, however, implies regional rather than local effects. Global events that occurred at the Pleistocene/Holocene boundary seem to be a likely explanation; however, two problems arise. First, untangling cause and effect between climatic and vegetational factors, which are closely linked, and second, the possibility that a change occurred in the birds' vagility.

It is perhaps easier to conceive that the two species of *Lagopus* changed size due to climate change and its direct effect on vegetation rather than to changes in the bird's degree of sedentariness. The birds appear to have reacted in much the same way as did many mammals that survived the Holocene/Pleistocene boundary by becoming smaller. It is suggested herein that the change in seasonal length and vegetation type was the primary reason for this, and not temperature. The birds in the northern areas of Europe today, and particularly in mountainous regions further south in the case of *L. mutus,* probably exist at much the same temperatures as they did in the Pleistocene in southern Europe. This would eliminate temperature as the primary causal factor of size decrease in the genus over this period, because birds of comparable size to those of the Pleistocene are not present in northern Europe today. Dietary shifts caused by vegetational changes are proposed herein as the most significant factor leading to size reduction. It therefore seems reasonable to suggest that the birds in the genus *Lagopus* in the Palearctic today are relictual populations that originally evolved and diversified into *Lagopus lagopus* and *L. mutus* on the steppe-tundras of the late–middle and late Pleistocene.

Bocheński (1974) and Mourer-Chauviré (1975a) had previously demonstrated allometric trends in European Pleistocene *Lagopus,* but the suggestion of a major reduction in size at the Pleistocene/Holocene boundary over most of Europe is new, as is the suggestion that it was due to the vegetational changes described above.

This work has implications for the taxonomic use of allometric differences in skeletal elements. Often such differences are given greater significance than are mere size differences. The example described above clearly shows that a change in size may not be conferred to all elements equally. Therefore, dimensions thought to be significant should be considered in terms of their relationship to body size before taxonomic decisions are taken. Furthermore, allometric changes have been observed by neontologists to occur over short periods of time, for example, the increased bill size observed in *Geospiza fortis* Gould on the island of Daphne Major, Galapagos, as a result of strong selection through differential survival of large-seeded plants in response to a drought (Grant, 1986). These allometric changes have no taxonomic significance but simply represent organisms adapting to the complex pattern of natural selective pressures acting on any given skeletal dimension. Thus, caution should be used when interpreting allometric differences seen in fossils because the differences seen between Pleistocene and Holocene *Lagopus* are of the type that have sometimes been considered to have taxonomic significance.

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A New Genus for the Incredible Teratorn (Aves: Teratornithidae)

Kenneth E. Campbell, Jr., Eric Scott,
and Kathleen B. Springer

ABSTRACT

A partial humerus of a giant flying bird from Blancan (upper Pliocene) deposits of California is determined to be a teratorn, although the humerus differs from those of other known genera of the family Teratornithidae in the position of the attachment of the M. latissimus dorsi and in the shape of the humeral shaft. The new specimen is referred to the Incredible Teratorn, *Teratornis incredibilis* Howard (1952), and a reexamination of all the specimens previously referred to this taxon reveals sufficient grounds to erect a new genus for this species. The size of the new partial humerus suggests that the bird had a wingspan of approximately 5 m, which is the same estimate previously given for the Incredible Teratorn.

Introduction

Teratorns are members of an extinct family of giant flying birds, the Teratornithidae (Miller, 1925), which currently is placed within the order Ciconiiformes (Jollie, 1976–1977; Rea, 1983; Olson, 1985; Emslie, 1988). Three genera have been recognized in the family: *Teratornis* L. Miller (1909), *Cathartornis* L. Miller (1910), and *Argentavis* Campbell and Tonni (1980). One species has been assigned to each of the latter two genera, whereas two species have been assigned to *Teratornis*: *T. merriami* L. Miller (1910) and *T. incredibilis* Howard (1952). Teratorns were the largest flying birds known, with the largest, *Argentavis magnificens* Campbell and Tonni (1980), reaching a wingspan of 6–8 m and a weight of 72–79 kg (Campbell and Tonni, 1980; Campbell and Marcus, 1992). Our current understanding of teratorns has been summarized by Campbell and Tonni (1980, 1982, 1983) and Campbell (1995).

The discovery of a partial humerus of a teratorn of a size similar to that estimated for *Teratornis incredibilis* allows us to clarify the status of that species, to which five specimens of widely different ages (late Pliocene to late Pleistocene) have previously been referred. The holotype of the species, an os carpi ulnare (cuneiform) (Howard, 1952), is the most diagnostic specimen, whereas the four referred specimens are much less so. Although these specimens, namely, the proximal end of an ulna, the distal end of a radius, the fragmentary proximal end of a carpometacarpus, and the anterior portion of a beak, were not very diagnostic, they were identified as teratorns and were referred to *T. incredibilis* primarily on the basis of size (Howard, 1963, 1972; Emslie, 1995; Jefferson, 1995). A sixth specimen, the fragmentary distal end of a right carpometacarpus recently discovered in upper Pliocene deposits of central Mexico and described below, is assigned herein to this species. A seventh specimen, a vertebra, previously referred to *T. incredibilis* (Heaton, 1984) was later reassigned to *T. merriami* (Emslie and Heaton, 1987). This specimen was not seen by us.

In spite of being rather fragmentary, the new specimen clearly possesses characters that unite it with the teratorns. At the same time, other characters clearly distinguish it from humeri of the genus *Teratornis,* which suggests that it represents a genus distinct from *Teratornis.* We took the opportunity this specimen provided to reexamine all specimens referred to *T. incredibilis*, and we found grounds for placing all of them in a new genus.

Osteological terminology is from Baumel (1993) and Howard (1980).

ACKNOWLEDGMENTS.—Fossil mammals from Murrieta were identified by R.L. Reynolds, San Bernardino County Museum; additional identifications were provided by C.A. Repenning, United States Geological Survey. Paleontologic Resource Assessment Program (PRAP) mitigation was conducted in cooperation with H. Meyers of the Kulberg Group, Temecula. We thank R. Chandler, Georgia College and State University, and O. Carranza-Castañeda, Instituto de Geología, Universidad Na-

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Systematics

Order CICONIIFORMES

Family TERATORNITHIDAE

Aiolornis, new genus

TYPE SPECIES.—*Teratornis incredibilis* Howard, 1952; type by original description.

REFERRED SPECIES.—None.

ETYMOLOGY.—*Aiolos*, Greek, masculine, god of the winds; *ornis*, Greek, masculine, bird.

EMENDED DIAGNOSIS.—Placed in the family Teratornithidae and differing from genera of the Vulturidae by having the os carpi ulnare with the following characters (from Howard, 1952:51): (1) attachment for Lig. ulno-ulnocarpale long, diagonal, and ridge-like (short, almost papilla-like in the Vulturidae); and (2) external prominence and attachment for Lig. ulno-ulnocarpale in close proximity (broad space separating the two in the Vulturidae).

Differs from *Teratornis* by having the os carpi ulnare with (1) external prominence a long, prominent ridge forming one end of and extending from the facies articularis ulnaris to very near the attachment for Lig. ulno-ulnocarpale (short, rounded, not contacting facies articularis ulnaris in *Teratornis*); (2) attachment for Lig. ulno-ulnocarpale proportionately longer, more prominently protruding from body of bone; (3) facies articularis ulnaris narrowing slightly distad, more concave, with dorsal rim notably lower than ventral rim (narrows abruptly, less concave, with dorsal rim only slightly lower than ventral rim in *Teratornis*); (4) facies articularis metacarpalis a slightly elongated oval, with long axis nearly aligned with long axis of facies articularis ulnaris, with external end very near facies articularis ulnaris, and lying at greater angle to facies articularis ulnaris (markedly elongated oval with long axis at low angle to that of facies articularis ulnaris and external end at some distance from facies articularis ulnaris in *Teratornis*); and (5) with ventral surface of bone bordering and surrounding incisura metacarpalis nearly flat (markedly concave in *Teratornis*).

Aiolornis incredibilis (Howard, 1952), new combination

HOLOTYPE.—Complete right os carpi ulnare, LACM(CIT) 5067.

TYPE LOCALITY.—Section 7-F-310 of LACM(CIT) locality 251, Smith Creek Cave, Snake Range, 54.4 km north of Baker, White Pine County, Nevada.

AGE.—Rancholabrean NALMA (North American Land Mammal Age).

DIAGNOSIS.—As for genus.

REFERRED MATERIAL.—*Left humerus:* Proximal end and portion of shaft, missing caput and much of crista deltopectoralis (Figure 1); SBCM A2239-2829, Section of Earth Sciences.

The specimen was collected by Quintin Lake (PRAP), April 1993, from locality SBCM 05.006.399, which is located approximately 1 km northeast of Murrieta, Riverside County, California, at an approximate elevation of 368 m. The locality lies within the unsurveyed Temecula Land Grant (Figure 2), within the SW¼, NE¼, SW¼ section 9, T. 7S, R. 3W, San Bernardino Base and Meridian. The specimen was exposed in situ in an erosional gully approximately 0.15 m below grade.

The partial humerus came from sediments of an unnamed sandstone and conglomerate formation that unconformably underlies the middle Pleistocene Pauba Formation and may unconformably overlie the lower Pliocene Temecula Arkose in the Elsinore Fault Zone (Kennedy, 1977). Two faunal components have been recognized from the unnamed sandstone formation, one dating to the late Blancan NALMA (late Pliocene, as interpreted by Lundelius et al., 1987) and the other to the Irvingtonian NALMA (early Pleistocene) (Scott and Cox, 1993). The partial humerus is derived from sediments that are late Blancan in age (pre-Olduvai subchron, 2.6–1.9 Ma), based on sites producing Blancan faunas in the area immediately adjacent to SBCM 05.006.399. These localities (SBCM 05.006.156, 05.006.157, 05.006.158, 05.006.159, 05.006.397) are all located within 15 m of SBCM 05.006.399 and have yielded *Hypolagus* sp., *Prodipodomys* sp., *Mimomys* (*Ophiomys*) *parvus* R. Wilson, and *Sigmodon minor* Gidley, but they lack any Pleistocene or later indicator taxa, such as *Microtus* sp. or *Mammuthus* sp. (Scott and Cox, 1993).

The partial humerus is placed in the family Teratornithidae based on the following characters: (1) crista bicipitalis elongated and prominently bulbous for entire length; (2) planus intertuberculare smooth, broad, and symmetrically and deeply convex in transverse section from caput to middle of crista deltopectoralis; (3) crista deltopectoralis low, very stout, curving ventrad on facies anterioris of corpus humeri just distal to end of crista bicipitalis, and tapering off gradually as it crosses to near midline of corpus humeri; and (4) distal insertion for M. pectoralis long, broad, and near midline of facies anterioris of corpus humeri.

Other avian taxa, such as some of the orders Procellariiformes, Pelecaniformes, and Ciconiiformes, resemble teratorns somewhat in having a bulbous crista bicipitalis. In these taxa, however, the bulbous portion is more limited, being present only at the distal end of the crista bicipitalis. In *Teratornis* the bulbous portion occupies the entire length of the crista bicipitalis and is more pronounced; it is missing from the only known humerus of *Argentavis*. Although most of the bulbous

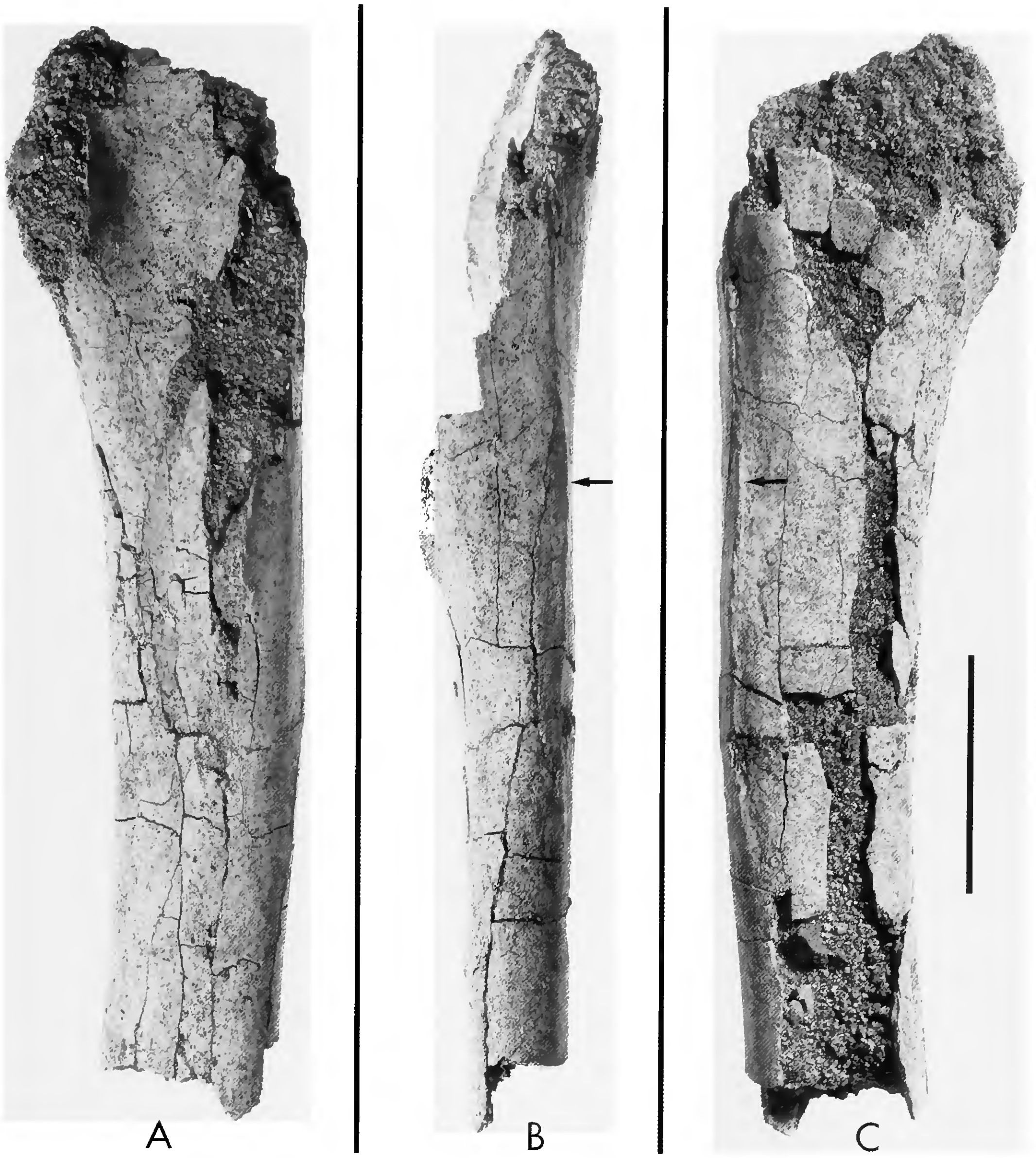

FIGURE 1.—New partial humerus referred to *Aiolornis incredibilis:* A, anterior, B, dorsal, and C, posterior views. The position of the line of insertion of M. latissimus dorsi (arrows) is unique among teratorns. Scale bar=5 cm.

portion in the partial humerus under discussion is missing, enough of the base is present to document its presence and its size. Similarly, some other avian taxa have a proportionately broad and convex planus intertuberculare, but we know of none that approaches the symmetrical, smooth, deep convexity seen in teratorns. We know of no other group of birds in which the crista deltopectoralis curves ventrad onto the facies anterioris of the corpus humeri. Among the New World vultures, condors share the trait of having a large distal insertion for M. pectoralis, but it is much smaller, more oval or tear-drop shaped, and positioned closer to the facies dorsalis of the humerus.

The partial humerus differs from *Argentavis* and *Teratornis,* the only two of the three genera of the family for which the humerus is known, by the following: (1) facies dorsalis fairly flat for length of attachment of M. latissimus dorsi, becoming slightly convex near its distal end (sloping anteriad proximally, changing to convex distally in *Argentavis* and *Teratornis*); (2) facies posterioris and facies dorsalis meet at near right angle, with line of insertion of M. latissimus dorsi following a well-defined "corner" of margo anteriodorsalis (line of insertion at angle to margo dorsalis, crossing facies posterioris from distal to proximal in *Argentavis* and *Teratornis*); (3) corpus humeri in

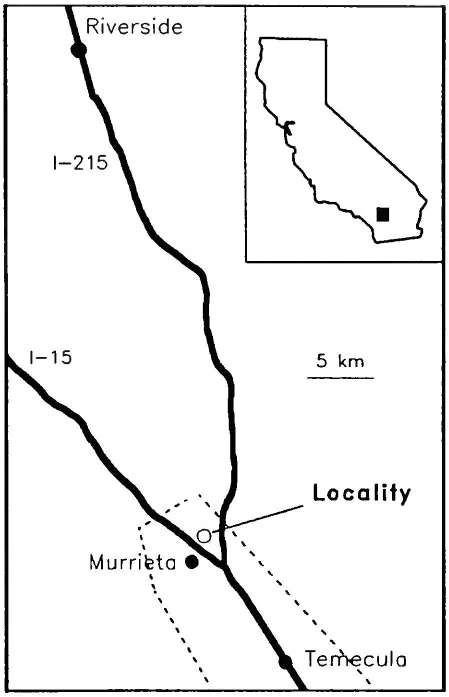

FIGURE 2.—Map showing location of locality SBCM 05.006.399 for the new partial humerus referred to *Aiolornis incredibilis.* Dashed line indicates unsurveyed boundary of Temecula Land Grant.

transverse section through nutrient foramen on margo ventralis at midshaft a flattened oval not quite twice as wide as deep (more egg-shaped, with margo ventralis slightly narrower than margo dorsalis in *Argentavis;* nearly round in *Teratornis*) (Figure 3); (4) corpus humeri less curved proximally in both horizontal and vertical planes; and (5) attachment of M. pectoralis with distal portion a broad, flattened area (area damaged but appears similar in *Argentavis;* narrow, steeply sloping on distal end of crista deltopectoralis in *Teratornis*). These characters hold in comparison with all humeri of *Teratornis* from Rancho La Brea, California (*n*=>50).

Although the position of the M. latissimus dorsi is so markedly different from that seen in known teratorns, even to the point of leading one to question whether or not the humerus might even be from a new, unknown family, in the absence of additional characters the presence of the four teratorn autapomorphies listed above are sufficient grounds for placing the specimen with the teratorns.

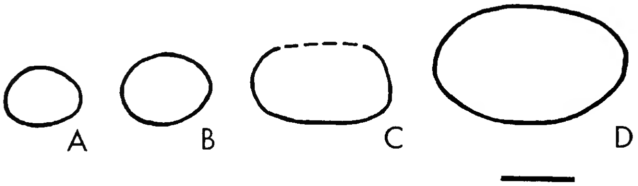

FIGURE 3.—Comparison of the size and shape of the cross section of the humeral shaft in the plane of the nutrient foramen in a vulturid (A) and teratorns (B–D): A, California Condor, *Gymnogyps californianus;* B, Merriam's Teratorn, *Teratornis merriami;* C, *Aiolornis incredibilis;* D, *Argentavis magnificens.* Scale bar=2 cm.

Measurements of this specimen are limited to shaft width and depth in the plane of the midshaft nutrient foramen on the facies ventralis: 37.8 mm and 22.0±1 mm, respectively. Comparable measurements for the single specimen of *Argentavis* are 52.2 mm and 32.8 mm, respectively, and measurements for *Teratornis merriami* ($n=16$) are 23.2–28.9 mm ($\bar{x}=24.9$ mm) and 18.3–23.0 mm ($\bar{x}=19.9$ mm), respectively.

Right radius: Distal end, Anza-Borrego Desert State Park Paleontological Collection, ABDSP(LACM) 1318/V3803, from Irvingtonian (middle Pleistocene, or 1.5–1.0 Ma (Savage and Curtis, 1970:223)) deposits at the 3600-ft level of the Vallecito Creek area, Anza-Borrego Desert State Park, referred to *Teratornis incredibilis* by Howard (1963). Emended description, in comparison with *T. merriami,* as follows: distal contour straighter, less rounded at corners; ligamental prominence extending more proximad, significantly elevated above and more markedly set off from shaft and more elevated than central ligamental attachment in anterior view (elevational differences slightly magnified by loss of surface bone on central ligamental attachment; both areas of attachment at about same level in *Teratornis*) (bone slightly crushed along proximal edge of prominence, but this cannot account for sharp drop to shaft); shaft immediately above distal end flat in anterior view; internal edge of shaft proximal to internal end of scapholunar facet broad, channeled, or slightly convex transversely, which gives way to knife-like ridge proximad, with interno-anterior edge formed by long, prominent attachment of Lig. radioulnare interosseum +Lig. ulno-radiocarpale (edge very narrow in *Teratornis,* sloping steeply mediad with attachment of Lig. radioulnare interosseum+Lig. ulno-radiocarpale a broad, flat area halfway between edge and midline of bone that is slightly elevated proximally); depression occurs between attachment of Lig. radioulnare interosseum + Lig. ulno-radiocarpale and midline of bone (accentuated, but not caused by crushing) (absent in *Teratornis*); central ligamental prominence more elevated and extending closer to distal end before dropping off than in *Teratornis;* external edge of shaft proximal to ligamental prominence with linear convexity; and shaft significantly more curved in anterior view and slightly more curved in external view (some of the curvature, but not much, may be a result of distortion in preservation).

Premaxillary: Anza-Borrego Desert State Park Paleontological Collection, ABDSP(LACM) 6747/V26697, from Blancan (late Pliocene, or 3.5–3.2 Ma (Savage and Curtis, 1970:223; Evernden et al., 1964:164)) deposits at the 7000–8000-ft level of the Fish Creek beds in the Anza-Borrego Desert State Park, referred to *Teratornis incredibilis* by Howard (1972).

Emended description as follows: markedly compressed, deep beak; palatal surface fairly flat (more concave than in *Terator-*

nis but not highly vaulted as in vulturids), with prominent central ridge, or septum (which is only slightly developed anteriorly in *Teratornis*), but lacking distinct median groove posterior to ridge (as present in *Teratornis*); crista tomialis wider in transverse section and more deeply grooved and more symmetrical anteriorly than in *Teratornis* but forming comparable enclosure of deep, narrow channel in anteriormost portion of beak, in region of sharp curvature.

In teratorns, the crista tomialis forms a sharp ridge external to the region of the anterior narial border, but farther anterior, about halfway to tip of beak, this ridge declines in prominence, and the median portion of the grooved crista tomialis forms a sharper ridge. The point of this transition represents the posteriormost portion of this specimen of beak that is preserved, which suggests that the specimen came from a bird with a proportionately much deeper beak than seen in *Teratornis*.

Left ulna: Proximal end and partial proximal shaft (Figure 4), Anza-Borrego Desert State Park Paleontological Collection, ABDSP (IVCM) 519/5660, from Vallecito member of the Palm Spring Formation (Woodward, 1963), June Wash area of the Vallecito-Fish Creek Basin. Specimen from Vallecito Creek local fauna (Jefferson, 1995), dating to about 1.8–0.9 Ma.

This ulna is severely crushed, but enough of the original structure remains to determine that it differs from that of *Teratornis* by having (1) olecranon long and very broad; (2) cotyla ventralis lying at a much steeper angle to the long axis of the shaft; and (3) cotyla dorsalis wider and relatively shallow. Although the specimen is quite crushed, most of the bone of the proximal end is present so it is possible to approximate closely its original shape. The cotyla ventralis may be slightly rotated as a result of crushing, but the original shape, in ventral view, is clearly preserved. The amount of bone present suggests that the proximal end was less deep anterioposteriorly immediately distal to the cotyla ventralis, and the tuberculum Lig. collat. ventralis was much less bulbous, than in *Teratornis*. In addition, it appears that the olecranon was much more compressed anteroposteriorly, although some post-mortem crushing has taken place.

A total of about 26 cm of the ulna is preserved, in four pieces, although only two of the four pieces actually fit together. Two of the shaft fragments have feather papillae, but the smallest does not. The small diameter of the smallest fragment, which has no recognizable features, suggests that it may not even be part of the ulna, an idea supported by the presence of a fifth fragment that is unidentifiable to element, but which is definitely not part of an ulna.

Right carpometacarpus: Fragmentary distal end, Universidad Nacional Autonoma de Mexico, Instituto de Geología, Museo de Paleontología, IGCU-6133, from locality GTO.31, Blancan, Rancho Viejo area, State of Gaunajuato, Mexico, about 240 km NNW of Mexico, Distrito Federal.

This specimen is too fragmentary to provide much information, but it is clearly a teratorn. It differs from carpometacarpi of *Teratornis* by having (1) the facies articularis digitalis major with the medial rise more elongated and elevated and more distinctly set off from the anterior portion; and (2) the os metacarpale minoris with the distal area of fusion with the os metacarpale majus proportionately shorter than in *Teratornis* and the distal end more massive, projecting distad more distinctly and at a greater angle from the os metacarpale majus. The single known partial carpometacarpus of *Argentavis* is too poorly preserved for comparison. For further details on the fauna associ-

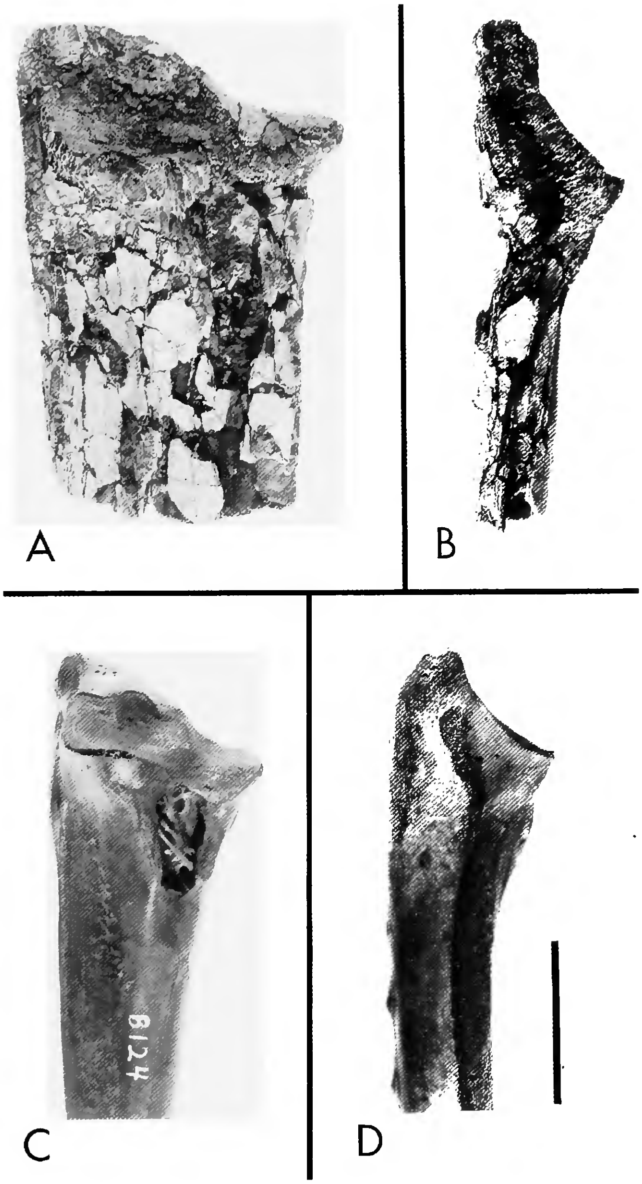

FIGURE 4.—A,B, proximal end of the ulna referred to *Aiolornis incredibilis* (ABDSP(IVCM) 519/5660): A, anterior view; B, ventral view. C,D, ulna of *Teratornis merriami* (George C. Page Museum, B124): C, anterior view; D, ventral view. Note the differences between the olecranons and the orientation of the cotylae ventralis. Scale bar=3 cm.

ated with this specimen, see Miller and Carranza-Castañeda (1984).

Right carpometacarpus: Fragmentary proximal end, including only trochlea carpalis and area immediately distal to it, Florida Museum of Natural History, UF 123874, Leisey Shell Pit 3, Hillsborough County, Florida, Bermont Formation, Irvingtonian (between 1.66 and 1.4 Ma (MacFadden, 1995)).

This specimen was originally described and figured by Emslie (1995:316–317), who referred it to *Teratornis* sp. cf. *T. incredibilis* on the basis of its similarity to *Teratornis merriami* and its size (~40% larger than *T. merriami*). We see no reason to doubt that this specimen is a teratorn, but little else can be said about it.

Discussion

Howard (1952) described *Teratornis incredibilis* on the basis of the complete os carpi ulnare (cuneiform) noted above, allocating the species to *Teratornis* on the basis of its general similarity to *T. merriami.* The much greater size of the specimen (43% larger than the same bone of *T. merriami*) and other characters clearly established its distinction as a separate species (Howard, 1952). Howard (1963, 1972) also referred to *Teratornis incredibilis* the distal end of a radius and the anterior portion of a beak discussed above on the basis of their general similarity to *T. merriami* and the fact that both of these specimens were about 40% larger than comparable bones of the latter species. Although Howard (1972:343) considered the possibility of generic separation of the larger species from *Teratornis,* she considered all three specimens she had assigned to *T. incredibilis* too undiagnostic or too poorly preserved to justify establishing a new genus.

After restudying the holotype and three specimens previously referred to *Teratornis incredibilis* we concluded that the differences seen between *T. incredibilis* and *T. merriami* are such that the erection of a new genus for the former was warranted. In reexamining the holotypical os carpi ulnare we found that the characters noted above for *Aiolornis* differ from those of *Teratornis* at a level comparable to the differences seen among the os carpi ulnare of the living genera of the family Vulturidae, which are easily identified to genus, and the differences hold for all specimens of the element from Rancho La Brea examined (*n*=24). The unique characters of the humerus, ulna, radius, and carpometacarpus assigned to *Aiolornis incredibilis,* however, suggest that that species may have had different flight adaptations from *Teratornis merriami.* Because the os carpi ulnare is a bone integral to the flight of any bird, we would have expected greater character differences to be reflected in the os carpi ulnare of *Aiolornis,* which would serve to separate it more readily from *Teratornis.* For this reason we would not be surprised to find in the future that the older (Blancan and Irvingtonian) specimens herein referred to *Aiolornis incredibilis* actually are referrable to another genus and species.

The other genus and species of teratorn, *Cathartornis gracilis,* is known only from tarsometatarsi, one complete and one distal end, from the late Pleistocene asphalt deposits at Rancho La Brea, California. Although the length of the holotypical tarsometatarsus of *C. gracilis* falls within the size range of tarsometatarsi of *Teratornis merriami,* it is much more slender and has several features that distinguish it from its more heavily built contemporary. Miller and Howard (1938:169) reevaluated the status of *Cathartornis* and concluded "that *Cathartornis* is markedly similar to *Teratornis merriami,* though it is undoubtedly a distinct species. We consider it also to be generically distinct." Some of the characters listed as separating the two genera are not particularly convincing, however, and with more specimens of teratorns available now than at the time of Miller and Howard's study, the case for maintaining *Cathartornis* as a separate genus is weak. Resolution of the status of *Cathartornis* is deferred pending completion of the studies of the teratorns of Rancho La Brea by KEC. Given the marked similarity of *Cathartornis* to *Teratornis,* we considered assignment to *Cathartornis* of the specimens now referred to *Aiolornis* inappropriate.

The size of the Incredible Teratorn, *Aiolornis incredibilis,* remains its most remarkable known feature, even though we know there was at least one larger species of teratorn. Howard (1952) estimated the size of *A. incredibilis* to be 43% larger than *Teratornis merriami* based on the holotypical os carpi ulnare, which would give a wingspan of about 5 m. She estimated (Howard, 1972:343) the radius she referred to *A. incredibilis* to be "approximately 40% broader than a large radius of *T. merriami.*" The beak she referred to *A. incredibilis* was estimated to be "43% larger than the largest of four measurable specimens of *T. merriami,*" based on what Howard (1972:343) considered the best available measurement. The ulna that Jefferson (1995:94) referred to *A. incredibilis* was said to be "about 57% larger than the average (39.6) of five measured specimens of *Teratornis merriami* from Rancho La Brea." Unfortunately, it is not possible to draw a direct size comparison between the partial humerus of *A. incredibilis* and humeri of *T. merriami.* The only accurate measurements that can be taken from the holotype of *A. incredibilis* are the width and depth near midshaft, and the width to depth proportions of the shaft are so different among the known genera of teratorns (Figure 3) as to make such a size comparison meaningless. Neither is it possible to determine accurately the size of the bird from which came the carpometacarpi referred to *A. incredibilis* because of the poor state of preservation of those specimens. A reasonable "eyeball" estimate, however, suggests that both of these specimens came from a bird with a wingspan intermediate between that of *T. merriami* (3.5–4 m) and *Argentavis magnificens* (6–8 m). This gives a wingspan estimate of 5.0–5.5 m for *A. incredibilis,* which conforms with that estimated from the other specimens referred to this species.

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The Fossil Record of Condors (Ciconiiformes: Vulturidae) in Argentina

Claudia P. Tambussi and Jorge I. Noriega

ABSTRACT

At present, the fossil record indicates that condors probably originated in North America, and their fossil history in South America has been traced to the early?–middle Pliocene (Montehermosan?–Chapadmalalan Age) of the Pampean region (Argentina). The great diversity of condors that occurred in the late Cenozoic of this region comprises three genera and at least four species, namely, *Dryornis pampeanus* Moreno and Mercerat, *Vultur gryphus* Linnaeus, *Geronogyps reliquus* Campbell, and an indeterminate vulturid probably belonging to a new genus and species. The presence of *Geronogyps reliquus* (up to now restricted to the Pleistocene of Peru) in the Pleistocene sediments of the Pampean region extends considerably the geographic range of the species.

Introduction

New World vultures (Vulturidae=Cathartidae auct.) are widely distributed in the Americas, ranging from Canada to Tierra del Fuego in Argentina, and are most diverse in tropical regions of South America. All species are adapted to feeding on carrion, but they present different and exceptional specializations in their habits of scavenging (Hertel, 1992, 1994).

New World vultures are closely related in habits and appearance to the Old World vultures (Accipitridae: Aegypiinae and Gypaetinae) due to convergent evolution. Vulturids show close phylogenetic relationships with the ciconiid storks (Ligon, 1967; Rea, 1983; Olson, 1985; Emslie, 1988a; Sibley and Ahlquist, 1990), whereas the Old World Vultures show close affinities to hawks and eagles (Brown and Amadon, 1968). Some analyses, however, do not agree with moving the Vulturidae from the Falconiformes to the Ciconiiformes (Griffiths, 1994, and the literature cited therein). We do not discuss this controversy but instead adopt the view that condors are Ciconiiformes.

Vulturids are represented by seven living species (Sibley and Monroe, 1990; nomenclature for species' binomials of modern birds mentioned herein follows Sibley and Monroe, 1990). The two largest species, the condors, are characterized by having long, broad wings and short tails and by certain osteological features of the cranium (Emslie, 1988a; Hertel, 1992) and include the California Condor, *Gymnogyps californianus,* and the Andean Condor, *Vultur gryphus,* from North America and South America, respectively.

The earliest fossil vulture with affinities to condors is *Hadrogyps aigialeus* Emslie from the middle Miocene of California. Two other pre-Pleistocene unequivocal condors were described from the late Miocene of Florida (*Pliogyps charon* Becker) and the middle Pliocene of Kansas (*Pliogyps fisheri* Tordoff). Based on the geographic distribution of recent and fossil species, Emslie (1988a, 1988b) suggested that condors probably originated in North America and may have participated in the Great American Biotic Interchange in the early–middle Pliocene. In accordance with the latter hypothesis, condors in Argentina are restricted to the Pliocene to late Pleistocene of the Pampean region, far from the modern area of distribution of the recent species, with the earliest fossil history being the early?–middle Pliocene (Montehermosan?–Chapamalalan Age) of Argentina, with the presence of *Dryornis pampeanus* Moreno and Mercerat.

The purpose of the present study is to summarize the diversity of the previously described condors from Argentina and to describe new specimens.

MATERIALS AND METHODS

Specimens of fossil and extant vultures were examined at the Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.; Department of Ornithology, American

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Museum of Natural History, New York, New York, U.S; Departamento Científico Paleontología Vertebrados and Departamento Científico Zoología Vertebrados of Museo de La Plata (MLP), La Plata, Argentina; Museo Municipal de Ciencias Naturales de Monte Hermoso (MMH), Monte Hermoso, Argentina; Casa de Cultura de Médanos (CCM), Municipalidad de Villarino, Argentina; Sección Ornitología and Sección Paleontología Vertebrados, Museo Bernardino Rivadavia, Buenos Aires, Argentina, and Royal Ontario Museum (ROM), Toronto, Canada.

The comparative material included skeletons of the following living vultures (number of specimens in parentheses): *Vultur gryphus* (8), *Gymnogyps californianus* (5), *Sarcoramphus papa* (1), *Coragyps atratus* (3), *Cathartes aura* (3), *Cathartes burrovianus* (1) and the ciconiids *Ciconia maguari* (2), *Mycteria americana* (2), and *Jabiru mycteria* (1). Fossil specimens examined are discussed below; they included *Geronogyps reliquus* Campbell, *Gymnogyps howardae* Campbell, and *Dryornis pampeanus* Moreno and Mercerat. Comparisons were made with original material except *Gymnogyps kofordi* Emslie, for which illustrations and published descriptions were used. All measurements were taken with vernier calipers to the nearest 0.1 mm and are given in millimeters. Anatomical terminology follows mainly Baumel and Witmer (1993) but also Fisher (1946).

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Systematic Paleontology

Order CICONIIFORMES

Family VULTURIDAE

The fossil record of condors in the Pliocene–Pleistocene of the Pampean region (Figures 1, 2) comprises five taxa, which are discussed below.

Dryornis pampeanus Moreno and Mercerat, 1891

LECTOTYPE.—Distal end of right humerus, MLP 20-169 (Figure 3).

LOCALITY.—Farola de Monte Hermoso (39°S, 61°50′W), Coronel Rosales County, Buenos Aires Province.

HORIZON AND AGE.—Early?–middle Pliocene (Montehermosan?–Chapadmalalan Age; see Cione and Tonni, 1995, for detailed stratigraphic analysis).

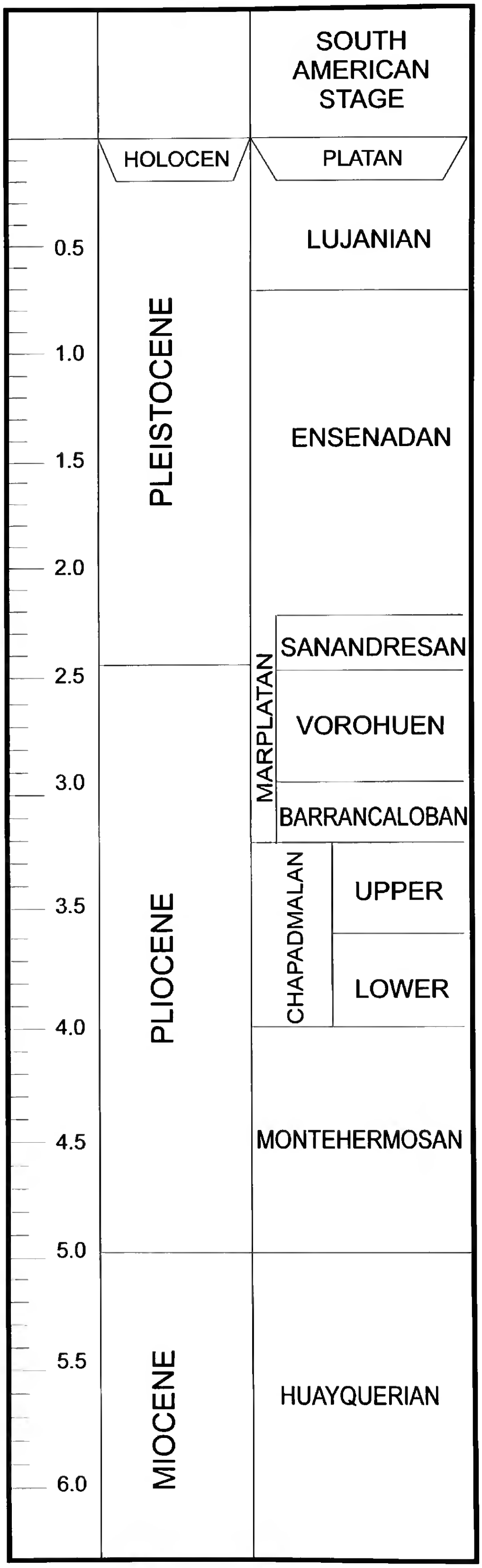

FIGURE 1.—Chronostratigraphic units of the upper Cenozoic of South America.

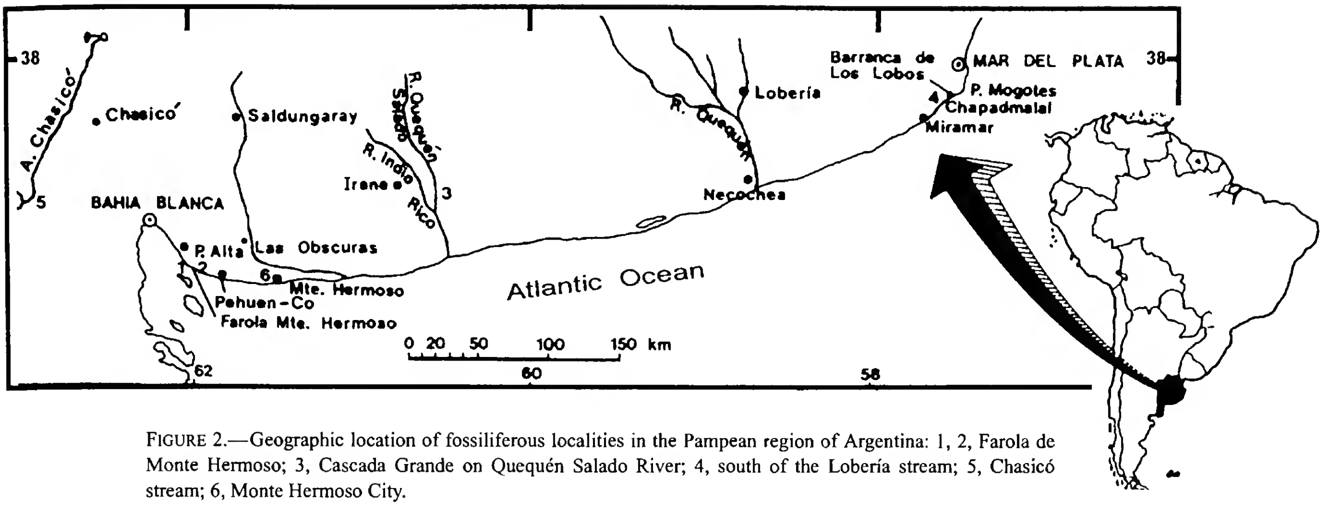

FIGURE 2.—Geographic location of fossiliferous localities in the Pampean region of Argentina: 1, 2, Farola de Monte Hermoso; 3, Cascada Grande on Quequén Salado River; 4, south of the Lobería stream; 5, Chasicó stream; 6, Monte Hermoso City.

REMARKS.—Moreno and Mercerat (1891) originally described *Dryornis pampeanus* based on a distal end of a left humerus (lectotype, MLP 20-169) and an abraded distal end of a right femur (MLP 20-170). As was pointed out previously by Patterson and Kraglievich (1960) and by Brodkorb (1967), the assignment of the femur (MLP 20-170) to a condor was erroneous. Our reexamination of this specimen agrees with prior revisions in attributing it to a phorusrhacoid bird.

Dryornis pampeanus is recognized by having a humerus with the following characters: (1) size similar to that of *Vultur gryphus*, but distal shaft width just proximal to the epicondylus dorsalis greater; (2) condylus dorsalis longer and straighter than in *Vultur, Gymnogyps*, or *Geronogyps;* (3) condylus ventralis narrower than in *Vultur* or *Gymnogyps*, similar to *Geronogyps;* slightly rotated anteriad, giving moderately flexed distal end as in *Geronogyps, Gymnogyps*, and *Vultur*, with marked flexion of distal end of humerus; (4) epicondylus dorsalis rounded as in *Gymnogyps* and less protrudent proximally than in *Vultur, Gymnogyps*, or *Geronogyps;* (5) insertions of M. brachialis anticus, M. pronator brevis (=M. p. superficialis), and M. flexor carpi ulnaris deeper than in *Gymnogyps* or *Geronogyps;* (6) fossa M. brachialis less extended laterally than in all species compared; (7) sulcus scapulotricipitalis less marked than in *Geronogyps* or *Vultur;* (8) fossa olecrani relatively more excavated and proximal, and less extended laterally, than in *Vultur, Gymnogyps*, or *Geronogyps;* and (9) intercondylar furrow nearly straight.

Historically there has been some agreement that *Dryornis pampeanus* is a valid genus within the Vulturidae (see Tonni, 1980; Emslie, 1988a). Our direct comparison of the material with other known fossil and living vultures supports the anatomical distinctness of *Dryornis pampeanus* from the other members of the family. Thus, based on the set of characters listed above, we consider *Dryornis pampeanus* to be a valid genus and species and to be one of the earliest fossil condors in South America.

Vultur gryphus Linnaeus, 1758

REFERRED MATERIAL.—Proximal end of humerus, MLP 48-XII-16-225 (Figure 4); Farola de Monte Hermoso (39°S, 61°50′W), Coronel Rosales County, Buenos Aires Province; early–middle Pliocence (Montehermosan?–Chapadmalalan Age.

Shaft of Ulna, MLP 63-VI-10-15; Cascada Grande locality on the right margin of Quequén Salado River (38°30′S, 60°30′W), Coronel Dorrego County, Buenos Aires Province; middle Pliocene (Lower Chapadmalalan Age).

REMARKS.—The humerus, which comes from the same locality as *Dryornis pampeanus*, was attributed to *Vultur gryphus* by Tambussi (1989), Tambussi et al. (1993), and Tambussi and Noriega (1996). The ulna shaft was referred to *Vultur gryphus* by Tambussi (1989) and shows 12 papillae remigiales ventrales and caudales (of secondary remiges). The cross section of the shaft is triangular and forms a smooth, sigmoid curve.

cf. *Vultur* sp.

REFERRED MATERIAL.—Distal end of femur, MMH 561; seashore close to Monte Hermoso city (39°S, 61°15′W); late Pleistocene (Lujanian Age).

REMARKS.—Tonni (1984) pointed out that this femur is indistinguishable from that of *Vultur*, but it is too badly preserved for a more accurate identification.

VULTURIDAE, genus and species indeterminate

REFERRED MATERIAL.—Incomplete right ulna and articulated proximal end of radius, MLP 90-X-1-1 (Figures 5, 6), collected by Ulyses Pardinas and Maximiliano Lezcano; south of the mouth of Arroyo Lobería (38°15′S, 57°40′W); middle Pliocene (Upper Chapadmalalan Age).

MEASUREMENTS (in mm).—*Ulna:* Total length as preserved, 253; width of proximal end, 40.8; width of midshaft,

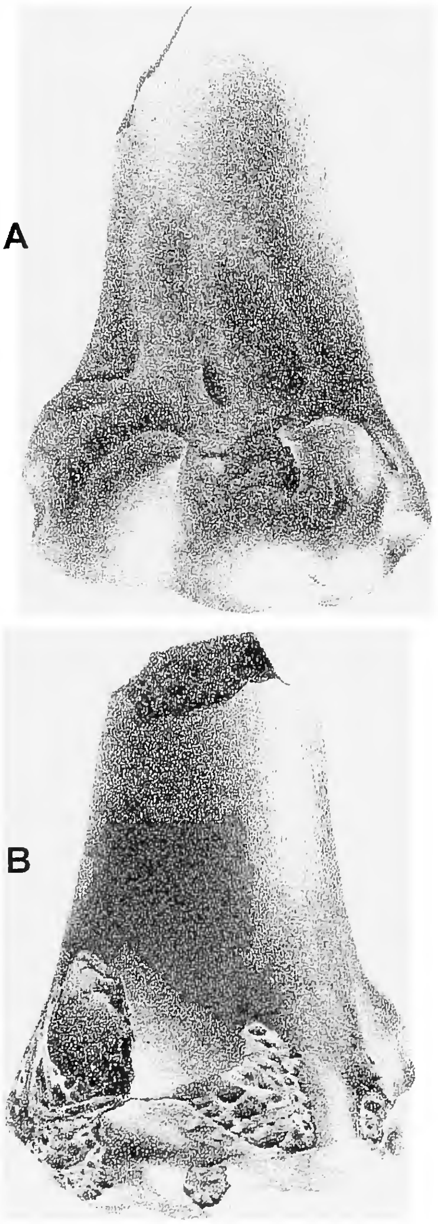

FIGURE 3.—Distal end of humerus of *Dryornis pampeanus* (MLP 20-169; lectotype): *a*, palmar view; *b*, anconal view.

FIGURE 4.—Proximal end of humerus of *Vultur gryphus* (MLP 48-XII-16-225) in anconal view. Scale bar=1 cm.

15.8; depth of midshaft, 16.4. *Radius:* Distance between head and capital tuberosity, 21.

DESCRIPTION.—The ulna differs from those of other condor genera by having the following features: (1) olecranon developed as in *Vultur*, larger than in *Gymnogyps* or *Geronogyps;* (2) olecranon directed medially; (3) the humero-ulnar depression well excavated; (4) incisura radialis shallower than in *Vultur, Gymnogyps,* or *Geronogyps* and located less medially; (5) impressio brachialis beginning more proximally than in *Vultur* and lacking foramina, unlike *Vultur, Geronogyps,* or *Gymnogyps;* (6) base of the processus cotylaris dorsalis palmarly excavated; and (7) papillae remigiales situated on midline of dorsal surface, but situated more mediad in *Vultur.* The bone is damaged at the level of the prominence for the tubercullum lig. collateralis ventralis. There are only 12 anconal papillae for attachment of secondary remiges preserved.

The radius is characterized by having (1) strong tuberculum bicipitali radii, as in *Geronogyps;* (2) deep and rounded bicipital attachment; (3) capital tuberosity (in the sense of Howard, 1929) prominent and limited internally by a deep notch, as in *Geronogyps;* and (4) capital tuberosity doubly pierced with large foramina.

REMARKS.—The preserved bones of MLP 90-X-1-1 are approximately 20% longer than those of either modern condors or *Geronogyps.* The features mentioned below make the fossil too different to be referred to any recent genus of fossil vultures; nevertheless, it would be imprudent to name a new genus and species until more complete material is recovered.

Geronogyps reliquus Campbell, 1979

REFERRED MATERIAL.—Left humerus, partially broken, CCM Nro 95-VI-5-1 and 95-VI-5-4 (Figure 7); left margin of Arroyo Chasicó, close to its mouth (38°30′S, 63°W), Villarino County, Buenos Aires Province; Pleistocene, sensu lato.

MEASUREMENTS (in mm).—Depth of head, 19; distance between tuberculum dorsale and insertion of M. scapulohumera-

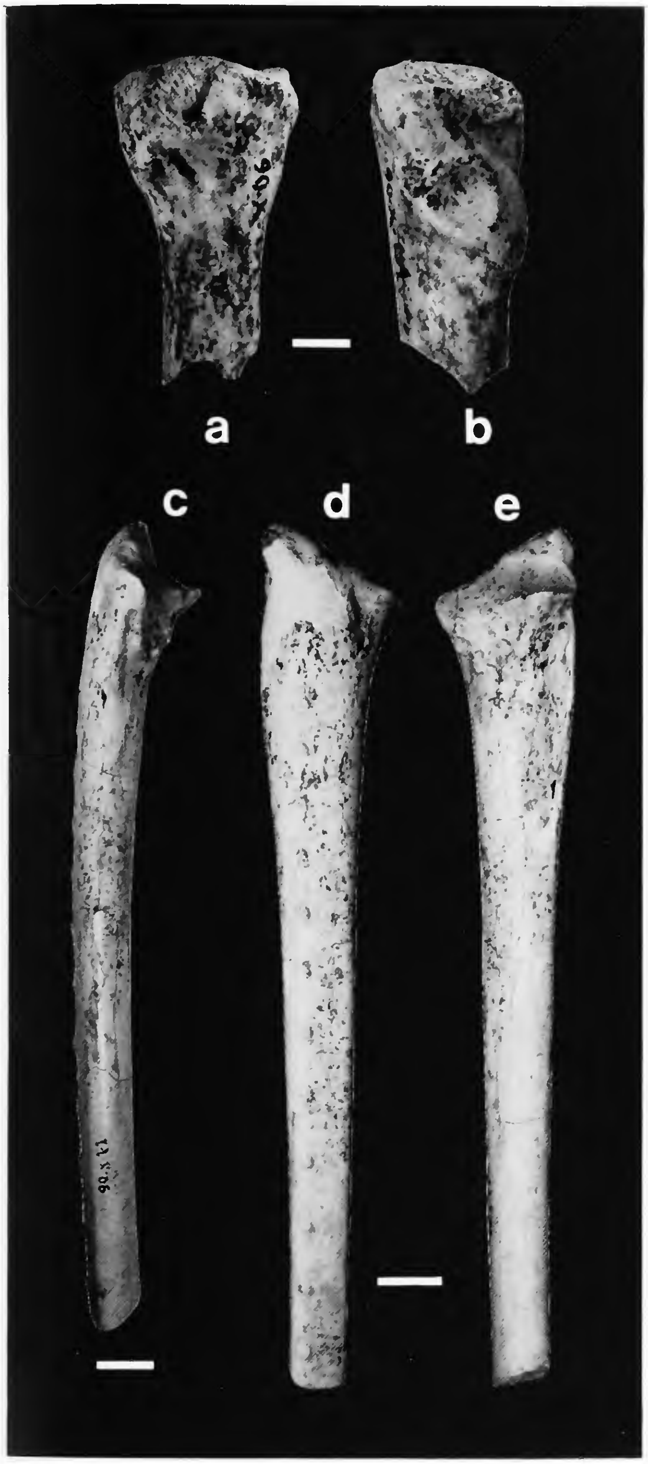

FIGURE 5.—Vulturidae, probably a new genus and species (MLP 90-X-1-1). Proximal end of radius: *a*, anconal view; *b*, palmar view. Proximal end of ulna and shaft: *c*, external view; *d*, palmar view; *e*, anconal view. Scale bar=1 cm.

lis, 61; width of midshaft, 20.8; depth of midshaft, 16.3; distal width, 46.9.

REMARKS.—Before now, *Geronogyps* was known only from the Pleistocene sediments of the Talara Tar Seeps, Peru (Campbell, 1979). Campbell established this genus based on a complete tarsometatarsus, with the distal end of a left humerus and the proximal and distal ends of two right humeri as paratypes. Because the paratypes are badly crushed, the specimens reported herein bring additional information about the morphology of *Geronogyps reliquus*.

The following characters of *Geronogyps reliquus*, given by Campbell (1979), are present in the Argentinian specimen: (1) margo caudalis dropping off sharply on both sides, whereas more rounded in *Vultur* and *Gymnogyps;* (2) attachment of M. proscapulohumeralis brevis more proximal than in *Vultur;* (3) crista deltopectoralis flaring distally, not flaring as much in *Vultur* or in *Gymnogyps;* (4) shaft ventral to M. pectoralis superficialis not depressed, unlike *Vultur* and similar to *Gymnogyps;* (5) condylus dorsalis wide and short, whereas narrow and long in *Vultur* and *Gymnogyps;* (6) condylus ventralis short (very long in *Vultur* and moderately long in *Gymnogyps*); (7) epicondylus dorsalis long and not angular, unlike *Vultur;* (8) condylus ventralis gently rotated anteriad, resulting in moderately flexed distal end, as in *Gymnogyps* (greatly rotated in *Vultur*); and (9) impression of M. brachialis shallower than in *Vultur* or *Gymnogyps.*

Discussion and Conclusions

Condors, one of the primary scavenging lineages of birds, are large-sized vulturids with past and present distributions restricted to the New World. The fact that the temporal range of condors is less extensive in South America (middle–late Pliocene) than in North America (middle Miocene), and that their absence from the richly fossiliferous Paleogene and early Neogene outcroppings of Argentina does not seem to be related to taphonomic problems, could probably be considered a reaffirmance of Emslie's idea (1988a) about a North American origin for the group. Condors may have participated in the Great American Biotic Interchange (GABI) during Pliocene times (Webb and Marshall, 1982; Emslie, 1988a), moving from north to south across open savanna environments; however, the presence of a fossil condor, *Antillovultur varonai* Arredondo (1971), from the late Pleistocene of Cuba, proves that condors can cross water barriers. This fact, together with the evidence of a significant interchange of pre-Pliocene volant bird families between both Americas before the formation of a land connection (Rasmussen and Kay, 1992), seems to weaken the hypothesis that condors were part of the latest events of the GABI. Our analysis does not make it possible to bring arguments in favor of, or against, this hypothesis.

The fossil record summarized above indicates that a great diversity of condors occurred in the late Cenozoic of the Pampean region of Argentina, including three genera and at least four species: *Dryornis pampeanus, Vultur gryphus, Gerono-*

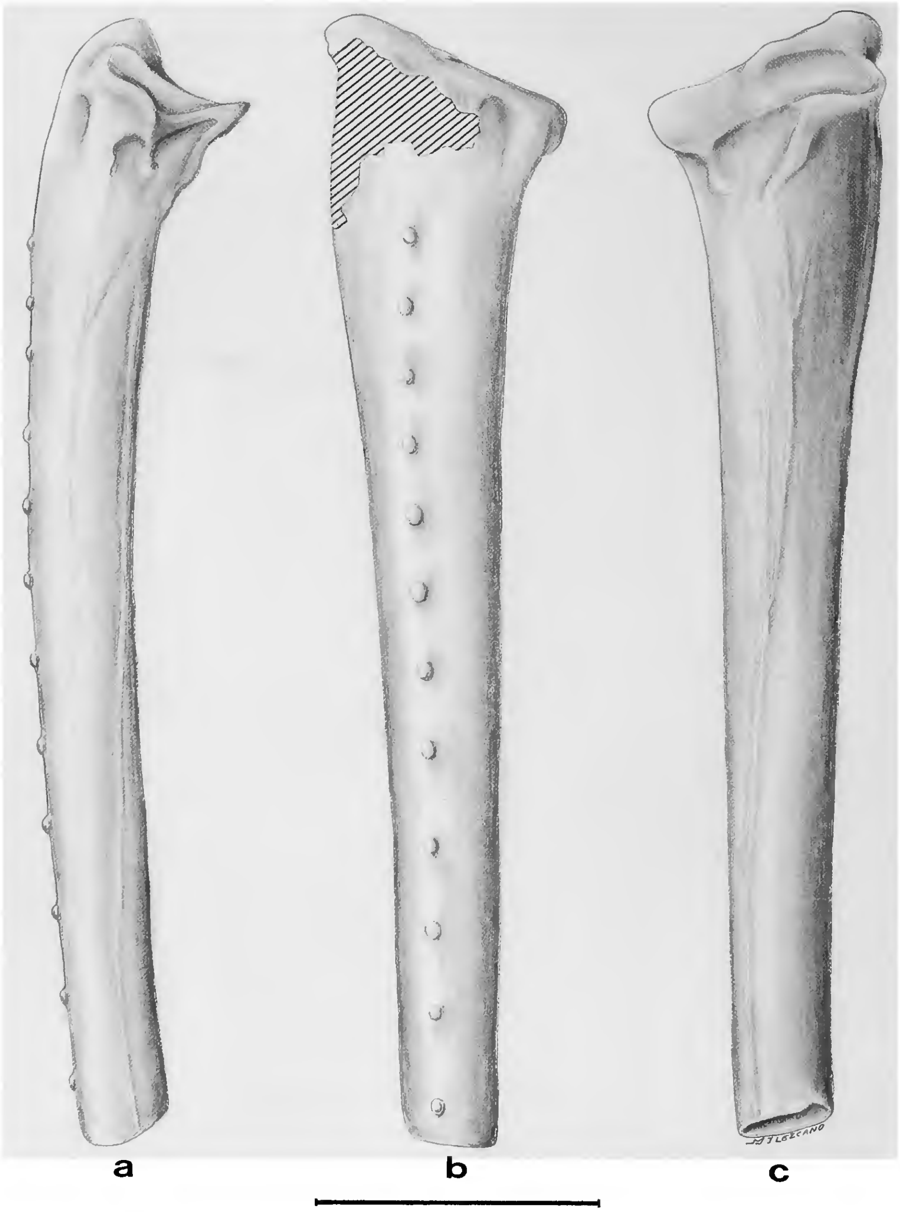

FIGURE 6.—Vulturidae, probably a new genus and species (MLP 90-X-1-1). Proximal end of ulna and shaft: *a*, external view; *b*, palmar view; *c*, anconal view. Scale bar=5 cm.

gyps reliquus, and an indeterminate vulturid that probably represents a new genus and species.

Dryornis pampeanus and *Vultur gryphus*, from the early?–middle Pliocene, constitute the earliest record of condors in South America. The remaining two taxa come from Pleistocene and middle Pliocene sediments, respectively.

The presence of *Geronogyps reliquus* (up to now restricted to the Pleistocene of Peru) in the Pleistocene sediments of the Pampean region extends considerably the geographic range of the species. Thus, condors were more widely distributed during the early?–middle Pliocene and Pleistocene than they are at present.

Only one condor species now survives in South America, *Vultur gryphus*, and its distribution is restricted to Andean regions and arid steppes of Patagonia. It has been hypothesized that the decline in condor diversity and the retraction of *Vultur gryphus* from the Pampean region is due to climatic changes and/or to the extinction of megaherbivorous mammals, which were likely their main food source (as carrion) (Emslie, 1987; Tonni and Noriega, 1998).

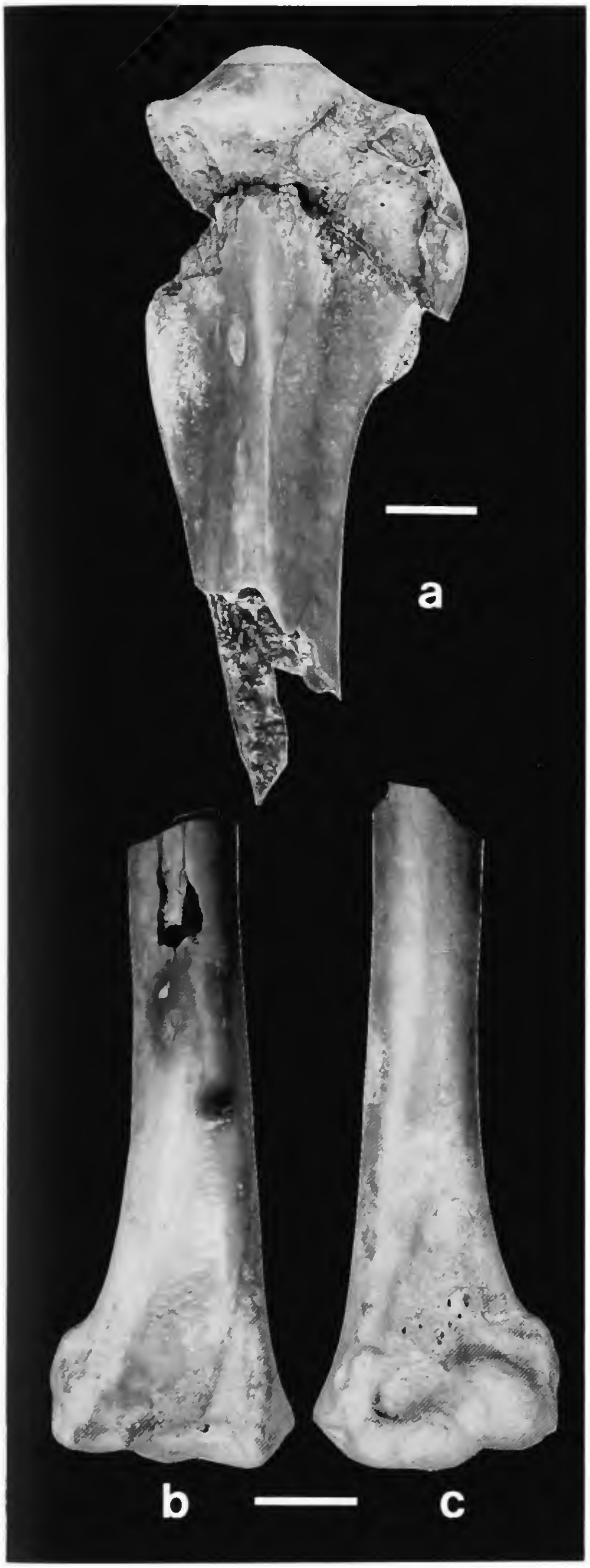

FIGURE 7.—Referred humerus of *Geronogyps reliquus* (CCM 95-VI-5-1 (*a*), CCM 95-VI-5-4 (*b,c*)): *a*, proximal end, anconal view; *b*, distal end, anconal view; *c*, distal end, palmar view. Scale bars=1 cm.

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Two New Fossil Eagles from the Late Pliocene (Late Blancan) of Florida and Arizona and Their Biogeographic Implications

Steven D. Emslie and Nicholas J. Czaplewski

ABSTRACT

Two new species of fossil eagles are described from the late Pliocene of Florida and Arizona, adding new information on the paleoecology of these regions. *Aquila bivia,* new species, is known from 33 skeletal elements from Inglis 1A, Citrus County, Florida, and from a partial skeleton from 111 Ranch, Graham County, Arizona. It was a large eagle, approximately 10%–15% larger than females of modern *A. chrysaetos* (Linnaeus), and it is the first valid fossil species in this genus to be described from North America. *Amplibuteo concordatus,* new species, is known from 13 skeletal elements from Haile 7C, Alachua County, and Inglis 1C, Citrus County, Florida, and from three specimens from Duncan, Greenlee County, Arizona. It is the third species of the genus to be described, and it represents the earliest occurrence of this genus. These two new taxa add to a growing list of vertebrates with fossil distributions in both the Florida peninsula and western North America, which reflects a corridor of common habitat that once united these regions. This corridor initially developed during glacial intervals in the late Pliocene, when numerous taxa of mammals, birds, reptiles, and plants first appear in the fossil record of Florida. The corridor probably was composed largely of dry thorn-scrub and savannah communities, but it also may have had a mosaic of lakes, wetlands, and hammocks that allowed dispersal of a variety of species that reflect these communities.

Introduction

The fossil record in Florida and the southwestern United States indicates that numerous species of mammals, reptiles, and plants were shared between these regions during the Pliocene and Pleistocene (Neill, 1957; Blair, 1958; Marshall et al., 1982; Marshall, 1985; Meylan, 1982). This distributional pattern has been explained as the result of the Gulf Coast corridor, a broad expanse of savannah and xeric thorn-scrub habitat that extended through Central America, Mexico, and the southern portion of the United States (Blair, 1958; Mares, 1985; Webb, 1985). This corridor allowed the dispersal of taxa between the Florida peninsula and the western United States and between North and South America during the Great American Biotic Interchange, which began at about 2.5 Ma (Stehli and Webb, 1985).

The fossil record of birds during this period is less well known, although similar dispersals have been documented (Vuilleumier, 1985; Emslie, 1996). For example, the phorusrhacoid *Titanis walleri* Brodkorb is a representative of a South American group that reached Florida and Texas during the Plio-Pleistocene (Brodkorb, 1963; Baskin, 1995). An unusual group of condor-like vultures, the teratorns, also may have been from a South American lineage that entered North America by the late Pliocene (Campbell and Tonni, 1981; Vuilleumier, 1985; Emslie, 1988). Recent paleontological investigations in Florida and Arizona have indicated that considerably more avian taxa were shared between North and South America and the western and eastern United States during the Plio-Pleistocene than previously have been documented (Emslie, 1998). Herein, we describe two new species of eagles from the late Pliocene of Florida and Arizona. As with mammalian taxa, these and other avian fossils indicate an extensive common habitat that once extended across the southern United States in the late Pliocene.

METHODS.—Comparative analyses of fossil and recent skeletal material was completed at the Florida Museum of Natural History (FLMNH), University of Florida (UF), Gainesville, where the fossils are housed; the National Museum of Natural History (USNM; collections of the former United States National Museum), Smithsonian Institution, Washington, D.C.; the Museums of Paleontology (UMMP) and Zoology (UMMZ), University of Michigan, Ann Arbor; the Museum of Northern Arizona (MNA), Flagstaff; the University of California, Los

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Angeles (UCLA); and the George C. Page and Los Angeles County Museum of Natural History (LACM), California. Other fossils examined are in the collections of the American Museum of Natural History (AMNH), New York, and the Oklahoma Museum of Natural History (OMNH), Norman. Specimens were measured with digital calipers to the nearest 0.1 mm; all measurements are self-descriptive except proximal depth of the coracoid, which was taken from the glenoid facet to the brachial tuberosity. Comparative material for *Amplibuteo hibbardi* Campbell was not available, and character determinations for skeletal elements are based on the published descriptions and illustrations in Campbell (1979). Osteological terminology follows that of Howard (1929), with certain modifications. Nomenclature for species' binomials and English names of modern birds follows Sibley and Monroe (1990).

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AVES

ACCIPITRIDAE

Amplibuteo Campbell, 1979

Genus characterized by having the carpometacarpus with metacarpal III merging with the distal symphysis at an angle, a tendinal groove that curves proximally to the anterior surface of metacarpal II, the humerus with the shaft relatively straight and excavated at the distal end of the median crest, a broad pneumatic foramen, a deep excavation on the internal side of the impression for M. brachialis anticus, and a prominent deltoid crest as described for *Morphnus* (Howard, 1932). Includes two species, *A. woodwardi* and *A. hibbardi,* formerly referred to *Morphnus* (see Campbell, 1979); *A. concordatus,* new species; and one undescribed species.

Amplibuteo concordatus, new species

HOLOTYPE.—Right carpometacarpus, UF 159426 (Figure 1A; Table 1).

TYPE LOCALITY.—Haile 7C, section 24, T. 9S, R. 17E, Alachua County, Florida (FLMNH Vertebrate Paleontology Locality number AL109; Figure 2).

FIGURE 1.—A, Holotypical right carpometacarpus (UF 159426) of *Amplibuteo concordatus* from Haile 7C, Alachua County, Florida, in internal (left) and external (right) views; B, paratypical left carpometacarpus (AMNH 10395) from Duncan 4-19, Greenlee County, Arizona, in internal (left) and external (right) views. For each specimen, scale = ×1, bar = 1 cm.

TABLE 1.—Measurements (mm) of pectoral and wing elements of *Amplibuteo woodwardi* (sample size (*n*), mean ($\bar{x}$), and standard deviation (s.d.)) from Rancho La Brea, California, compared with *A. concordatus*, new species. Measurements of the carpometacarpus for *A. woodwardi* are in Emslie (1995). (L=length, PW=proximal width, PD=proximal depth; LWS=least width of shaft, LDS=least depth of shaft, DW=distal width, DD=distal depth.)

Element	L	PW	PD	LWS	LDS	DW	DD
Coracoid							
Amplibuteo woodwardi							
n	5	–	5	5	5	4	4
$\bar{x}$+s.d.	76.4±2.3	–	21.1±1.2	12.3±0.7	7.8±0.4	34.9±1.1	9.6±0.7
range	74.5–80.7	–	20.2–23.2	11.4–13.3	7.3–8.4	33.5–36.1	8.8–10.3
Amplibuteo concordatus							
UF 159404	–	–	18.4	–	–	–	–
UF 165529	–	–	16.4	9.0	–	–	–
AMNH 10399	72.5	–	17.9	10.6	6.4	–	8.2
Humerus							
Amplibuteo woodwardi							
n	1	6	6	3	3	4	4
$\bar{x}$±s.d.	207.0	40.0±2.4	12.3±0.5	14.5±0.7	12.6±0.3	35.8±1.8	17.9±0.7
range	–	37.4–42.7	11.5–12.8	13.7–15.0	12.3–12.8	34.1–37.5	17.3–18.8
Amplibuteo concordatus							
UF 159406(right)	163.3	33.3	9.0	13.1	10.4	26.7	14.2
UF 159407(left)	162.7	34.2	9.0	12.3	10.8	26.7	14.2
UF 165542	–	32.6	8.8	12.1	9.5	–	–
Ulna							
Amplibuteo woodwardi							
n	–	5	5	5	5	4	4
$\bar{x}$±s.d.	–	24.3±0.6	19.0±0.7	10.3±1.5	10.7±0.5	16.3±1.4	17.3±0.9
range	–	23.9–25.0	18.2–19.5	8.9–12.3	10.0–11.1	13.9–17.4	15.9–17.9
Amplibuteo concordatus							
UF 121743	177.4	17.9	14.6	9.0	8.4	14.7	12.7
Radius							
Amplibuteo woodwardi							
LACM H7419	–	11.6	8.5	–	–	–	–
LACM H7414	–	11.1	8.2	–	–	–	–
LACM D2057	–	–	–	6.0	4.9	14.3	6.7
LACM D4872	–	–	–	6.2	5.3	15.9	7.6
Amplibuteo concordatus							
UF 159408	–	–	–	5.4	4.0	13.5	5.8
AMNH 10398	–	–	–	–	–	13.3	6.1
Carpometacarpus							
Amplibuteo concordatus							
UF 159426	93.2	9.5	21.1	7.9	5.2	11.8	13.1
AMNH 10395	96.4	9.5	21.9	8.0	5.2	12.5	13.9

HORIZON AND AGE.—Late Pliocene (late Blancan), 2.2–2.0 Ma (Morgan and Hulbert, 1995; Hulbert, 1997; Emslie, 1998).

MEASUREMENTS OF HOLOTYPE.—See Table 1.

PARATYPES.—*Haile 7C:* Humeral end of left coracoid, UF 159404; left furcula, UF 159403; carina of sternum, UF 159402; right and left humeri (matching) with shafts broken, UF 159406, 159407 (Figure 3B); right and left ulnae (matching), UF 121743, UF 159405; distal end of left radius, UF 159408; partial synsacrum, UF 159427.

Inglis 1C (section 10, T. 17S, R. 16E, Citrus County, Florida (FLMNH Vertebrate Paleontology Locality number CI019; Figure 2)): Associated right coracoid and fragmentary manubrium of sternum, UF 165529; left humerus missing distal end, UF 165542 (Figure 3A); left fibula, UF 165577. Locality dates to late Pliocene (early Irvingtonian, 2.0–1.6 Ma) based on vertebrate biochronology similar to that of Inglis 1A.

Duncan 4-19 (south locality, west of Railroad Wash, Greenlee County, Arizona (Figure 2)): Right coracoid, AMNH 10399; distal end of left radius, AMNH 10398; left carpometacarpus, AMNH 10395. Locality dates to late Pliocene, 3.7–3.2 Ma (Blancan III of Repenning, 1987).

MEASUREMENTS OF PARATYPES.—See Table 1.

ETYMOLOGY.—From Latin, *concordatus*, agree together or harmonize, in reference to the close similarity of the fossil material both from the two Florida localities and from Arizona.

DIAGNOSIS.—Differs from *Amplibuteo woodwardi* (L. Miller) and *A. hibbardi* in the following characteristics. Carpometacarpus (UF 159426, AMNH 10395; Figure 1) with metacarpal I relatively large, with little or no proximal curvature; deep, narrow fossa present on internal surface of metacarpal I below pisiform process; internal ligamental fossa moderately to deeply excavated; and area between pisiform and

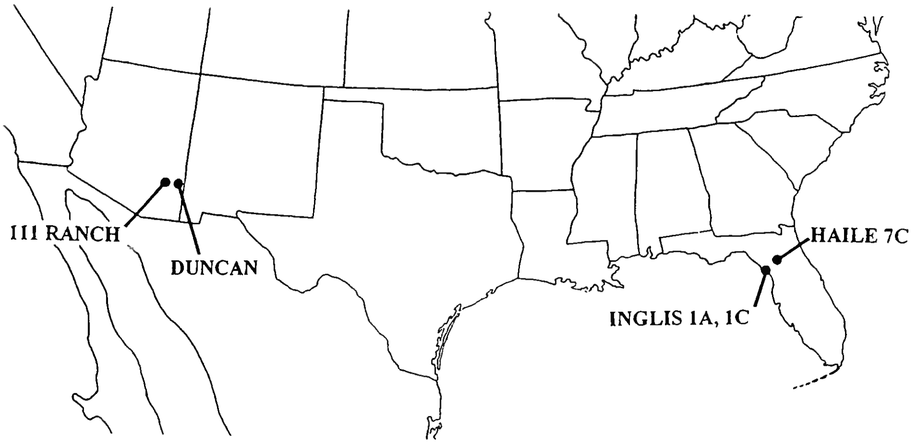

FIGURE 2.—Locations of late Pliocene fossil localities discussed in the text.

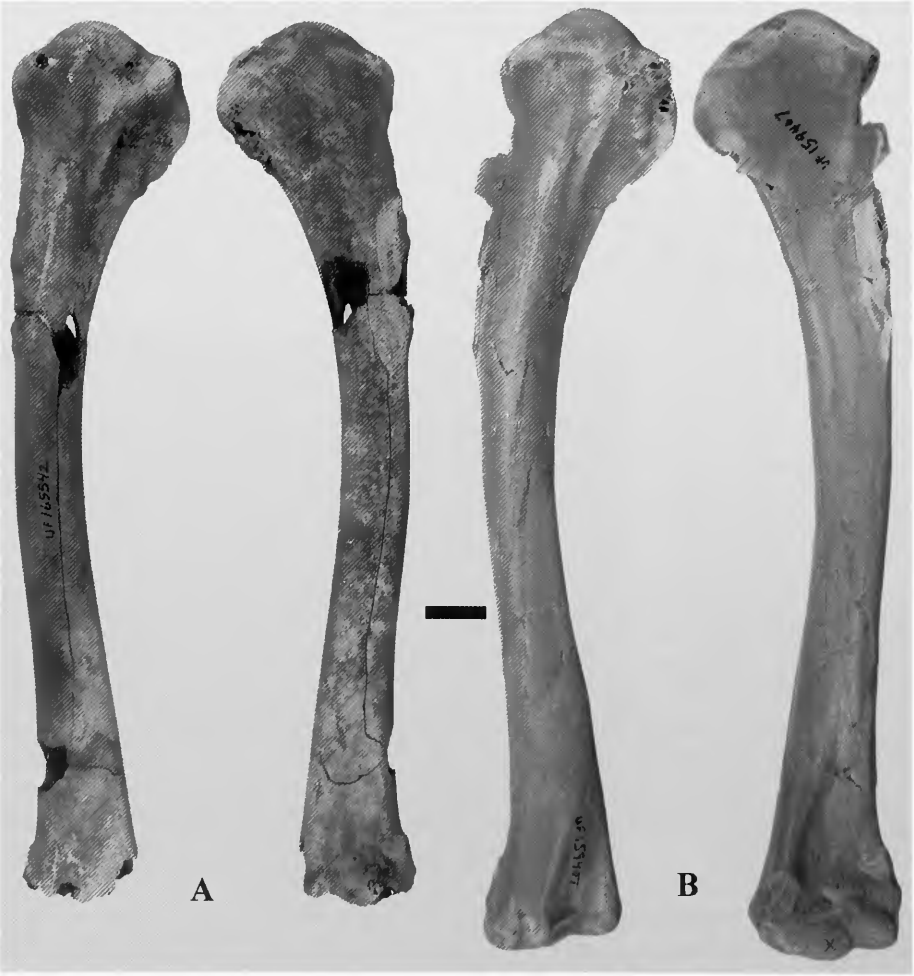

FIGURE 3.—Paratypical humeri of *Amplibuteo concordatus* from Florida: A, left humerus (UF 165542) from Inglis 1C, Citrus County; B, left humerus (UF 159407) from Haile 7C, Alachua County. For each specimen, scale=×1, bar=1 cm.

carpal trochlea relatively small (carpometacarpus larger, metacarpal I relatively smaller, with distinct proximal curvature, fossa below pisiform shallow and broad, area of internal ligamental fossa relatively greater in *Amplibuteo woodwardi* (*n*=4) and *A. hibbardi*). Coracoid with relatively short, narrow coraco-humeral surface (long and broad in *A. woodwardi* (*n*=5), short and broad in *A. hibbardi*); pneumatic foramina below brachial tuberosity small and indistinct (shallow to deep in *A. woodwardi*). Humerus (Figure 3) with internal tuberosity relatively narrow and less blunt (large and blunt in *A. woodwardi* (*n*=9), rounded in *A. hibbardi*); distinct excavation at distal end of medial bicipital crest (deep in *A. hibbardi;* deep to shallow or absent in *A. woodwardi*); ligamental furrow relatively narrow and deep (furrow broad, shallow to deep in *A. woodwardi*); bicipital crest merges with shaft immediately below pneumatic foramen (merges with shaft more distal to pneumatic foramen, forming a distinct flange, in *A. woodwardi* and *A. hibbardi*); attachment for anterior articular ligament relatively flat, long, and narrow (flat to convex, short and broad to long and narrow in *A. woodwardi,* short and rounded in *A. hibbardi*); impression of M. brachialis anticus relatively narrow (broad in *A. woodwardi*); and entepicondylar and ectepicondylar prominences relatively small (larger and more robust in *A. woodwardi*). Ulna with bicipital attachment relatively high on shaft (attachment more distal on shaft in *A. woodwardi* (*n*=3) and *A. hibbardi*); prominence for anterior articular ligament relatively small (large and robust in *A. woodwardi* and *A. hibbardi*); distal external condyle relatively long and narrow (short and broad in *A. woodwardi* and *A. hibbardi*); and carpal and radial tuberosities prominent (reduced in *A. woodwardi,* more prominent in *A. hibbardi*). Radius with ligamental prominence relatively small and blunt (large with more distal extension in *A. woodwardi* (*n*=2) and *A. hibbardi*); scapholunar facet in distal view relatively short and narrow (long and broad in *A. woodwardi*).

COMPARATIVE MATERIAL.—*Morphnus guianensis* (Daudin), skeleton, USNM 432243, unsexed; LACM 91788, skeleton, female. *Harpyhaliaetus solitarius* (Tschudi), partial skeleton with sternum, coracoid, proximal humerus, and femur, UCLA 41971, unsexed.

STATUS.—Extinct, known from fossils only.

REMARKS.—The material from Haile 7C is probably from a single individual based on similarities in the size and features of matching elements. At least one individual is represented from Inglis 1C, and the humerus (UF 165542) is slightly porous and incompletely ossified, indicating it is from a subadult. *Amplibuteo concordatus* was a small eagle compared to *A. woodwardi* or *A. hibbardi.* A third possible species of *Amplibuteo* (UF 102550), reported by Emslie (1995) from the late–early Irvingtonian Leisey Shell Pit 3B, is slightly larger than *A. concordatus* and smaller than *A. woodwardi* (see measurements in Emslie, 1995, table 11). It compares most closely with *A. woodwardi* except for the carpometacarpus, which is shorter and differs in characters as described by Emslie (1995). The carpometacarpus (UF 102550) from Leisey was compared with UF 159426 and AMNH 10395 and was found to differ in having a distinct proximal curvature of metacarpal I and having the fossa below the pisiform process broad and deep. These differences also suggest that the Leisey specimen represents a fourth, undescribed species of *Amplibuteo.*

Of the two other fossil species described in this genus, *A. woodwardi* is known from the late Pleistocene of Rancho La Brea, California, and the middle and late Pleistocene of Florida (Miller, 1911; Howard, 1932; Emslie, 1995); *A. hibbardi* is known only from the late Pleistocene Talara Tar Seeps, Peru (Campbell, 1979). The addition of *A. concordatus* to this record extends the geologic range of the genus into the late Pliocene. This species also was relatively long-lived, with a potential geologic range spanning 2.1 million years (between 3.7–1.6 Ma). The genus reached its greatest diversity in the Pleistocene of North and South America, when up to three species may have existed, although none of these apparently were sympatric based on the available evidence.

Campbell (1979) erected the genus *Amplibuteo,* with *A. hibbardi* of Peru as the type species, and at the same time transferred the fossil species *Morphnus woodwardi* from Rancho La Brea to the same new genus. His comparisons suggested that *Amplibuteo* is most closely related to *Buteo* and *Geranoaetus,* whereas *Morphnus* is closer to *Harpia* than to other genera.

Campbell's comparisons included one specimen of *Harpyhaliaetus solitarius,* from which only the tarsometatarsus was used in the generic diagnosis of *Amplibuteo.* We compared the sternum, coracoid, proximal end of the humerus, and femur of this species with those of *Morphnus guianensis, Amplibuteo woodwardi,* and *A. concordatus.* These comparisons indicate a closer similarity in skeletal characters between *Harpyhaliaetus* and *Amplibuteo* than previously has been recognized. Characters shared by these two genera include the sternum with the anterior carinal margin placed relatively far from the manubrium, the coracoid with the coracoidal fenestra positioned relatively far from the scapular facet, the humerus with a bicipital crest that merges with the shaft distally, giving the crest a distinct flange in *A. woodwardi* (although the crest merges immediately to a shaft with no flange in *A. concordatus* and *Harpyhaliaetus*), and the femur with a high trochanter and a trochanteric ridge extending far down the shaft.

These similarities raise the possibility that *Amplibuteo* may be closely related to or even congeneric with *Harpyhaliaetus,* of which additional modern skeletal specimens would be highly desirable. The high diversity of Accipitridae and the lack of adequate comparative skeletons for some species (e.g., *H. coronatus*), however, compound the problems associated with describing new taxa in this group, and additional, more detailed comparisons are needed with all accipitrid genera. The two species of *Harpyhaliaetus* are today confined to the Neotropics. The Crowned Solitary Eagle (*H. coronatus*) is found in savannah habitats from Bolivia to southern Argentina, whereas the Black Solitary Eagle (*H. solitarius*) occurs on mountain slopes from Mexico to Peru (Brown and Amadon, 1968). With little being known of the natural history of these species (Brown and Amadon, 1968), and comparative skeletal material being rare (Wood and Schnell, 1986), future additions to existing skeletal collections should provide further insight on the relationships between *Harpyhaliaetus* and *Amplibuteo.* Given these affinities, *Amplibuteo* probably is of Neotropical origin, although this suggestion is not yet supported by the fossil record.

Aquila Linnaeus

These fossils represent a large eagle that is referable to *Aquila,* and not *Haliaeetus,* by the following characters: cranium with relatively larger, more rounded foramen prooticum; mandible with symphysis broader and less tapered distally, and with relatively broader articular; scapula with external border of acromion more curved in proximal view; humerus with bicipital crest smaller and extending less distally on shaft, with median crest forming a longer border to the pneumatic fossa distally; ulna with relatively more pronounced prominence for anterior articular ligament and with external condyle extending farther proximally on the shaft; radius with bicipital tubercle located relatively farther distally on shaft; carpometacarpus with relatively broader and deeper excavation below pisiform process, internal border of carpal trochlea long, extending closer to metacarpal III; femur relatively longer, trochanter less pronounced; and tibiotarsus with tendinal bridge angled less medially and tendinal groove placed more internally than in *Haliaeetus.*

Aquila bivia, new species

HOLOTYPE.—Right carpometacarpus, UF 30015 (Figure 4; Table 2).

TYPE LOCALITY.—Inglis 1A, section 8, T. 17S, R. 16E, Citrus County, Florida (FLMNH Vertebrate Paleontology Locality number CI001; Figure 2).

HORIZON AND AGE.—Late Pliocene (early Irvingtonian), 2.0–1.6 Ma (Morgan and Hulbert, 1995).

MEASUREMENTS OF HOLOTYPE.—See Table 2.

PARATYPES.—*Inglis 1A:* Fragment of left cranium, UF 159544; articular end of left mandible, UF 30028; two mandibular symphyses, UF 30029, 30030; two proximal ends of left scapulae, UF 30026, 30027; shaft of left coracoid, UF 30034; anterior portion of carina of sternum, UF 30035; distal end (damaged) of right humerus, UF 30043; two proximal ends of left humeri, UF 30040, 30041; two proximal ends of left ulnae, UF 30023, 30024; distal end of left ulna, UF 30025; two proximal ends of right radii, UF 30038, 30039; distal end of left radius, UF 30036; proximal end of left radius, UF 30037; distal end of left carpometacarpus, UF 30014; three alar phalanges,

TABLE 2.—Measurements (mm) of modern and late Pleistocene (maximum lengths only, Rancho La Brea, from Howard, 1932) Golden Eagle (*Aquila chrysaetos*) carpometacarpi, femora, and tibiotarsi (sample size (*n*), mean ($\bar{x}$), and standard deviation (s.d.)) in comparison with fossils of *A. bivia*, new species, from Inglis 1A, Florida. (L=length, PW=proximal width, PD=proximal depth; LWS=least width of shaft, LDS=least depth of shaft, DW=distal width, DD=distal depth.)

Element	L	PW	PD	LWS	LDS	DW	DD
Carpometacarpus							
Aquila chrysaetos							
n=10; ♀, 5?							
$\bar{x}$±s.d	103.0±4.4	10.4±0.7	26.0±1.2	8.4±0.4	6.1±0.2	13.7±0.6	15.4±0.8
range	97.6–112.5	9.5–11.7	24.1–24.8	7.9–9.2	5.7–6.5	12.8–14.8	13.8–16.6
maximum	112.9						
Aquila bivia							
UF 30015	119.6	12.5	29.9	10.3	6.7	15.1	17.9
Femur							
Aquila chrysaetos							
n=12; 7♀, 5?							
$\bar{x}$±s.d	129.7±4.5	28.0±1.3	19.5±1.2	13.5±0.8	12.7±0.7	30.1±1.5	22.3±1.2
range	120.8–134.6	25.1–30.1	17.7–21.7	12.5–15.0	11.4–13.6	27.3–32.3	20.6–24.8
maximum	135.8						
Aquila bivia							
UF 30019	140.1	29.3	20.7	14.1	13.8	29.6	22.8
Tibiotarsus							
Aquila chrysaetos							
n=14; 7♀, 7?							
$\bar{x}$ ±s.d.	164.2±5.1	–	–	11.3±0.5	7.7±0.4	22.9±1.3	15.6±0.8
range	155.6–172.7	–	–	10.4–12.1	7.1–8.3	20.7–26.0	14.3–16.6
maximum	172.8						
Aquila bivia							
UF 30012	180.6	–	–	11.6	8.3	21.3	12.5

Figure 4.—Holotypical right carpometacarpus (UF 30015) of *Aquila bivia* from Inglis 1A, Citrus County, Florida, in internal (left) and external (right) views. Scale=×1, bar=1 cm.

UF 30031–30033; two proximal ends of right femora, UF 30020, 30021; distal end of right femur, UF 30022; left femur, UF 30019 (Figure 5B; Table 2); right tibiotarsus, UF 30012 (Figure 5A; Table 2); proximal end of right fibula, UF 30013; right metatarsal I, UF 30018; right phalanx 1 of digit I, UF 30016; left ungual phalanx of digit II, UF 30017; right phalanx 2 of digit II, UF 30045; left phalanx 1 of digit III, UF 30046; phalanx 3 of digit III, UF 30044; phalanx 1 of digit IV, UF 30047; ungual phalanx of digit IV, UF 30048. At least two adults represented.

111 Ranch (East Ravine at Dry Mountain, Graham County, Arizona (OMNH Locality V818; Figure 2)): Partial associated skeleton (OMNH 50271) including proximal and distal ends of a right carpometacarpus, right and left ulnares, right radiale, proximal end of left tarsometatarsus; right metatarsal I, phalanx 1 and ungual of digit I, phalanx 2 and ungual of digit II, phalanges 1–3 and ungual of digit III, phalanges 2–4 and ungual of digit IV; left metatarsal I and phalanx 1 of digit I, phalanx 2 and ungual of digit II, phalanx 3 (partial) of digit III, and phalanges 2–4 of digit IV.

This locality is within greenish clay in the Gila Conglomerate at the approximate level of paleomagnetic samples 112 and 113, East Ravine, of Galusha et al. (1984). This section has reversed polarity throughout and represents Chron C2r, or slightly above the 2.47 Ma Dry Mountain Ash Bed (Izett, 1981; Galusha et al., 1984; Tomida, 1987). One adult (from associated material) is represented.

Measurements of Paratypes.—See Table 1.

Etymology.—From Latin, *bivius, -a, -um,* two-wayed, in reference to the distribution of the fossil specimens in Florida and Arizona.

Diagnosis.—The species is diagnosed by the following characters. Carpometacarpus (UF 30015, OMNH 50271; Figure 4) with relatively deep external ligamental attachment with pronounced proximal border, metacarpal I relatively long and robust, pit below pollical facet on metacarpal II, relatively large prominence for muscle attachment of proximal internal edge of metacarpal III (ligamental attachment shallow and proximal border less pronounced, metacarpal I relatively shorter and less robust, absence of pit below pollical facet on metacarpal II, and prominence for muscle attachment small in *Aquila chrysaetos, A. rapax, A. heliaca, A. verreauxii,* and *A. audax*). Femur with relatively long and slender shaft (shaft shorter and more robust in *A. chrysaetos*) and with broad, deeply excavated popliteal area (area narrower and moderately excavated in *A. chrysaetos;* Figure 5B). Tibiotarsus with relatively long, narrow shaft (shaft shorter and more robust in *A. chrysaetos;* Figure 5A). Size relatively large compared with *Aquila chrysaetos, A. rapax, A. heliaca, A. verreauxii,* or *A. audax.*

Comparative Material.—*Haliaeetus leucocephalus* (Linnaeus); USNM 611999, USNM 489276, 1 male and 1 female. *Aquila rapax* (Temminck), USNM 430406, 430532, 488147, 488148, 1 male, 3 females. *Aquila heliaca* Savigny, USNM 488808, female. *Aquila chrysaetos* (Linnaeus), UF 19399, 23961, 23962, 23964, 1 male, 3 females; USNM 17721, 17983, 18194, 18802, 19251, 19394, 19399, 19724, 19777, 288513, 319967, 320978, 343130, 491476, 500354, 500355, 500367, 502292, 612086, 5 males, 5 females, 9 unsexed; LACM 89953, female. *Aquila audax* (Latham), USNM 344883, unsexed. *Aquila verreauxii* Lesson, USNM 612539, unsexed.

Status.—Extinct, known from fossils only.

Remarks.—*Aquila bivia* was a large eagle that was closely related to the Golden Eagle (*A. chrysaetos*), but it was 10%–15% larger than females of that species and had limb elements that do not overlap with those of *A. chrysaetos* in length (Table 2). A large series of late Pleistocene eagle bones from Rancho La Brea that Howard (1947) recognized as a larger temporal form of *A. chrysaetos* also do not approach the length of the Inglis specimens (Table 2). Howard (1932) noted that the Rancho La Brea eagle had relatively longer wings and shorter legs than did recent *A. chrysaetos,* but with a larger series of recent skeletons she later found that the limb proportions of the

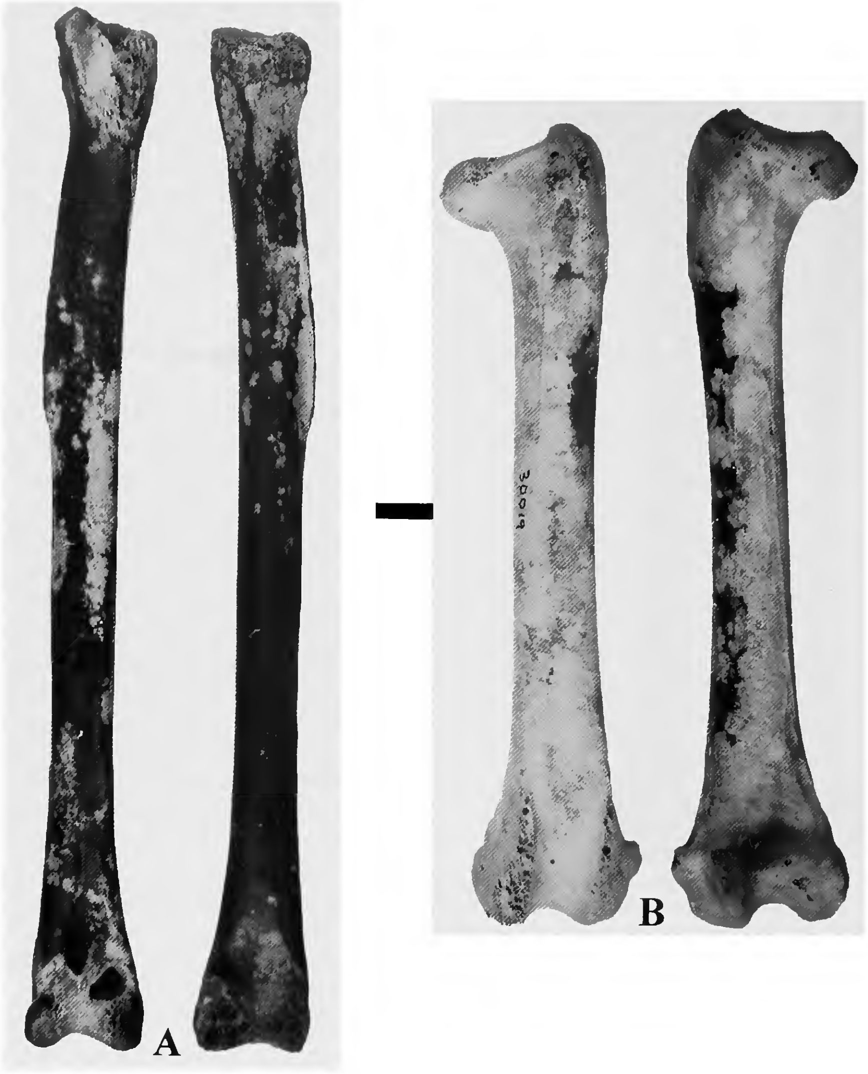

FIGURE 5.—Paratypes of *Aquila bivia* from Inglis 1A, Citrus County, Florida: A, right tibiotarsus (UF 30012); B, left femur (UF 30019), in anterior (left) and posterior (right) views. For each specimen, scale= ×0.75, bar=1cm.

fossil eagle did not differ significantly from those of the modern one (Howard, 1947).

The ratio of carpometacarpus to femur length of recent *Aquila chrysaetos* shows considerable variation (range, 0.79–0.85; *n*=11). The maximum lengths of these elements given by Howard (1932) for the Rancho La Brea eagle give a ratio of 0.83, or within the range of the modern species. If the carpometacarpus (UF 30015) and femur (UF 30019) of *A. bivia* are assumed to be from the same individual, they give a ratio of 0.85 and are thus within the range of modern *A. chrysaetos*. The tibiotarsus (UF 30012) of *A. bivia*, however, is longer and proportionally more gracile compared to *A. chrysaetos* (Table 2), suggesting that the fossil species had relatively longer and more slender legs compared to other eagles of this genus.

This large eagle is the first valid fossil species of *Aquila* to be described from North America. Two named species, *A. ferox* and *A. lydekkeri*, described from North America by Shufeldt (1915), are now recognized as synonyms of *Minerva antiqua* Shufeldt, an Eocene owl in the extinct family Protostrigidae (Olson, 1985). *Aquila borrasi*, described from the late Pleistocene of Cuba by Arredondo (1970, 1976), was discussed by Olson and Hilgartner (1982), who suggested that it may be related to the large, extinct hawk *Titanohierax gloveralleni* Wetmore (1937) of the Bahamas. They also suggested that none of the Cuban material was properly placed in the genus *Aquila*.

We compared the paratypical femur of *A. borrasi* (Arredondo, 1970, fig. 7) to femora of *A. bivia* and found it to differ in its relatively greater size, shaft more distinctly flared toward the ends, and the relatively large proximal pneumatic foramen. This femur does not appear to represent any living genus of hawk, eagle, or vulture, and we agree with Olson and Hilgartner (1982) that it probably is referable to *Titanohierax*. Bickart referred six specimens to *Aquila* sp. A and sp. B from the late Miocene/early Pliocene Big Sandy Formation, Arizona. These specimens are described as equal in size to or smaller than *A. chrysaetos* and probably do not represent *A. bivia.*

Two other fossil species, *Aquila delphinensis* and *A. pennatoïdes,* described by Gaillard (1938), are known from the late Miocene of France, each only by the proximal end of the tarsometatarsus

These specimens were not available for comparison in this study, but their geographic location and age suggest that the Inglis fossils would not be referable to either of these species.

Discussion

The two new eagles described herein add to a growing list of living and extinct birds that indicate a former habitat corridor, extending from the Florida peninsula to western North America, that probably developed in the late Pliocene when climatic changes allowed xerophytes from the south to move northward and those from the north to move southward (Blair, 1958; Axelrod, 1979; Simpson and Neff, 1985). The resulting habitat apparently was a dry, thorn-scrub community and savannah as suggested by fossil and recent plant and animal distributions (Blair, 1958; Axelrod, 1979; Simpson and Neff, 1985) and was an important corridor for biotic dispersal during the Great American Biotic Interchange (Stehli and Webb, 1985).

Based on topography, probable avenues of northward dispersal of Neotropical elements into the southwestern and southeastern United States were along the coastal lowland corridors on the eastern and western margins of mainland Mexico (i.e., below the Sierra Madre Oriental along the Gulf of Mexico and below the Sierra Madre Occidental along the Gulf of California; Figure 6). From these areas of entry, late Blancan and early Irvingtonian invaders from the tropics spread into savannah habitats on the Mexican Plateau and in the present-day southern United States. They moved especially into the southeastern United States (particularly the Florida peninsula, where the vertebrate fossil record is best known, but later as far north as South Carolina) but also into the southern Great Plains and to a lesser extent into present-day Sonora, Mexico, and southern California, probably via the western corridor. Some of these taxa dispersed as far north as present-day Idaho, although the greatest diversity extends no farther north than the Texas panhandle (Figure 6).

Before now, the greatest evidence for the Gulf Coast corridor was shown primarily by mammalian faunas of the late Blancan and early Irvingtonian Land Mammal Ages in North America (Webb and Wilkins, 1984; Morgan, 1991; Figure 6, Table 3). Florida fossil faunas are characterized more by Neotropical influences during this period than by northern or western faunal elements (Webb and Wilkins, 1984; Morgan, 1991). The fossil herpetofauna from Inglis 1A, however, indicates greater influence from xeric habitats in the western United States during the early phase of the Plio-Pleistocene (15 of 31 species identified; Meylan, 1982).

Less has been documented in relation to fossil avifaunas in the Plio-Pleistocene, but evidence so far indicates similar disperal routes and timing as for the mammals. Vuilleumeir (1985) found that representatives of only three South American groups, the teratorns (*Teratornis* spp.), caracaras (*Caracara plancus* (J.F. Miller) and *Milvago readei* (Brodkorb)), and phorusrhacids (*Titanis walleri*), are known from the fossil record of Florida, and that there was a greater influence of North American taxa on South American avifaunas than the reverse. New fossil records indicate that additional extant Neotropical taxa, representing lowland forest and aquatic habitats, inhabited Florida during the Plio-Pleistocene. These taxa include the Least Grebe (*Tachybaptus dominicus* (Linnaeus)) and Great Black-hawk (*Buteogallus urubitinga* (Gmelin)) from Inglis 1A, Ringed Kingfisher (*Ceryle torquata* (Linnaeus)) from Haile 7C, and Gray-breasted Crake (cf. *Laterallus exilis* (Temminck)) from Haile 16A (early Irvingtonian, 1.6–1.0 Ma; Carr, 1981; Emslie, 1998). Other extant species that first appear in the late Pliocene (Inglis 1A) of Florida that have populations or closely related species in western North America are discussed by Emslie (1996, 1998).

Extinct birds from the late Pliocene and early Pleistocene of Florida that reflect a common habitat between the peninsula and the western United States include the first record of an extinct cormorant (*Phalacrocorax idahensis* Marsh) from Florida (Emslie, 1998) and two species of pygmy-owls (*Glaucidium* spp.), which represent the first occurrence of this genus in eastern North America (Carr, 1981; Emslie, 1998; Table 3). In addition, teratorns (*Teratornis* spp.) first appear in Florida and the western United States in the late Blancan and represent a group that probably originated in South America (Campbell and Tonni, 1981; Emslie, 1988). Other taxa that arrived in the peninsula during this period include condors (*Gymnogyps* spp.), an extinct accipitrid vulture (*Neophrontops slaughteri* Feduccia), *Aquila bivia* and *Amplibuteo concordatus,* described herein, a tropical hawk-eagle (*Spizaetus* sp.), an undescribed chachalaca (Cracidae, indet.), and an extinct turkey (*Meleagris leopoldi* A.H. Miller and Bowman/*M. anza* Howard) (Steadman, 1980; Carr, 1981; Emslie, 1988, 1992, 1998; Table 3).

As with the mammals, these extant and extinct taxa provide strong evidence that xeric, thorn-scrub and savannah habitats once existed between the Florida peninsula and western North America. Other species of mammals and birds that appeared in North America during this time, however, reflect aquatic and lowland tropical forest environments (Table 3). The presence of

TABLE 3.—Occurrence of mammalian taxa of presumed South American origin, and birds with Neotropical and western affinities, in faunas of late Pliocene to early Pleistocene (late Blancan to early Irvingtonian; 3.7–1.0 Ma) age in western North America and the Florida peninsula. References used to compile this table include Akersten (1972), Carranza-Castañeda and Miller (1988), Conrad (1980), Dalquest (1975), Downs and White (1968), Emslie (1988, 1992, 1995, 1998), Frazier (1981), Galusha et al. (1984), Gillette and Ray (1981), Hager (1974), Hirschfeld and Webb (1968), Hulbert (1992, 1997), Hulbert and Morgan (1993), Jefferson (1989), Johnson et al. (1975), Johnston and Savage (1955), Lindsay (1978, 1984a, 1984b), Lindsay and Tessman (1974), Lundelius et al. (1987), Miller and Carranza-Castañeda (1984), Montellano-Ballesteros and Carranza-Castañeda (1986), Morgan (1991), Morgan and Hulbert (1995), Opdyke et al. (1977), Robertson (1976), Schultz (1977, 1990), Schultz (1937), Seymour (1993), Skinner and Hibbard (1972), Tomida (1987), and Webb and Wilkins (1984). Inferred general habitat requirements for each taxon is indicated by superscript numbers as follows: ^{1}thorn-scrub and savannah, ^{2}lowland tropical forest and/or hammock, and ^{3}aquatic or semiaquatic. Habitat assignment is based on that of living counterparts and/or paleoecological and paleobiological information provided in American Ornithologists' Union (1998), Brown and Amadon (1968), Campbell and Tonni (1981), Delacour and Amadon (1973), Downing and White (1995), Kurtén and Anderson (1980), McDonald (1995), and Steadman (1980). (AZ=Arizona, CA=California, CO=Colorado, ID=Idaho, MX=Mexico, TX=Texas.)

Taxon	Florida								Western North America										
	Haile 7C	Haile 15A	Macasphalt Shell Pit	Santa Fe River	St. Petersburg Times	Inglis 1A, 1C	Haile 16A	Leisey, Pelican Road Shell Pits	111 Ranch; Red Knolls, AZ	San Pedro Valley Sites[a], AZ	Duncan, AZ	Anza-Borrego[b], CA	Cita Canyon; Red Corral, TX	Red Light; Hudspeth, TX	Blanco, TX	El Golfo de Santa Clara, MX	Rancho Viejo (Blancan), MX	Donnelly Ranch, CO	Grand View; Hagerman, ID
Mammals																			
Dasypus bellus^{1}	x	x	x	x		x	x	x											
Holmesina floridanus^{1}	x	x	x	x	x	x	x	x											
Glyptotherium arizonae^{3}	x			x	x	x		x		x									
Glyptotherium texanum^{3}									x				x	x	x				
Pachyarmatherium leiseyi^{1,2}							x	x											
Glossotherium chapadmalense^{1}		x	x	x		x			x						x				
Glossotherium garbanii^{1}																	x		
Glossotherium sp.^{1}													x	x			x		
Paramylodon harlani^{1}						x	x	x											
Megalonyx leptostomus^{2}	x		x	x	x	x							x		x			x	
Megalonyx wheatleyi^{2}							x	x								x			
Megalonyx sp.^{2}									x			x		x					
Eremotherium sp.^{2}	x					x	x	x											
Nothrotheriops texanus								x											
Nothrotheriops sp.^{1}												x				x			
Myrmecophaga tridactyla^{1}																x			
Erethizon bathygnathum^{2}										x									x
Erethizon kleini^{2}						x													
Erethizon dorsatum							x	x											
Erethizon poyeri^{2}	x											x							
Neochoerus dichroplax^{2,3}			x						x										
Neochoerus cordobai^{2,3}																	x		
Neochoerus sp.^{2,3}								x		x						x	x		
Hydrochaeris holmesi^{2,3}		x				x													
Birds																			
Phalacrocorax idahensis^{3}						x													x
Teratornis incredibilis^{1,3}								x				x							
Teratornis merriami^{1,3}								x											
Gymnogyps kofordi^{1}							x	x											
Gymnogyps sp.^{1}			x			x													
Neophrontops slaughteri^{1}						x													x
Amplibuteo concordatus^{1,2}	x					x					x								
Aquila bivia^{1}						x			x										
Spizaetus sp.^{2}			x																
Cracidae, indet.^{1}							x												
Meleagris leopoldi/anza^{1,2}	x					x						x	x						
Titanis walleri^{1}				x		x													
Glaucidium explorator^{1,2}						x													
Glaucidium sp.^{1,2}						x													

[a] Wolf Ranch, California Wash, Cal Tech, Benson, Mendevil Ranch, McRae Wash, Curtis Ranch

[b] Upper Arroyo Seco, lower Vallecito Creek

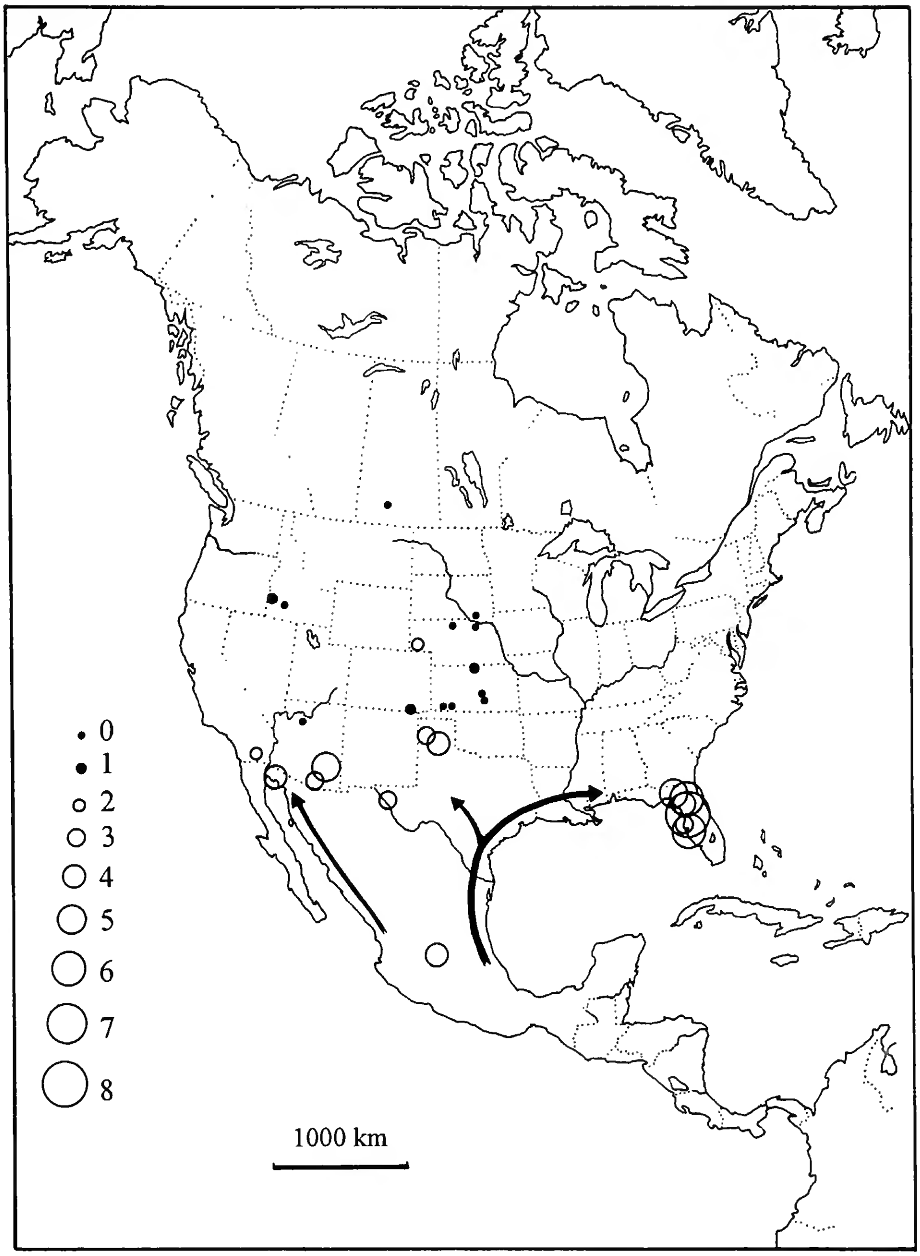

FIGURE 6.—Distribution of late Blancan to early Irvingtonian (ca. 2.5–1.0 Ma) local faunas in North America. Size of dot or circle indicates number of species of mammals of South American origin (Xenarthra, Caviomorpha) in the fauna. Local faunas include those listed in Table 3 plus Wellsch Valley, Saskatchewan; Delmont, South Dakota; Big Springs, Nebraska; Kentuck, Kansas; and Anita, Arizona. Arrows signify likely corridors of dispersal; the Gulf of Mexico terrestrial corridor would have been widened onto the continental shelf during glacial periods.

these taxa suggests that the Gulf Coast corridor was composed of a mosaic of communities, including dry thorn-scrub, hammocks, and aquatic zones (lakes and wetlands). Such a broad zone having patches of dry to moist habitats is unlike any such region today and probably developed in response to unusual climatic conditions during glacial intervals in the Plio-Pleistocene.

Conclusion

The record of birds in North America during the Great American Biotic Interchange indicates patterns for timing and dispersals that are similar to those known for other vertebrates and for plants. As with the mammals, the birds are largely presumed to represent a xeric, thorn-scrub and savannah environment that developed from the southwestern United States and northern Mexico across to the Florida peninsula during glacial intervals in the Pilocene and Pleistocene. This corridor probably accounts for the distributions of extant and extinct birds, including the two new eagles described herein, between the western United States and Florida. Other bird and mammal species suggest that a mosaic of habitats, including hammocks, lakes, and wetlands, also existed in this corridor. Subsequent climate change during interglacial intervals fragmented this broad habitat with concomitant isolation and extirpation of populations in the western United States and the Florida peninsula.

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A New Genus of Dwarf Megapode (Galliformes: Megapodiidae) from the Late Oligocene of Central Australia

Walter E. Boles and Tessa J. Ivison

ABSTRACT

The earliest fossil record of the Megapodiidae is from the Pliocene; most records are from the Quaternary. A recently identified megapode from late Oligocene deposits at Lake Pinpa, central Australia, is older than any previously reported megapode taxon and is only about two-thirds the size of the smallest living species. It probably inhabited riparian forests bordered by tropical savanna woodland in the Oligocene environment of Lake Pinpa, occupying a role similar to that of the Orange-footed Scrubfowl, *Megapodius reinwardt* Dumont, in tropical Australia today. Although the new fossil confirms the presence of the Megapodiidae in Australia as early as the late Oligocene, it provides no information on the origins and relationships of the family, or on the evolution of its distinctive method of incubation.

Introduction

The megapodes, or mound-builders, are among the more intriguing families of birds because they exhibit the practice, unique among birds, of incubating their eggs through the use of external heat sources (sun, decaying vegetation, volcanic heat, etc.) rather than body heat. The young hatch in a hyperprecocial state, receive no parental care from the adults, and are capable of flight within a few hours. This family has a circumscribed distribution: with one exception, it occurs only east of Wallace's Line, from Sulawesi through Australo-Papua and to Tonga and Samoa (recently extinct), and north to the Philippine Islands and Micronesia.

Several aspects of the biology and evolution of the Megapodiidae have been the subject of ongoing debate, including the relationships of the megapodes to other galliform families (e.g., Cracraft, 1973; Sibley and Ahlquist, 1990; Brom and Dekker, 1992; Jones et al., 1995), the origin of the family (either the Southern (Gondwanan) or the Northern Hemisphere (Cracraft, 1973; Olson, 1985)), and the factors responsible for its current distribution (whether competitive exclusion by pheasants (Phasianidae) (Olson, 1980) or predation by mammalian carnivores (Felidae, Viverridae) (Dekker, 1989)). It is now generally agreed that the megapodes' unusual incubation strategy was acquired secondarily, following the development of typical avian incubation strategies in early birds (Clark, 1964a, 1964b; Dekker and Brom, 1992). For a current review of these and other topics on the biology, classification, and evolution of the Megapodiidae, see Jones et al. (1995).

The 22 or so extant species are classified in six or seven genera (Sibley and Monroe, 1990; del Hoyo et al., 1994; Jones et al., 1995), although relationships among genera of megapodes are unresolved. A division between the "scrubfowl" and the other taxa (Clark, 1964a, 1964b) has not been confirmed (Brom and Dekker, 1992), nor has the position of the fossil genus *Progura* De Vis, 1888, been examined. The brush-turkeys comprise three genera, *Alectura* (monotypic, endemic to Australia), *Talegalla* (three species), and *Aepypodius* (two species), with the last two restricted to New Guinea. The single species of malleefowl, *Leipoa,* occurs only in Australia. Among the scrubfowl and their relatives, there are two monotypic genera: *Macrocephalon,* restricted to Sulawesi, Indonesia, and *Eulipoa* (Moluccas and Misool Island), which is often merged with *Megapodius. Megapodius* has the widest distribution, occurring in Australia and New Guinea, east to Tonga (with prehistorically extinct Holocene forms from as far as Samoa), north to the Philippine Islands and the Palau and Mariana islands in Micronesia, and west through Sulawesi and Lombok, Indonesia, with isolated populations on the Nicobar Islands. *Megapodius* also is the most diverse genus, with nine to 13 living species, depending on taxonomy (e.g., Peters, 1934; Sibley and Monroe, 1990; del Hoyo et al., 1994; Roselaar, 1994; Jones et al., 1995).

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The range of body sizes in the megapodes varies from the extinct *Progura gallinacea* De Vis (1888) of Australia, which reached the size of a turkey (*Meleagris*), to *Megapodius laperouse* of Micronesia, the smallest described species (28–30 cm). Steadman (1993a) reported an extinct, as yet undescribed species of *Megapodius* from the late Quaternary of 'Eua, Tonga, which was smaller than any other known megapode. The earliest known fossil occurrence of the Megapodiidae is from the Pliocene (Boles and Mackness, 1994); most records are from the Pleistocene. Because of its age and diminutive size, a recently identified megapode from late Oligocene deposits of central Australia, outside the current distribution of this family, is of considerable interest.

FOSSIL RECORD OF MEGAPODES

Mourer-Chauviré (1982) initially indicated the presence of the Megapodiidae in the Eocene-Oligocene deposits of Quercy, France. Later she regarded these as belonging to a more primitive family of galliforms, the Quercymegapodiidae (Mourer-Chauviré, 1992), consisting of the single genus *Quercymegapodius,* which she created for *Palaeocryptonyx depereti* Gaillard (1908), and a new species, *Q. brodkorbi* Mourer-Chauviré (1992). This family was interpreted as being the sister group of all the living Galliformes. Excluding the Quercymegapodiidae, there are no known occurrences of fossil megapodes outside Australia and the islands of the southwest Pacific.

The Pleistocene record of megapodes is dominated by the fossil genus *Progura. Progura gallinacea* was originally described by De Vis (1888) as a large pigeon. Van Tets (1974) recognized that the specimens belonged to a megapode larger than any living species. Additional material identified by De Vis as pigeons, as well as material he identified as storks or as bustards, also was included in this taxon (van Tets, 1974; van Tets and Rich, 1990). Specimens of a smaller but related form were described as *P. naracoortensis* by van Tets (1974), to which were referred fossils that previously had been attributed to *Alectura lathami* (Lydekker, 1891; Longman, 1945). It was later suggested (van Tets, 1984) that the two taxa of *Progura* actually represented a single, sexually dimorphic species. The only other Australian species in the fossil record is *Leipoa ocellata,* which has been recovered from late Pleistocene deposits in South Australia (van Tets, 1974). The only Tertiary records come from the Pliocene of Australia. De Vis (1889) described the fossil megapode *Chosornis praeteritus* from Chinchilla, Queensland, which van Tets (1974) later placed in the synonymy of the Pleistocene species *Progura gallinacea.* Boles and Mackness (1994) reported on the presence of *P.* cf. *naracoortensis* at Bluff Downs, Queensland.

A variety of fossil species of *Megapodius,* mostly extinct forms, are known from South Pacific islands from New Caledonia (Balouet and Olson, 1989) eastward into Polynesia (Steadman, 1989, 1993a, 1993b, 1995; see also Jones et al., 1995). Most of these sites are of Holocene age, and most or all of the extinctions were anthropogenic.

The enigmatic *Sylviornis neocaledoniae* of New Caledonia was first described as a ratite (Poplin, 1980) but later was considered to be a large, flightless megapode (Poplin and Mourer-Chauviré, 1985). Balouet and Olson (1989) and C. Mourer-Chauviré (pers. comm., 1996) believe that that *Sylviornis* belongs to the Galliformes but is best placed in its own family.

METHODS.—Measurements mostly follow those of Steadman (1980) and were made with digital calipers and rounded to the nearest 0.1 mm. Osteological nomenclature follows Baumel and Witmer (1993); taxonomic nomenclature for the Megapodiidae follows Jones et al. (1995). Comparisons were made with representatives of all extant genera of megapodes (*Macrocephalon maleo, Eulipoa wallacii, Alectura lathami, Leipoa ocellata, Talegalla jobiensis, T. fuscirostris, Aepypodius arfakianus, A. bruijni, Megapodius reinwardt, M. freycinet, M. eremita, M. pritchardi, M. cumingii, M. nicobarensis*) as well as with *Progura gallinacea.*

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Systematic Paleontology

Order GALLIFORMES

Family MEGAPODIIDAE

Because of the gracility of the trochleae of the tarsometatarsus described herein compared with those of some other megapodes, the Pinpa fossil bears a superficial resemblance to the tarsometatarsus of a medium-sized pigeon, such as the Wonga Pigeon, *Leucosarcia melanoleuca* Latham. Rich et al. (1991) originally placed it in the Columbidae, which is understandable because there are superficial similarities between the tarsometatarsus in these two families, as shown by De Vis's (1888) original description of the fossil megapode *Progura gallinacea* as a relative of the crowned pigeons (*Goura*). Van Tets (1974) discussed characters that differentiate the two groups.

The tarsometatarsus in the Megapodiidae may be identified by the following combination of characters: three cristae hypotarsi (medialis large) and four sulci hypotarsi (medialis broad), only one of which is enclosed; distal extension of crista medialis hypotarsi along the shaft flat and virtually absent; shaft dorsoplantarly compressed; depression on plantar face; fossa metatarsi I distinct; and trochleae metatarsi II and IV with equal distal extension. This suite of features separates the Megapodiidae from other living and most extinct Galliformes. The fossil and other Megapodiidae differ from the Quercymegapodiidae by having the crista metatarsi medialis projecting further plantarly, trochlea metatarsi II not globular, and trochleae metatarsi II and IV with equal distal extension (characters from Mourer-Chauviré, 1992). In species of the Gallinuloididae the depression on the plantar surface is more extensive than in the Megapodiidae.

The Megapodiidae also differ from the Columbidae by lacking an indentation on the medial border of the shaft distal to the fossa metatarsi I and by having the sulcus hypotarsi in the same dorsoplantar line as the eminentia intercondylaris (in proximal view) rather than offset laterally; also, the trochlea metatarsi II is more in the same lateromedial line as trochleae metatarsi III and IV (in distal view) instead of being recessed plantarly and rotated medially.

The fossil exhibits a suite of characters unlike those found in other genera of the Megapodiidae, for which reason it is recognized as a new genus.

Ngawupodius, new genus

TYPE SPECIES.—*Ngawupodius minya*, new species, by original designation and monotypy.

ETYMOLOGY.—*Ngawu*, in South Australia an Aboriginal name for the Malleefowl *Leipoa ocellata* (see Peter and Peter, 1993), and *-podius*, Latinized Greek, "footed," in allusion to the similarities between the tarsometarsi of these taxa.

DIAGNOSIS.—The proximal end is medially flared less than in *Megapodius* or *Progura* but is more so than in *Alectura*. The shape and size of the cotyla medialis are about the same as the cotyla lateralis in proximal view; the dorsal rim is not produced as far dorsally, and the medial rim is thin, unlike the conditions in *Leipoa* or *Alectura*. The sulcus hypotarsi is proportionally small in proximal view compared with all the modern taxa. The robustness of the lateral side of the hypotarsus in proximal view is blocky, unlike that in *Megapodius*. The plantar extension of the crista medialis hypotarsi is greater than in *Alectura, Talegalla, Aepypodius,* or *Macrocephalon* but is less than in *Megapodius, Eulipoa,* or *Leipoa*. The relative plantar extension of the crista lateralis hypotarsi differs from that in *Alectura, Talegalla, Aepypodius,* or *Progura* in being about one-half that of the crista medialis. The distally projecting process on the distal end of the hypotarsus is smaller than that in *Megapodius*. The dorsoventral compression of the shaft is greater than in *Talegalla* or *Aepypodius*. The sides of the shaft are relatively parallel and do not widen toward the distal end, unlike *Alectura, Leipoa, Aepypodius, Talegalla, Macrocephalon,* or *Progura*. The relative development of the tuberositas M. tibialis cranialis is shorter in the fossil than in the modern forms. The fossa metatarsi I is not as distinct as in *Megapodius, Leipoa,* or *Progura* and has little medial extension. The trochleae are gracile and are not swollen as in the other genera, particularly *Megapodius*. The trochlea metatarsi II is at the same level as the trochlea metatarsi IV, rather than slightly above, when viewed either distally (unlike *Megapodius, Leipoa,* or *Talegalla*) or dorsally (unlike *Megapodius, Leipoa, Aepypodius,* or *Progura*). The trochlea metatarsi II is neither inflated nor globular as it is in *Megapodius* or *Eulipoa*, and it does not diverge strongly medially, unlike *Alectura, Leipoa, Aepypodius, Talegalla, Macrocephalon,* or *Progura*. The trochlea metatarsi IV does not project laterally, unlike *Megapodius* or *Eulipoa*. The articular groove of the trochlea metatarsi IV is moderately well developed, more so than in *Alectura, Leipoa, Aepypodius, Talegalla,* or *Progura*, but is less distinct than in *Megapodius*.

Ngawupodius minya, new species

FIGURE 1A–C

HOLOTYPE.—Complete right tarsometatarsus, Paleontology Collection of the Museum of Victoria (MV), Melbourne, P160493. Collected by I. Parker on 12 May 1979.

TYPE LOCALITY.—South end of Lake Pinpa, South Australia (31°08′31″S, 140°12′47″E; T.H. Rich, pers. comm., 1996).

HORIZON.—Namba Formation, Ericmas Fauna, late Oligocene.

ETYMOLOGY.—*Minya*, in South Australia an Aboriginal word for "small" (Reed, 1977); for the purposes of nomenclature, *minya* should be considered to be without gender.

DIAGNOSIS.—As for the genus.

DESCRIPTION.—The fossil is from an adult bird because the surface lacks porosity, the tarsal cap is completely fused to the proximal end of the metatarsals, the hypotarsus is fully formed, and the metatarsals are fully fused over their entire length. In immature *Leipoa ocellata*, the tarsometatarsi may approach the size in that of adult birds yet still be highly porous and incompletely fused.

Total length 40.2 mm; proximal width 8.1 mm; distal width 9.5 mm; distal depth 5.7 mm. Eminentia intercondylaris low, about same height as rim of cotyla medialis; both higher than rim of cotyla lateralis. Depth of crista hypotarsi medialis about one-half that of proximal end of bone (proximal depth to hypotarsus 4.4 mm; proximal depth with hypotarsus 8.0 mm), with laterally directed projection at end. In proximal view, sulcus medialis hypotarsi slightly laterad of eminentia intercondylaris, three shallow sulci lateralis hypotarsi and two low cristae lateralis hypotarsi on rather square hypotarsus. In lateral view, hypotarsus short (5.1 mm). Ridge extending distally from hypotarsus on facies plantaris very low. Shaft broad (midshaft width, 4.3 mm; shaft width at proximal edge of fossa metatarsi I, 4.5 mm) but dorsoplantarly flattened (midshaft depth, 2.6 mm; shaft depth at proximal edge of fossa metatarsi I, 2.8 mm), markedly so on medial side; lateral margin straight, medial margin somewhat concave distally to fossa metatarsi I; distal to fossa produced more medially. Fossa metatarsi I elongate (5.8 mm). Fos-

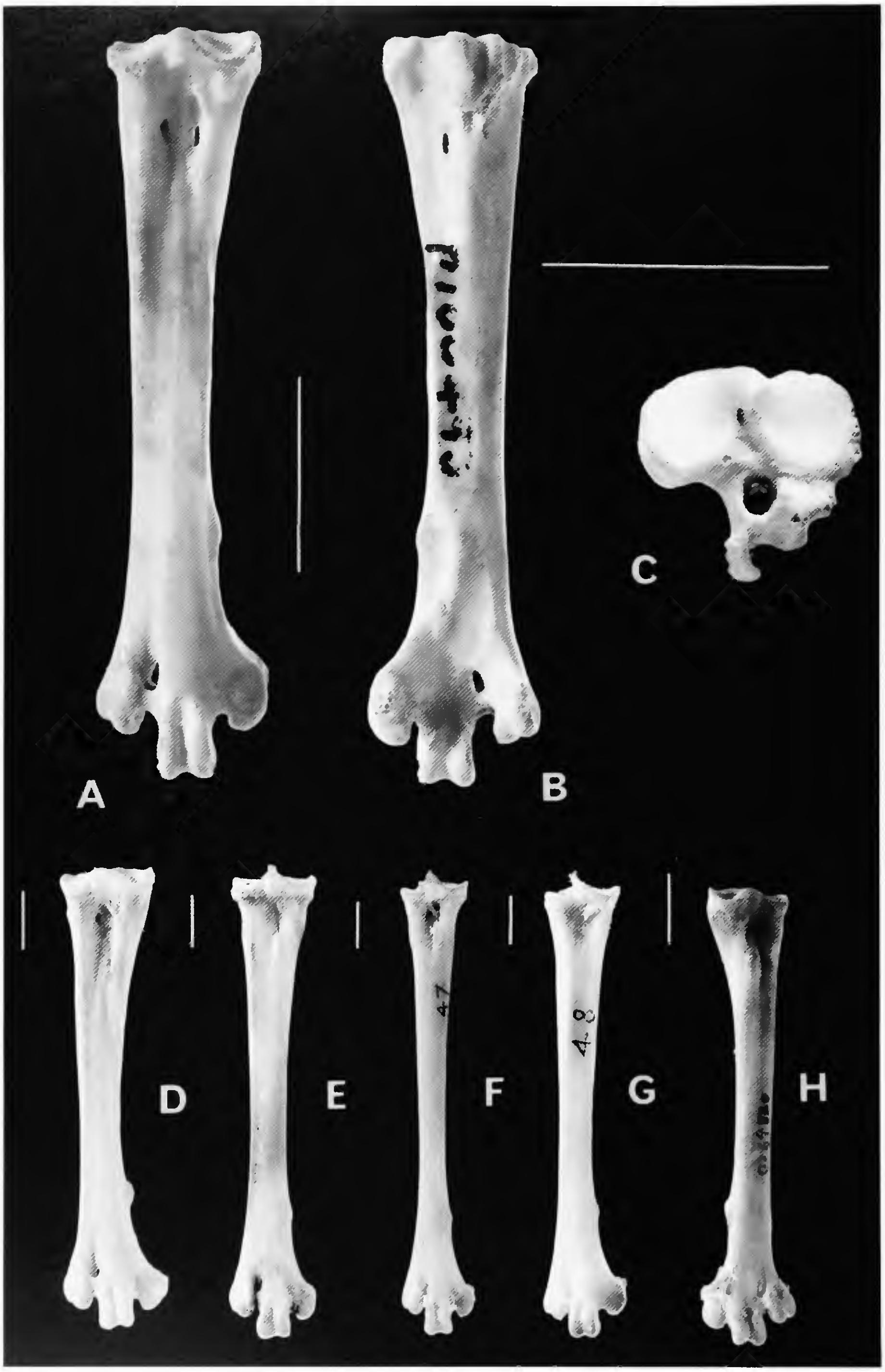

FIGURE 1.—Tarsometatarsus of fossil and recent megapodes. A–C, *Ngawupodius minya* (holotype, MV P160493), dorsal, plantar, and proximal views, respectively. D–H, dorsal views, recent species: D, *Leipoa ocellata;* E, *Alectura lathami;* F, *Aepypodius arfakianus;* G, *Talegalla jobiensis;* H, *Megapodius reinwardt.* Bars = 10 mm.

sa supratrochlearis plantaris shallow, extending from between trochleae on distal end of plantar surface proximally to about proximal end of facet. Trochlea metatarsi II strongly divergent, trochlea metatarsi IV less so; distal and plantar extensions about equal; articular grooves obsolete. Trochlea metatarsi III about twice as long as other trochleae, strongly grooved.

The fossil is larger than the known tarsometatarsal specimens of *Quercymegapodius* (*Q. depereti:* total length 30.0 mm, distal width 5.8 mm, distal depth 3.75 mm; Mourer-Chauviré, 1992).

Discussion

GEOGRAPHIC SETTING AND GEOLOGY

Northeastern South Australia has produced a number of important fossil sites, ranging in age from Oligocene-Miocene to Pleistocene, many of which have yielded avian remains. The fossil megapode was recovered from Lake Pinpa, one of several localities in the Tarkarooloo Basin where outcrops of the Namba Formation are exposed. The formation is divisible into two members, the upper resting disconformably on the lower. Green claystones and dolomitic claystones at the top of the lower member have yielded vertebrate remains designated as the Pinpa Fauna. A sequence of thin-bedded, fine- to medium-grained sands cut into the lower member, and it is these basal sands of the upper member that have produced the Ericmas Fauna (type locality Ericmas Quarry, Lake Namba; 31°12'S,140°14'E), from which the megapode bone was recovered. For details of the geology, dating, and other vertebrate remains, see Callen and Tedford (1976), Tedford et al. (1977), Woodburne et al. (1985), and references therein.

The age of the Ericmas Fauna was originally placed at middle Miocene on the basis of its position above the Pinpa Fauna, and, where there are comparable species, species in the Ericmas Fauna appear less primitive. The lower member of the Namba Formation contains pollen floras similar to Balcombian-Batesfordian (middle Miocene) deposits in Victoria and South Australia. Tedford et al. (1977) put a maximum age of ca.14–16 Ma on vertebrates higher in the formation. Woodburne et al. (1985) considered the Ericmas Fauna to be middle Miocene in age. Subsequent work, however, has led to a revision of these dates. Studies on the central Australian Etadunna Formation (East Lake Eyre Basin), considered to be roughly contemporaneous with the Namba Formation, led Woodburne et al. (1993) to place its age at late Oligocene. These authors considered the Ditjimanka Fauna (Lake Palankarinna) from the Etadunna Formation and the Ericmas Fauna to be "approximate correlatives" (ca. 24–26 Ma).

The Lake Pinpa site, like most others in central Australia, is characterized by lacustrine/fluviatile deposits. The bones have been disarticulated post-mortem and have been transported varying distances. The faunal summary by Rich et al. (1991) showed that there was a large aquatic component, represented by several species of lungfish (*Neoceratodus*), teleost fish, chelid turtles, crocodiles, the primitive platypus *Obdurodon insignis* Woodburne and Tedford (1975), and a dolphin (Rhabdosteidae). Terrestrial forms included marsupials of the families Dasyuridae, Phascolarctidae, Diprotodontidae, Pseudocheiridae, and Petauridae. The only other bird thus far reported was assigned to the Anseriformes (Rich et al., 1991) and has not yet been studied. In contrast, the Pinpa Fauna has abundant bird remains, including grebes, pelicans, cormorants, waterfowl, rails, burhinids, and flamingos.

RECONSTRUCTION OF *Ngawupodius* AND ITS ENVIRONMENT

Living megapodes were used as the basis of an attempt to reconstruct the general size and proportions of *Ngawupodius.* Because skeletons of certain taxa were not available, published tarsal measurements from skins were substituted; these give close approximations of the length of the tarsometatarsus. Weights and body lengths are less precise measurements but can serve as approximate indicators of size and permit some rough values to be obtained; data were taken from Marchant and Higgins (1993), Jones et al. (1995), and specimens.

The tarsometatarsus of *Ngawupodius* is smaller in absolute terms than those of other described taxa (Table 1; Figure 1). It

TABLE 1.—Measurements (mm) of the tarsometatarsus in *Ngawupodius minya* and recent species of megapodes, giving mean ($\bar{x}$), range, and sample size (*n*).

Species	Total length			Proximal width			Distal width			Midshaft width		
	$\bar{x}$	range	*n*	$\bar{x}$	range	*n*	$\bar{x}$	range	*n*	$\bar{x}$	range	*n*
Ngawupodius minya	40.2	–	1	8.1	–	1	9.5	–	1	4.3	–	1
Megapodius reinwardt	59.8	–	1	10.6	–	1	12.2	–	1	4.5	–	1
Megapodius eremita	64.6	–	1	11.9	–	1	13.7	–	1	5.2	–	1
Megapodius freycinet	69.2	–	1	12.7	–	1	14.0	–	1	5.4	–	1
Megapodius pritchardi	58.6	58.1–59.0	2	9.2	9.0–9.4	2	10.8	10.8	2	3.9	3.8–3.9	2
Megapodius cumingii	67.0	61.1–72.8	2	11.6	10.3–12.9	2	13.5	12.2–14.8	2	5.4	4.6–6.1	2
Megapodius nicobarensis	68.2	–	1	12.9	–	1	14.3	–	1	5.9	–	1
Eulipoa wallacii	61.2	–	1	10.2	–	1	12.3	–	1	4.5	–	1
Macrocephalon maleo	87.6	86.6–88.6	2	16.0	15.9–16.0	2	16.7	16.1–17.2	2	6.2	6.0–6.3	2
Alectura lathami	96.9	88.2–103.3	5	17.6	16.5–18.6	5	18.1	16.5–18.7	6	7.3	7.1–7.7	3
Talegalla jobiensis	87.7	85.0–90.4	2	14.8	14.7–14.8	2	16.3	15.4–17.1	2	6.3	5.8–6.7	2
Talegalla fuscirostris	–	–	–	–	–	–	16.0	–	1	5.3	–	1
Aepypodius bruijni	108.4	–	1	16.2	–	1	17.9	–	1	6.8	–	1
Aepypodius arfakianus	97.0	–	1	14.8	–	1	16.0	–	1	6.2	–	1
Leipoa ocellata	75.3	71.2–76.7	3	15.9	15.3–16.3	3	17.5	16.1–18.3	3	6.8	6.5–7.1	2
Progura gallinacea	–	–	–	25.5	–	1	28.4	–	1	–	–	–

is about 80% of the external tarsal length of females of *Megapodius laperouse laperouse* (50–55 mm), the smallest living species of megapode. The proximal and distal widths of the tarsometatarsus of *Ngawupodius* are proportionally great compared to its total length: about 21% for both measurements, at the top of the range among megapodes (15%–21%). Likewise, *Ngawupodius* has a proportionally wide middle shaft (10.6% of total length, range of megapodes 6%–11%; 45% of distal width, 38%–45% in other species). In these proportions *Ngawupodius* resembles only *Leipoa* (Figure 1D). Comparisons with *Progura* are not possible from existing material. The structure and length of the tarsometatarsus in *Leipoa* may be related to its more open habitat, and the resemblances to *Ngawupodius* could be coincidental.

Given what is known of living species, a general range of size can be proposed for *Ngawupodius.* If it had disproportionally short legs, as in *Leipoa,* then it may have been similar in body length and weight to the smallest species of *Megapodius.* If the leg proportions were more typical of the other megapodes, then estimates of about 225–235 mm overall length and 230–330 g are reasonable. The small, undescribed species of *Megapodius* from 'Eua, Tonga, appears to have been of comparable size to *Ngawupodius minya* (D. Steadman, pers. comm., 1996).

On the basis of pollen of grasses and subtropical rainforest flora from the lower member of the Namba Formation, Tedford et al. (1977:56) suggested a paleohabitat of "riparian forests with savannas on better drained fluviatiles." Some related but specifically distinct mammals in the faunas of the two members were inferred by Tedford et al. (1977) to indicate that the division between them recorded both a change in the depositional environment and a significant time gap. If the general vegetation in the upper member remained much the same as that suggested by the pollen from the lower member, then it is tempting to envisage a situation much like that in northern Australia today. The Orange-footed Scrubfowl, *Megapodius reinwardt,* frequents riparian forests bordered by tropical savanna woodland. *Ngawupodius* may have occupied a similar habitat in the Oligocene environment of Lake Pinpa.

The extinction of *Ngawupodius* was neither through competition with pheasants nor predation by felids. The only phasianids known from the Australian fossil record or occurring in a natural state in Australia today are small quail of the genus *Coturnix* (up to 120 g). These are too small to compete actively with megapodes, even *Ngawupodius. Coturnix* is known from other late-Oligocene-aged central Australian sites, although not Lake Pinpa. Pheasants, partridges, or other galliforms of a size comparable to any of the megapodes are not known from Australia. Likewise, the Felidae and Viverridae do not occur in Australia, and there is no evidence that marsupial carnivores have a particularly deleterious effect on megapode populations. Marsupial carnivores were well represented in Australia during the Oligocene and also have been found in the Ericmas Fauna (Dasyuridae).

If it left no descendants, the eventual extinction of *Ngawupodius* may be related to a changing environment. With the late Miocene drying of Australia, the wet forest vegetation that apparently was its habitat was lost from the center of the continent. Similar habitats are now restricted to parts of eastern and northern Australia. Other central Australian birds that were lost after these climatic alterations were aquatic forms (e.g., flamingos, Phoenicopteridae). It is not yet possible to verify the loss of other terrestrial birds because these are not well represented, and existing material has yet to be studied in any depth.

The morphology of *Ngawupodius* holds no clues to its relationships within the family; it shares osteological characters with most genera of megapodes. Until a complete phylogenetic analysis of the Megapodiidae is performed, the polarities of these characters will not be known. Likewise, whether *Ngawupodius* was ancestral to any of the living forms, and if so, how directly, cannot be determined. Similarities in proportions and its occurrence in central Australia raise the possibility that *Ngawupodius* may have been a direct ancestor of *Leipoa.* Conversely, *Ngawupodius* may have represented a distinct lineage within the family. There is general agreement that, regardless of their center of origin, megapodes were isolated in Australo-Papua for an extended period, which we know now to extend at least to the late Oligocene, *Ngawupodius* being the oldest known member of the Megapodiidae.

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A New Genus and Species of the Family Jungornithidae (Apodiformes) from the Late Eocene of the Northern Caucasus, with Comments on the Ancestry of Hummingbirds

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ABSTRACT

Argornis caucasicus, a new genus and species of the family Jungornithidae (Apodiformes), is based on an incomplete, articulated skeleton of the shoulder girdle and wing from the late Eocene of the northern Caucasus. The holotype includes the manus, which was previously unknown in the Jungornithidae. In comparison with early Oligocene *Jungornis,* the new form is less advanced evolutionarily, and, in particular, it lacks certain characters shared by *Jungornis* and the Trochilidae. An emended diagnosis of the family Jungornithidae is given. Taking into account that both *Jungornis* and *Argornis* possess an apodid-like deltopectoral crest, revealing their highly developed ability for gliding flight, the appearance of trochilid-like features in *Jungornis* demonstrates a real possibility that hovering specializations developed from gliding adaptations. This conclusion conforms with the results of a comparative analysis of the transformation of forelimb muscles in three modern apodiform families.

Introduction

Jungornis tesselatus Karhu, 1988, a bizarre Paleogene apodiform referred to its own family, was described from an incomplete, articulated skeleton of the shoulder girdle and forelimb from the early Oligocene of the northern Caucasus. The second genus and species of the family Jungornithidae described, *Palescyvus escampensis* Karhu, 1988, was based on a single coracoid from the late Eocene of the Phosphorites du Quercy, France, that Mourer-Chauviré (1978) had previously assigned to *Cypselavus gallicus* Gaillard.

The Jungornithidae possess features in common with such evolutionarily advanced families as the Apodidae and Trochilidae; the Jungornithidae also demonstrate a clear resemblance to the comparatively generalized apodiform family Hemiprocnidae, and even to the Caprimulgidae. An unusual combination of characters in the Jungornithidae, some of which are shared separately either with the Apodidae or with the Trochilidae, has been considered evidence in favor of the common origin of these three families (Karhu, 1988, 1992a, 1992b). Further investigation of the apodiform flight apparatus has revealed, in particular, that an important part of the morphofunctional specializations in hummingbirds represents subsequent stages of development from the apodid-like adaptations (Karhu, 1992a). This contradicts the principal conclusion of Cohn (1968) that the similarity between the true swifts and hummingbirds is the result of convergence.

In 1993, a new genus and species of jungornithid, described herein, was found in a late Eocene locality, Gorny Luch, northern Caucasus, that has yielded an abundant marine ichthyofauna (Bannikov, 1993). This discovery provides important data concerning the morphological specialization of the flight apparatus in the Jungornithidae. Taking into account the essential similarities between the Jungornithidae and Trochilidae, an older example of the former family may shed light on the early evolution of hummingbirds.

METHODS.—Comparative study of the forelimb muscles in modern Apodiformes is very important for analysis of evolutionary trends. The forelimb muscles of the following species were studied (number of specimens is in parentheses): Hemiprocnidae: *Hemiprocne mystacea* (1), *Hemiprocne comata* (1); Apodidae: *Collocalia lowi* (1), *Hirundapus caudacutus* (1), *Chaetura pelagica* (1), *Chaetura brachyura* (1), *Apus apus* (4), *Apus pacificus* (1); Trochilidae: *Chlorostilbon ricordii* (1), *Chlorostilbon* sp. (1), *Heliomaster longirostris* (1), and *Papho-*

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sia helenae (1). Muscle dissections were stained by the method of Bock and Shear (1972), and magnifications from ×8 to ×50, mainly ×16 and ×25, were used. The analysis of forelimb muscles also utilizes data from Cohn (1968) and from Zusi and Bentz (1982, 1984). This paper presents a brief summary of the unpublished results of the investigation of the forelimb muscles in apodiforms (Karhu, 1992a) (see "Forelimb Muscles: Tendencies of Transformation," below).

Anatomical terminology used in the descriptions generally follows Baumel et al. (1993).

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Systematic Paleontology

Order APODIFORMES

Suborder APODI

Family JUNGORNITHIDAE

TYPE GENUS.—*Jungornis* Karhu, 1988.

EMENDED DIAGNOSIS.—Apex carinae moderately developed. Facies articulares coracoidei widely spaced and separated from rostri sterni. Sulci carinae well pronounced. Proc. acrocoracoideus claviculae placed along dorsal margin of scapus, being considerably narrower than scapus in dorsoventral dimension; concave facies articularis acrocoracoidea claviculae oriented caudolaterally. Facies articularis humeralis scapulae directed cranioventrally. Proc. acrocoracoideus between facies articularis clavicularis and impressio lig. acrocoracohumeralis stretched mediolaterally. Proc. lateralis coracoidei well pronounced, protruding noticeably laterad beyond level of angulus lateralis. Facies articularis sternalis coracoidei wide, with distinctly outlined angulus medialis projecting sternally approximately to same level as angulus lateralis. Caput humeri directed caudally. Crista deltopectoralis high and proximally placed. Proc. supracondylaris dorsalis distally placed. Proximoventral border of cotyla ventralis ulnae not pronounced. Phalanx proximalis digiti majoris bifenestrated.

INCLUDED GENERA.—*Jungornis* Karhu, 1988; *Palescyvus* Karhu, 1988; *Argornis,* new genus.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION.—Upper Eocene and lower Oligocene, northern Caucasus, Russia; upper Eocene, Phosphorites du Quercy, France.

REMARKS.—In comparison with the former diagnosis of the family Jungornithidae (Karhu, 1988), the emendation omits the presence of the distal enlargement of the middle of the caput humeri and the proximity of the tuberculum supracondylare ventrale and tuberculum M. pronator superficialis. It adds points concerning the development of proc. lateralis coracoidei, orientation of the caput humeri, position of proc. supracondylaris dorsalis, development of the proximoventral border of the cotyla ventralis ulnae, and fenestration of the proximal phalanx of the major digit.

Argornis, new genus

TYPE SPECIES.—*Argornis caucasicus,* new species.

DISTRIBUTION.—Upper Eocene; northern Caucasus, Russia.

ETYMOLOGY.—From the Greek *argos,* swift, and *ornis,* bird; the gender is masculine.

DIAGNOSIS.—Facies articularis acrocoracoidei claviculae lengthened mediolaterally. Acromion scapulae with cranial margin beveled laterally and crista lig. acrocoraco-acromiale well developed. Dorsal side of medial part of proc. acrococoracoideus forms high, caudally projecting crest, with mediolaterally narrow base. Facies articularis sternalis coracoidei saddle-shaped, with only medial part of crista ventralis protruding ventrad. Angulus lateralis of sternal facet projecting a little more distally than angulus medialis. Ventral part of caput humeri oriented perpendicularly to long axis of bone, whereas dorsal part oriented obliquely to it, being placed more distally relative to ventral part; distal border of caput humeri clearly outlined. Tuberculum M. tensor propatagialis pars brevis well pronounced and placed just distal to proc. supracondylaris dorsalis humeri. Tuberculum M. pronator superficialis clearly detached from tuberculum supracondylare ventrale humeri. Tuberculum supracondylare ventrale adjoins condylus ventralis humeri. Epicondylus ventralis markedly prominent ventrad. Proc. flexorius projects slightly distally beyond condylus ventralis. Tuberculum lig. collateralis ventralis ulnae relatively small and weakly protruding ventrad. Tuberculum bicipitale brachii radii with impression of M. biceps brachii.

COMPARISON.—*Clavicula:* In *Argornis* the facies articularis acrocoracoidei is more elongated mediolaterally, narrower dorsoventrally, and directed more caudally than it is in *Jungornis,* in which it is a rounded, caudolaterally orientated facet. The overall configuration of the facies articularis acrocoracoidei is very unusual in both *Jungornis* and *Argornis* in comparison with other known Apodiformes, and it appears to be closest to that in the Caprimulgidae.

Scapula: The cranial margin of the acromion is strongly beveled laterally in *Argornis,* whereas in *Jungornis* the margin is thickened. The crista lig. acrocoraco-acromiale is well developed in *Argornis,* but it is not pronounced in *Jungornis.* In *Argornis* the facies articularis humeralis is relatively longer craniocaudally and wider dorsoventrally in comparison with *Jungornis.*

Coracoid: The overall configuration is close to that in *Jungornis.* In these genera the shaft is relatively slender, and the mediolateral width of the processus acrocoracoideus exceeds the distance between the angulus medialis and the angulus lateralis of the sternal facet (Figure 3C,D), whereas in *Palescyvus* the shaft is stouter, and the acrocoracoid is narrower than the sternal facet in frontal aspect (Figure 3E). In *Argornis* the dorsal crest of the medial portion of the acrocoracoid protrudes caudally almost to the level of the middle of the dorsal aperture of the canalis triosseus, and the base of this crest does not reach laterally to the level of the medial border of the impressio lig. acrocoracohumerale. In *Jungornis* the crest projects much less caudad, and its base is relatively wider, extending laterad to the level of the medial edge of the impression mentioned above. In *Palescyvus* the medial portion of the acrocoracoid curves strongly caudally but lacks a pronounced dorsal crest. The base of the proc. procoracoideus is relatively wider in *Argornis* in comparison with either *Jungornis* or *Palescyvus.* The facies articularis sternalis is saddle-shaped in *Argornis* but is concave in *Jungornis.* In *Argornis* only the medial part of the crista ventralis of the sternal facet protrudes ventrad, whereas in *Jungornis* the entire crista ventralis forms a ventral convexity. The ratio of the greatest dorsoventral width of the sternal facet to the distance between the angulus medialis and angulus lateralis is smaller in *Argornis* than it is in *Jungornis.* The angulus medialis is rounded in *Argornis* and in *Palescyvus,* whereas in *Jungornis* it is moderately sharpened. The angulus lateralis projects slightly distad beyond the level of the angulus medialis in *Argornis;* in *Jungornis* and *Palescyvus* the angulus medialis and angulus lateralis are placed approximately on the same level (Figure 3C–E).

Humerus: In *Argornis* the humeral shaft is more slender, and both the proximal and distal ends are relatively narrower in comparison with *Jungornis* (Figure 2E–G,R). The smaller, ventral part of the caput humeri is situated perpendicularly to the long axis of the bone in *Argornis,* unlike in *Jungornis,* in which the entire caput humeri is transversely placed (Figure 2H,R). There is no distal enlargement of the middle of the caput humeri on the facies caudalis in *Argornis* as there is in *Jungornis.* In *Argornis* the clearly pronounced tuberculum of M. tensor propatagialis pars brevis adjoins distally the base of the proc. supracondylaris dorsalis. This process in *Jungornis* is adjoined distally by a high thin crest, and the insertion of M. tensor propatagialis pars brevis is not marked. Tuberculum M. pronator superficialis is low and is clearly separated from the tuberculum supracondylare ventrale in *Argornis,* whereas in *Jungornis* the former protrudes strongly proximad and fuses with the proximal part of the tuberculum supracondylare ventrale. In *Argornis* the tuberculum supracondylare ventrale adjoins the base of the condylus ventralis ventroproximally, but in *Jungornis* it is placed more proximally and is well separated from the base of the condylus ventralis. In *Argornis* the condylus ventralis projects distad beyond the condylus dorsalis, whereas the distal borders of both condyli are placed on the same level in *Jungornis.* In *Argornis* the epicondylus ventralis protrudes strongly ventrad, is widened proximodistally, and is fused distally with the proc. flexorius, unlike the much smaller and detached epicondylus ventralis of *Jungornis.* The proc. flexorius projects distad less in *Argornis* than in *Jungornis.*

Ulna: In *Argornis* the tuberculum lig. collaterale ventrale is smaller and protrudes less ventrad in comparison with *Jungornis.*

Radius: In contrast to *Jungornis,* there is an impression of M. biceps brachii on the ventrocranial surface of the tuberculum bicipitale brachii in *Argornis.*

REMARKS.—An extremely peculiar morphology of the sternocoracoidal articulation is among the most characteristic features of the Apodiformes sensu Wetmore, 1960 (Lucas, 1893; Lowe, 1939; Cohn, 1968; Karhu, 1988, 1992a). In the Apodiformes, the sternum possesses a weakly saddle-shaped or convex facies articularis coracoidei instead of the coracoidal sulcus of most birds. Consequently, the coracoid has a more or less dorsoventrally widened facies articularis sternalis that is slightly saddle-shaped, or concave, and placed on the whole perpendicularly to the long axis of the bone. There is a single exception: in *Aegialornis* the coracoid has the sternal facet ventrally widened near the angulus medialis, whereas its greater part is wedge-shaped in dorsoventral section, as is typical for most birds.

The structure of the sternal facet of the coracoid is considerably more generalized in *Argornis* in comparison with *Jungornis.* In *Jungornis* the overall configuration of the facies articularis sternalis is apodid-like, with the entire ventral margin convex ventrad but to a lesser degree than in true swifts. In *Argornis* the coracoid possesses a facies articularis sternalis that is widened by a ventral prominence in its medial part only, which is similar to the most generalized type within Apodiformes as demonstrated by *Aegialornis. Argornis* differs from *Aegialornis,* however, in having the dorsal edge of the sternal facet situated much more sternally (Figure 3A,C).

The other relatively generalized character of the coracoid in *Argornis* is the placement of the angulus lateralis slightly beyond the level of the angulus medialis (Figure 3C). In *Jungornis* and *Palescyvus* the angulus lateralis and angulus medialis are on the same level relative to the long axis of the bone (Figure 3D,E), which was pointed out as a distinctive familial character in the former diagnosis of the Jungornithidae (Karhu, 1988). In the Hemiprocnidae and Apodidae, as well as in the Eocene genus *Aegialornis,* the angulus lateralis protrudes considerably more sternally than does the angulus medialis (Figure 3A,B,F).

All three known genera of the Jungornithidae are clearly distinguished from other fossil and modern Apodiformes by the presence of a well-developed proc. lateralis in the sternal part of the coracoid (Figure 3).

In caudal aspect, the overall configuration of the caput humeri in *Argornis* is most similar to that in *Hemiprocne:* the smaller ventral part of the head is placed approximately perpendicular to the long axis of the bone, whereas its greater part is placed obliquely and more distally relative to the ventral part of the head. At the same time, *Argornis* differs from *Hemiprocne* in having the caput humeri directed mainly caudally, in contrast to *Hemiprocne* in which it is directed apically. Both *Argornis* and *Jungornis* have a relatively distally placed proc. supracondylaris dorsalis, similar to that in *Aegialornis.* In comparison with other Apodiformes, *Argornis* possesses the most distally situated tuberculum supracondylare ventrale, revealing a tendency toward the proximal displacement found in all apodiform families.

In *Argornis* and *Jungornis* the cotyla ventralis ulnae has a slightly pronounced ventroproximal edge. The Trochilidae possess a similar structure of the cotyla ventralis in this regard, whereas in the Hemiprocnidae and Apodidae its ventroproximal edge is well marked.

Argornis caucasicus, new species

FIGURES 1, 2A–P, 3C

HOLOTYPE.—Incomplete, partially crushed articulated skeleton including the vertebral column, shoulder girdle, and forelimbs; Paleontological Institute of the Russian Academy of Sciences, PIN 4425-18.

TYPE LOCALITY.—Gorny Luch, left bank of Pshekha River, northern Caucasus, Russia.

HORIZON.—Kuma (Kumsky) horizon, upper Eocene (Bannikov, 1993).

MEASUREMENTS (in mm).—Clavicle, minimum width 0.5, maximum width 0.9; scapula, dorsoventral width of cranial end 2.4; coracoid, length 10.0, diameter of midshaft 0.9 by 1.0, mediolateral width of sternal end 2.6, dorsoventral width of sternal end 1.2, distance between tips of angulus medialis and angulus lateralis 1.8; humerus, length 10.4, proximal dorsoventral width 4.1, distal dorsoventral width 3.3; ulna, length 16.0; radius, length 15.1, diameter of midshaft 0.5 by 0.7; carpometacarpus, length 11.6, craniocaudal width through extensor process 3.8, craniocaudal width of midshaft of major metacarpal 1.1; proximal phalanx of major digit, length through articular surfaces 6.4, maximum length 7.2, craniocaudal width at middle 2.4; distal phalanx of major digit, length 6.3; phalanx of minor digit, length 3.0.

Judging from the length of the coracoid, A. *caucasicus* may have been approximately the same overall size as *Palescyvus escampensis,* which has a coracoid 10.1 mm long (Harrison, 1984, table 2), although in *A. caucasicus* the coracoid is somewhat more slender, suggesting smaller body size. *Argornis caucasicus* noticeably exceeds *Jungornis tesselatus* in all corresponding measurements.

ETYMOLOGY.—After Caucasus, the geographic area of the type locality.

DESCRIPTION.—Remains of the vertebral column, sternum, and ribs are too fragmentary and badly damaged for description of their features.

Clavicula: The scapus claviculae is flattened mediolaterally and smoothly widened toward the extremitas omalis. The transition between the clavicular shaft and the proc. acromialis is not pronounced. The proc. acrocoracoideus protrudes strongly laterad, its base approximately one-half the dorsoventral width of the clavicular shaft. The facies articularis acrocoracoideus is flattened dorsoventrally and is concave mediolaterally.

Scapula: The acromion protrudes a little beyond the level of the cranial border of the tuberculum coracoideum. The dorsal margin of the acromial tip is curved laterad, with the crista lig. acrocoraco-acromiale short craniocaudally. The tuberculum coracoideum passes gradually into the proc. glenoidalis. The dorsocaudal part of the proc. glenoidalis protrudes strongly laterad. The facies articularis humeralis is widened ventrocaudad, being directed cranioventrally and turned slightly laterally.

Coracoid: The facies articularis clavicularis is convex. The well-marked cotyla scapularis is rounded and moderately concave. The proc. procoracoideus is long, its base stretches caudad almost to the level of the cranial border of the impressio M. sternocoracoidei. The foramen supracoracoidei, situated in the middle of the base of the procoracoid, opens ventrally into a groove that extends along the base. The sulcus supracoracoideus is well developed craniad of the level of the foramen supracoracoidei. The impression of M. supracoracoidei is deep and sharply outlined. The proc. lateralis is obtuse-angled in frontal aspect. The facies articularis sternalis is subdivided asymmetrically into a smaller medial and a larger lateral part by a saddle-like ridge that extends lateroventrad from the angulus medialis. The larger lateral part is concave in both mediolateral and dorsoventral dimensions.

Humerus: The tuberculum dorsale is displaced distad from the dorsal part of the caput humeri. The crista deltopectoralis is high and tapering, with a concave proximal edge. The tip of the crista deltopectoralis is approximately on the level of the middle of the impression of the tendon of M. supracoracoideus. The proc. supracondylaris dorsalis occurs about one-quarter of the length of the humerus from its distal end. The tuberculum M. pronator superficialis is placed approximately on the level of the tuberculum M. tensor propatagialis pars brevis. The sulcus intercondylaris is narrow and shallow. The proc. flexorius is blunt and widened dorsoventrally. The cranial surfaces of the tuberculum supracondylare ventrale and epicondylus ventralis are fused continuously, as are the cranial surfaces of the epicondylus ventralis and proc. flexorius. The fossa of M. brachia-

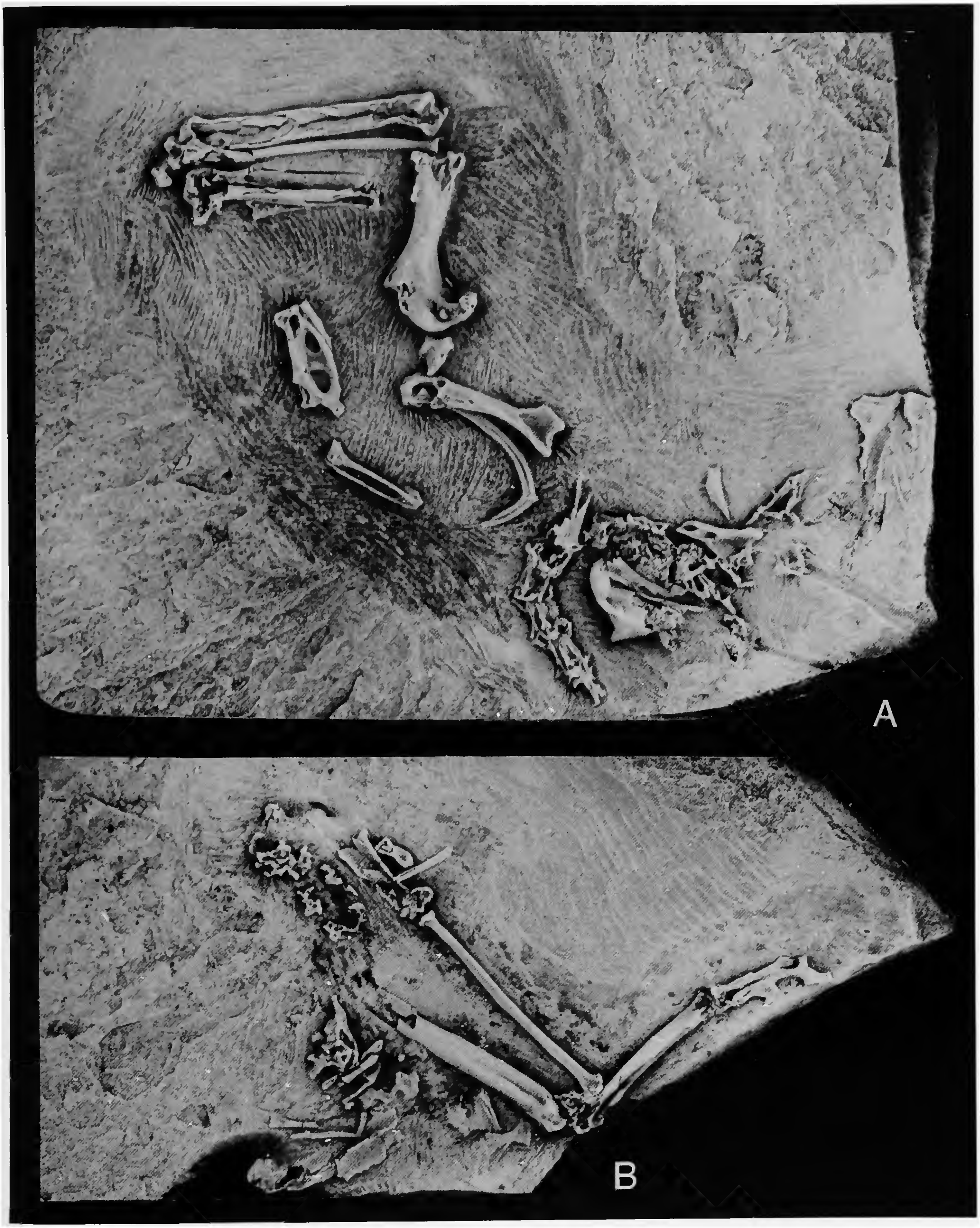

FIGURE 1.—*Argornis caucasicus*, new genus, new species, holotype (PIN 4425-18), partial skeleton: A,B, two complementary slabs (×3; specimen coated with ammonium chloride).

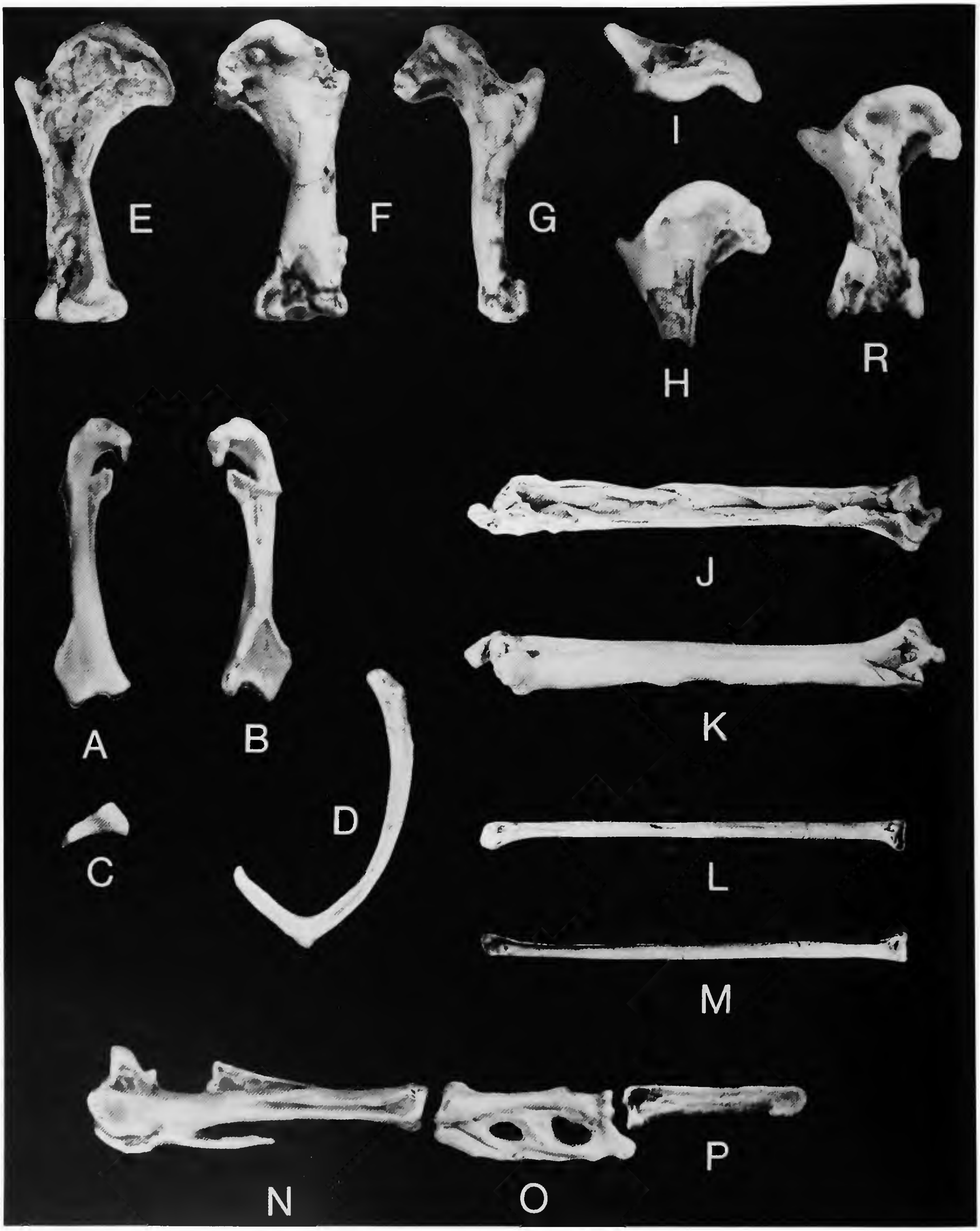

FIGURE 2.—Elements of shoulder girdle and forelimb (A–P) of *Argornis caucasicus,* new genus, new species (holotype, PIN 4425-18), and humerus (R) of *Jungornis tesselatus.* A–C, right coracoid in ventral (A), dorsal (B), and sternal (C) views; D, right clavicle with sternal part of left bone; E–G, right humerus in cranial (E), caudal (F), and dorsal (G) views; I,H, proximal part of left humerus in caudal (H) and proximal (I) views; J,K, right ulna in cranial (J) and caudal (K) views; L,M, right radius in dorsal (L) and ventral (M) views; N, right carpometacarpus and phalanx of alular digit, dorsal view; O, right proximal phalanx of major digit and phalanx of minor digit, dorsal view; P, right distal phalanx of major digit, dorsal view; R, left humerus of *Jungornis tesselatus* (holotype, PIN 1413-208), caudal view (×5; specimens coated with ammonium chloride).

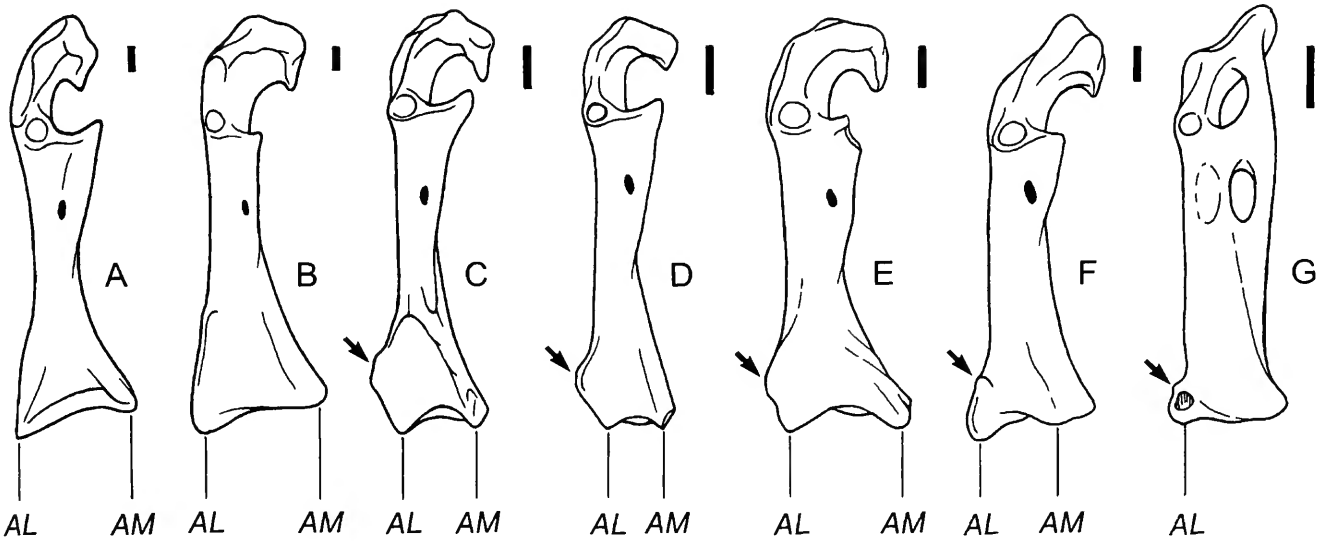

FIGURE 3.—Comparison of coracoid of Apodiformes: A, *Aegialornis gallicus;* B, *Hemiprocne mystacea;* C, *Argornis caucasicus,* new genus, new species; D, *Jungornis tesselatus;* E, *Palescyvus escampensis;* F, *Apus apus;* G, *Archilochus colubris.* AM=angulus medialis, AL=angulus lateralis. Arrows indicate proc. lateralis. Left side, dorsal view, standardized for comparison. (Scale=1 mm.)

lis is not pronounced. The sulcus of M. humerotricipitis is wide and shallow.

Ulna: The shaft is slender and straight. Both ends are relatively narrow. The olecranon is tapered, with a narrow base. The cotyla ventralis is shallow. The ridge separating the cotyla dorsalis and cotyla ventralis is low and smooth. The tuberculum bicipitale is located close to the distal border of the cotyla ventralis. There is a deep fossa for M. ulnometacarpalis ventralis on the caudoventral side of the proximal end.

Radius: The shaft is thin and slightly bowed craniad. Both ends are relatively narrow. The tuberculum bicipitale adjoins the ventral border of the cotyla humeralis.

Carpi ulnare: The proximal margin of the corpus is noticeably beveled, so that the proximal border of the facies articularis ulnaris lies much more distally than the base of the proc. muscularis.

Carpometacarpus: The metacarpale majus is slender, slightly bowed craniad, and beveled ventrocaudally. The protuberantia metacarpalis projects dorsally, is proximodistally elongated, and is placed somewhat distad to the middle of the craniodorsal surface of the major metacarpal. A well-developed sulcus tendinosus begins just proximocaudally of the protuberantia metacarpalis and passes distad and somewhat caudad, where it widens into a clearly outlined and relatively deep depression on the dorsal side of the distal end of the major metacarpal. There is a pronounced tuberculum of M. extensor metacarpi ulnaris on the caudal margin of the major metacarpal just opposite the distal border of the proximal symphysis. The cranial margin of the labrum dorsale of the trochlea carpalis bears the impression of M. ulnometacarpalis ventralis. The caudal margin of the facies articularis digitalis major is deeply concave. The distal part of metacarpale minus is absent in the holotype; however, the facies articulares metacarpales of the proximal phalanx of the major digit and of the minor digit are on the same level in the holotype, which suggests that corresponding facies articulares digitales major and minor also should be level relative to the long axis of the carpometacarpus.

Ossa digorum manus: The phalanx digiti alulae is damaged too badly to recognize any structural peculiarities.

Two large oval fenestrae of the phalanx proximalis digiti majoris are separated by a dorsally pronounced, obliquely oriented pila transversa. There is a well-developed proc. distalis on the caudal margin. The caudal edge of the facies articularis metacarpalis forms a deep middle concavity.

The phalanx distalis digiti majoris has a caudally enlarged proximal articulation and a caudally widened tip.

The phalanx digiti minoris is narrow and tapering. It curves along the caudal margin of the proximal phalanx of the major digit and extends to the level of the distal margin of the proximal fenestra. The facies articularis metacarpalis of phalanx digiti minoris is placed relative to the long axis of the manus on the same level as the metacarpal facet of the proximal phalanx of the major digit.

Forelimb Muscles: Tendencies of Transformation

Among the living Apodiformes, the most generalized configuration of the forelimb muscles is found in the Hemiprocnidae. The completeness of their set of forelimb muscles reveals a relatively low level of specialization. Many of their muscles demonstrate a comparatively simple inner structure. In particular, unlike the true swifts and hummingbirds, the crested swifts possess well-developed Mm. extensor longus alulae and ulnometacarpalis dorsalis. Both of these muscles usually sustain a reduction when the automatic conjunction of movements in the elbow and carpal joints becomes more efficient (Stegmann, 1970). The Hemiprocnidae also are characterized by relatively simple inner differentiation of such important flight muscles as M. pectoralis, M. flexor carpi ulnaris, and M. extensor metacarpi radialis. In the crested swifts, comparatively weak development of M. extensor digitorum communis, M. flexor digitorum profundus, and M. ulnometacarpalis ventralis is obviously associated with their limited role of resisting aerodynamic forces, whereas in the true swifts and hummingbirds these muscles also participate in active rotation of the manus and its major digit.

Certain flight muscles are developed in constant proportion to body size in all representatives of the families compared: M. rhomboideus superficialis, the group of Mm. serrati (with exception of M. serratus superficialis pars metapatagialis, it being absent in the hummingbirds), M. coracobrachialis caudalis, M. tensor propatagialis pars brevis, M. scapulotriceps, M. brachialis, M. expansor secundariorum, M. ectepicondylo-ulnaris, M. abductor alulae, and M. flexor digiti minoris. All three families are characterized by the weakness of both M. deltoideus minor and M. scapulohumeralis cranialis.

Relative development of the following flight muscles increases from the Hemiprocnidae to the Apodidae to the Trochilidae: M. subcoracoideus caput ventrale, M. pectoralis, M. supracoracoideus, M. humerotriceps, M. flexor digitorum profundus caput humerale, M. flexor carpi ulnaris, M. extensor metacarpi radialis, M. extensor digitorum communis, M. extensor longus digiti majoris, M. supinator, M. ulnometacarpalis ventralis, and M. abductor digiti majoris. Thus, in addition to an obvious and quite understandable hypertrophy of M. pectoralis and M. supracoracoideus, the reinforcement of the flight muscles in the true swifts and hummingbirds involves those that supinate the humerus and forearm, extend the elbow, extend and flex the wrist, rotate the manus, supinate the major digit of the manus, and flex the major digit and pronate its distal phalanx.

In the same sequence, the following muscles become relatively less developed: M. scapulohumeralis caudalis, M. rhomboideus profundus, M. deltoideus major, M. latissimus dorsi pars cranialis, M. biceps brachii, M. extensor longus alulae, M. ulnometacarpalis dorsalis, and M. flexor alulae. In the true swifts and hummingbirds, a relative weakness of the muscles that elevate and retract the humerus without causing rotation (M. latissimus dorsi pars caudalis, M. scapulohumeralis caudalis, M. deltoideus major) obviously results from a hypertrophy of both M. pectoralis and M. supracoracoideus. These two muscles provide mainly rotational mobility of the humerus relative to its long axis in the true swifts and hummingbirds, which correlates with the caudal orientation of the caput humeri and the shortening of the humeral shaft in these families (Karhu, 1992b). The retracting action of M. pectoralis grows as its sternal attachment widens caudally, increasing the amount of muscular fibers oriented in a craniodorsolateral direction.

In contrast to the large number of muscles with similar tendencies of specialization in both the Apodidae and the Trochilidae, there are few muscles in which specific reinforcement or reduction is unique either to the Apodidae or to the Trochilidae.

The Apodidae exceed the Trochilidae in relative development of M. coracobrachilais cranialis, M. subscapularis caput laterale, M. flexor digitorum superficialis, M. extensor metacarpi ulnaris, and M. interosseus ventralis. In the Apodidae, enlargement of the muscles listed above provides more efficient maintenance of the spread wing and prevents passive extension of the wrist and passive dorsal flexure of the major digit. These peculiar transformations of the flight muscles in the Apodidae correspond to their greater ability in gliding and fast, forward-flapping flight in comparison with the Trochilidae.

In comparison with the Apodidae, the Trochilidae have much better developed Mm. pronator superficialis and pronator profundus but less developed M. subscapularis, M. latissimus dorsi pars caudalis, M. tensor propatagialis pars longa, and M. interosseus dorsalis. In addition, the hummingbirds lack both propatagial parts of M. pectoralis, and M. flexor digitorum superficialis remains only as a short, stout tendon, attaching on the proximal part of the lig. humeroulnare. They have only two of the four alular muscles, namely, M. abductor alulae and M. adductor alulae, the latter being greatly reduced.

Reinforcement of Mm. pronator superficialis and pronator profundus in hummingbirds indicates an extensive rotational mobility of the forearm relative to the humerus. This conclusion conforms with the structure of the elbow joint in the hummingbirds, which allows significant rotational movements, unlike the more restricted mobility in the true swifts.

A conspicuous example of divergence between the Apodidae and Trochilidae is provided by M. biceps brachii. In living Apodiformes, only the crested swifts have the M. biceps brachii ending on both the proximal end of the ulna and the proximal end of the radius. In hummingbirds there is a single insertion on the ulna, whereas in the true swifts the insertion is on the radius. Taking into account that the double insertion of M. biceps brachii is typical for most birds, it is obviously more generalized, and a single insertion, either on the ulna or on the radius, represents a morphological specialization.

Discussion

The following features show the general level of specialization to be lower in *Argornis* than in *Jungornis:* coracoid with facies articularis sternalis saddle-shaped; sternal facet of coracoid relatively narrow dorsoventrally with only the medial part ventrally protruded; sternal facet of coracoid with the angulus lateralis projecting beyond the level of the angulus medialis; both proximal and distal ends of humerus relatively narrow; humeral shaft more slender; only the smaller ventral part of the caput humeri perpendicular to the long axis of the bone; the middle of the caput humeri without a distal protrusion on the caudal side; distal part of humerus without a dorsal crest; humerus with tuberculum M. pronator superficialis detached from tuberculum supracondylare ventrale; distal end of humerus with tuberculum supracondylare ventrale adjacent to the condylus ventralis; proc. flexorius of humerus projecting weakly distad; ulna with relatively small tuberculum lig. collateralis ventralis; and double insertion of M. biceps brachii on both the radius and ulna.

The Jungornithidae resemble the Apodidae in having a high, robust, tapering, and proximally placed deltopectoral crest. In the Apodidae the structure and position of the deltopectoral crest correlates with reinforcement of M. coracobrachialis cranialis and M. pectoralis, pars cranialis. All these features are among the characters that provide a highly developed ability for gliding flight in the true swifts (Karhu, 1992a). The similarity of structure and placement of the deltopectoral crest in the true swifts and jungornithids suggests that the latter could be well adapted for gliding flight, too.

At the same time, *Jungornis* and the Trochilidae share some essential characters that distinguish them from the Apodidae. The structure of the humeral head in *Jungornis* clearly demonstrates a trochilid-like specialization: presence of the distal enlargement on the caudal surface. In the Trochilidae this modification of the humeral head is associated with high specialization of the shoulder joint, which allows extreme supination of the adducted humerus during hovering flight (Cohn, 1968; Karhu, 1992a). In the Hemiprocnidae, Apodidae, and all known fossil genera, with the exception of *Jungornis*, the humeral head lacks any distal enlargement on the caudal surface.

Although *Argornis* possesses a double insertion of M. biceps brachii both on the ulna and on the radius, there is no sign of the radial insertion in *Jungornis*. This fact implies the presence of a single insertion on the ulna, although it cannot be determined directly because of poor preservation in the holotype of *Jungornis*. If so, it would represent another trochilid-like specialization within the Jungornithidae.

Taking into account that the trochilid-like characters under discussion are absent in the relatively more generalized jungornithid genus *Argornis*, their occurrence in *Jungornis* should be considered a result of intrafamilial evolution parallel to that in the Trochilidae. Because two jungornithid genera, *Argornis* and *Jungornis*, show obvious similarities to the Apodidae, the origin of trochilid-like features in the Jungornithidae demonstrates the feasibility of developing trochilid-like specializations from apodid-like adaptations. It suggests that the Trochilidae could have arisen from an apodid-like ancestor as well. This inference is supported by the analysis of evolutionary transformation of the forelimb muscles in the Apodiformes, which shows the widespread progression of certain specializations in the Trochilidae relative to the Apodidae. Agreement in the conclusions based on paleontological and myological data clearly contradicts the opinion of Cohn (1968) that similarities between the Apodidae and Trochilidae are convergent.

Both *Argornis* and *Jungornis* are similar to the Trochilidae and differ from the Apodidae in having the cotyla ventralis ulnae with a weakly pronounced ventroproximal edge. Owing to this peculiarity, the condylus ventralis of the humerus can slide ventroproximally relative to the ulna during the supination of the forearm. In the Apodidae the ventroproximal edge of the cotyla ventralis is prominent and strongly restricts the possible rotational movements of the elbow joint in the spread wing (Karhu, 1992a).

The position of the proc. supracondylaris dorsalis of the humerus is among the number of especially important characters in Apodiformes. The tendency for proximal displacement of this process is obviously conditioned by the proximal enlargement of the places of origin of M. extensor digitorum communis and the ventral head of M. extensor metacarpi radialis on the craniodorsal side of the distal part of the humerus. Very interesting indirect evidence of such a correlation is provided by *Jungornis*. Its humerus resembles the true swifts and hummingbirds in overall configuration, but it has the proc. supracondylaris dorsalis placed approximately on the same level as in *Aegialornis*, the most generalized genus of Apodiformes known (Karhu, 1992b). The relatively distal position of the proc. supracondylaris dorsalis in *Jungornis* may be explained by the presence of the high crest distally adjacent to the process. This crest allows enlargement of the place of origin of both extensors without proximal displacement of the supracondylar process. Hummingbirds, which have the best developed M. extensor digitorum communis and ventral head of M. extensor metacarpi radialis, demonstrate both conditions: proximal displacement of the proc. supracondylaris dorsalis, and muscle origin from the crest. In *Argornis* the supracondylar process is located distally, and the dorsal crest is absent, suggesting relatively weak development of both these muscles.

The well-developed distal process of the caudal margin of the proximal phalanx of the major digit indicates the presence of long first primaries in *Argornis* (Stegmann, 1965). Evidence for long first primaries in other Eocene apodiforms (e.g., Lydekker, 1891; Peters, 1985) suggests that the elongation of the distal part of the wing occurred in the early stages of apodiform evolution. In particular, this elongation might precede the divergence of humeral structure that distinguishes the hemiprocnid and apodid-trochilid directions of specialization of the flight apparatus within Apodiformes (Karhu, 1992a, 1992b).

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Selmes absurdipes, New Genus, New Species, a Sandcoleiform Bird from the Oil Shale of Messel (Germany, Middle Eocene)

D. Stefan Peters

ABSTRACT

Selmes absurdipes, new genus, new species, is established for two fossil specimens from Messel. The pamprodactyl foot, with unusually short toes and comparatively long tarsometatarsus and tibiotarsus, is the most characteristic feature of the new genus. Sandcoleiformes were not confined to North America and had a considerable morphological radiation. It might be appropriate to combine Sandcoleiformes and Coliiformes.

Introduction

Surprisingly, the great majority of fossil birds from the lake deposits of Grube Messel are land birds. Many of them are difficult to classify with extant taxa even on the ordinal level (Peters, 1991, 1992). Houde and Olson (1992) established the order Sandcoleiformes for a variety of species from the Eocene of North America. Some of these birds were previously assigned to various other higher taxa. Subsequently, an examination of several Messel birds revealed that the new order was not confined to North America. Two specimens of a supposed species of Sandcoleiformes from Messel are described herein. The anatomical terminology used is after Baumel et al. (1993) unless otherwise indicated.

ACKNOWLEDGMENTS.—I am indebted to S. Rietschel, Landessammlungen für Naturkunde, Karlsruhe, who kindly lent the paratype of *Selmes absurdipes.* I wish to thank Storrs Olson, Peter Houde, and an anonymous reviewer for their critical review of the manuscript.

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Systematics

SANDCOLEIFORMES

SANDCOLEIDAE

REMARKS.—Placed within order and family by the following characters: apertura nasi ossea large and holorhinal; rostrum maxillae distal to the nostrils rather short; mandibula curved (ventrally concave, dorsally convex) and with a short symphysis; fenestrae mandibulae absent; furcula thin and lacking a hypocleideum; olecranon short and blunt; papillae remigiales absent; processus intermetacarpalis absent; os metacarpale majus and o. m. minus subequal in distal extent; the three proximal phalanges of digit IV very short; phalanges unguales large and with strong flexor tubercles.

Selmes, new genus

FIGURES 1–3

TYPE SPECIES.—*Selmes absurdipes,* new species, the only known species of the genus.

ETYMOLOGY.—Anagram of Messel. *Selmes* should be treated as masculine in gender.

DIAGNOSIS.—The new genus differs from all known sandcoleiform genera by the unique morphology of its hind limbs. The tarsometatarsus is rather slender and is markedly longer than the longest toe; its distal end is only slightly broadened, approaching the condition of Coliiformes. Not only the proximal phalanges of toe IV but also the proximal two phalanges of toe III and the proximal phalanx of toe II are extremely short. Toes III and IV are of almost equal length. The foot is pamprodactyl and possibly was facultatively anisodactyl.

In addition, *Selmes* differs from *Sandcoleus* Houde and Olson, 1992, by having a comparatively shorter and thicker bill; it differs from *Chascacocolius* Houde and Olson, 1992, by having neither long processus retroarticulares mandibulae nor a marked epicondylus of humerus nor processus intermetacarpales.

FIGURE 1.—*Selmes absurdipes*, n. gen., n. sp. Holotype, SFM-ME 2375. Scale=2 cm. Photo, Forschungsinstitut Senckenberg, S. Tränkner.

Selmes absurdipes, new species

HOLOTYPE.—Slab with partly deformed skeleton, sternum and pelvis lacking, Forschungsinstitut Senckenberg SFM-ME 2375.

TYPE LOCALITY.—Ölschiefergrube Messel, Hessen, Germany.

HORIZON.—Lower middle Eocene, Lower Geiseltalium, Messel Formation.

PARATYPE.—Slab with postcranial skeleton, lacking most of

FIGURE 2.—*Selmes absurdipes*, n. gen., n. sp. Holotype, SFM-ME 2375. Coated with ammonium chloride. Scale=2 cm. Photo, Forschungsinstitut Senckenberg, S. Tränkner.

sternum and pelvis, Landessammlungen für Naturkunde Karlsruhe, ME 313.

ETYMOLOGY.—From the Latin *absurdus*, absurd, senseless, crazy; and *pes*, foot; noun used in apposition.

DESCRIPTION.—Both skeletons are fixed in slabs and are heavily crushed. In addition, the bones of the holotype are plastically deformed, a condition frequently encountered in fossils from Messel. For this reason, only approximate measurements can be given.

Skull: The calvaria is crushed and compressed rostrocaudally so that the rim of the orbita is bent off and is not inspectable; therefore, little can be said about the various processus and fossae. They apparently were not very prominent, however, because no indications of these structures can be traced on the preserved parts of the calvaria. In the orbita most of the annulus ossicularis sclerae is preserved and contains a black "pupil" of some organic matter (Figure 1). The bill is nearly conical. The apertura nasi ossea is similar to that of *Sandco-*

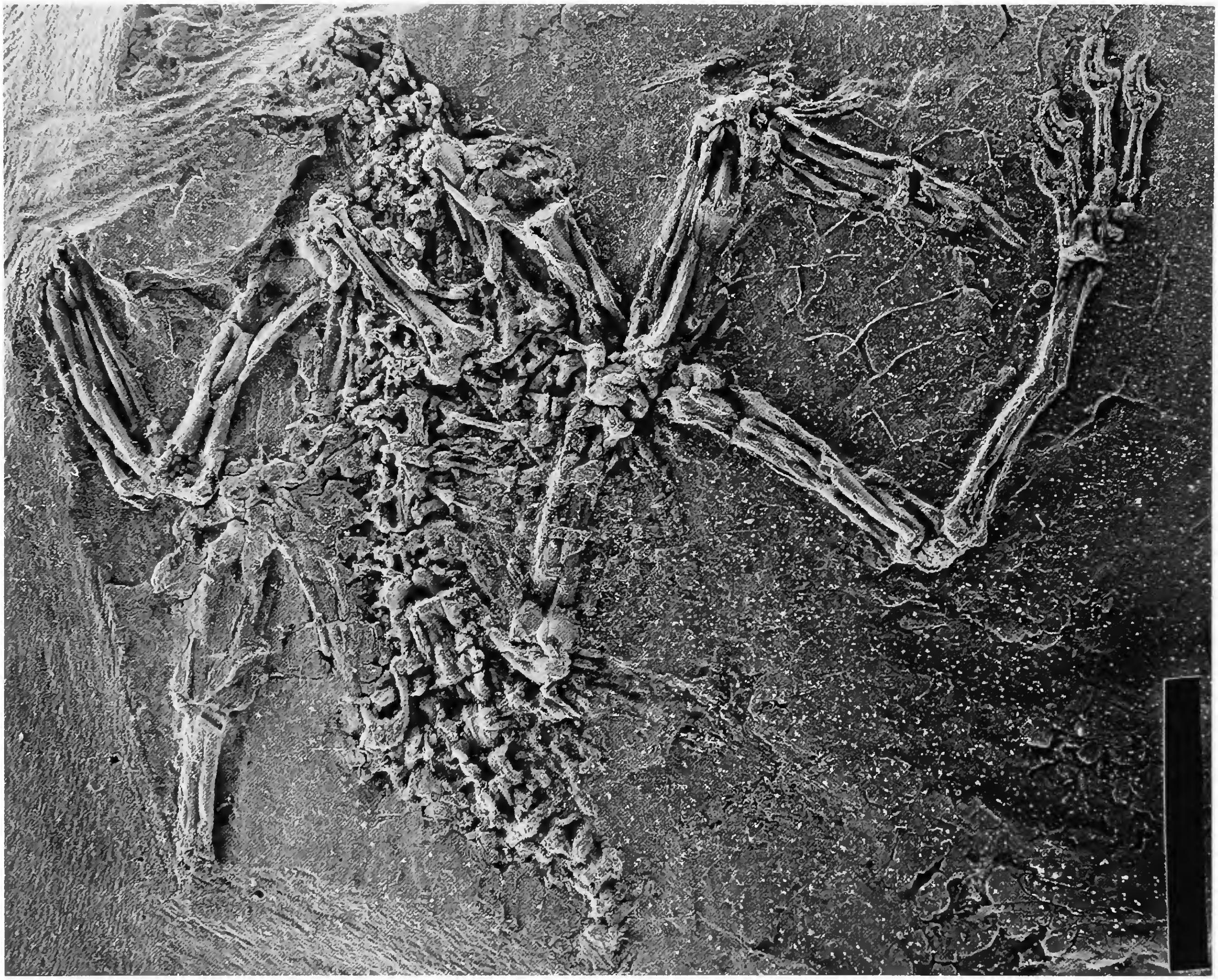

FIGURE 3.—*Selmes absurdipes*, n. gen., n. sp. Paratype, ME 313. Coated with ammonium chloride. Scale=2 cm. Photo, Forschungsinstitut Senckenberg, S. Tränkner.

leus copiosus Houde and Olson (1992, fig. 2). Most probably there was a septum nasi, otherwise it would be difficult to interpret the amorphous bony matter filling the nostril; however, a fragment of a strap-like structure might be a part of the palatinum. The dorsal outline of the rostrum maxillae is only moderately curved. The mandibula seems to be slightly more robust than the specimens figured by Houde and Olson (1992). There are no fenestrae mandibulae; some organic matter and shadows (Figures 1, 2) simulate apertures, but there are none. Measurements are as follows: maximal skull length 37.5 mm; nostril length 7.5 mm; mandibula length 26.5 mm.

Apparatus hyobranchialis: A considerable number of fragments of this structure are preserved. The paraglossum and the rostral end of the basihyale cannot be seen. The basihyale is rather broad and is not fused with the urohyale. The latter is a slender bone, tapering caudally, about 3.5 mm long. The right ceratobranchiale is completely preserved (6 mm long, rostral-end diameter 1 mm), whereas the caudal ends of both epibranchialia are lost (length of preserved part of right epibranchiale 6 mm, rostral-end diameter 0.5 mm).

Vertebrae: Although many vertebrae are preserved, they are very deformed and are almost useless for diagnostic purposes. Even their exact number cannot be ascertained. In the paratype the last free thoracic can be measured ventrally (length 3.5 mm). The synsacrum consists very probably of 11 vertebrae. There are at least five free caudal vertebrae. The pygostyle is not preserved.

Costae: Deformed fragments of four left ribs can be seen in the paratype. No processus uncinati can be detected.

Sternum: Pieces of the sternum are preserved only in the paratype. They are badly crushed, covering as a thin layer parts of the ribs and femur.

Furcula: The furcula is thin and U-shaped. There is no hypocleideum. In both specimens the dorsal ends of this bone are insufficiently preserved. The thickness of the scapus is continuously about 1 mm.

Coracoideum: In the holotype, fragments of the coracoids are deformed past recognition. In the paratype they are in better condition. They have a slender shaft and a rather small extremitas omalis. The presence of a processus procoracoideus is uncertain. Unfortunately, the lateral and medial parts of the extremitates sternales are only partly preserved. What can be seen, especially from the left coracoid of the paratype, suggests a broad sternal extremity. Maximal length of the coracoid is approximately 16 mm.

Scapula: Parts of the left scapula of the holotype and of both scapulae of the paratype are preserved. All three bones have an even, ribbon-like shape, without any terminal enlargement. They are 1.6–1.7 mm broad. The cranial extremities are hidden by other bones.

Humerus: All humeri have the cranial surfaces exposed. They are robust, slightly curved, and approach in shape the humerus of *Anneavis* Houde and Olson, 1992, but have the tuberculum dorsale and epicondylus dorsalis less prominent (fide Houde and Olson, 1992, fig. 8). The length is 21 mm and the midshaft width is 3 mm.

Ulna: The ulna is stout, only slightly curved, and of the same length as the humerus or slightly shorter.

Radius: The radius is straight and robust. The extremities are not well preserved.

Os carpi radiale and o. c. ulnare: In the holotype a deformed ossicle attached to the distal end of the left ulna might be the o. c. ulnare, and both carpalia are preserved in the right hand of the holotype and in the left hand of the paratype. Their condition is so bad, however, that no useful details can be detected.

Carpometacarpus: This is a robust bone. Apparently, the processus extensorius was only moderately protuberant. No processus intermetacarpalis is present. The proximal end of the os metacarpale minus has a rectangular flange projecting ventrally. A blurred structure in the paratype suggests that this flange might have been perforated, as in *Coracias garrulus* Linnaeus. The length is 14–15 mm, and the distal-end width is 4.5 mm.

Digitus alulae: In the holotype a small ossicle at the tip of the digit of the left hand very probably represents the second phalanx of this digit. The length of the first phalanx is 6 mm.

Digitus major: The proximal phalanx is not fenestrated and approaches the shape of that of Passeriformes. Measurements are as follows: phalanx proximalis length 6 mm, distal-end width 3 mm; phalanx distalis length 6 mm.

Digitus minor: The only phalanx is robust; it has a triangular outline and is about 3 mm long.

Pelvis: The small fragments in the paratype suggest that the pelvis was rather wide. Inferring from the position of the femora, the distance between the acetabula was about 11–12 mm.

Femur: No precise morphological details of this bone can be imparted. Its length is about 20 mm.

Tibiotarsus: This is a slender, straight bone. In the holotype the cranial aspect of the right tibiotarsus is exposed; in the paratype the lateral side of the left tibiotarsus can be seen. The latter one is broken near the distal end, and both fragments have slipped together. In the holotype, part of the proximal end can be seen. Apparently, the cristae cnemiales were not very prominent, similar to the condition in *Coracias*. The distal end in both specimens is very deformed. The length is 30 mm, and the midshaft width is 3 mm.

Fibula: Not preserved.

Tarsometatarsus: The tarsometatarsus also is comparatively slender and straight. In the holotype both tarsometatarsi have the dorsal aspect exposed, the left one in a reversed position. In the paratype the left tarsometatarsus is exposed lateroplantarly. Although the bones are plastically deformed, it can be seen that they had a small hypotarsus and an unusually small trochleae. Both the distal and the proximal ends of the bone are only slightly broader than the shaft. The length is 20–21.5 mm.

Ossa digitorum pedis: In the holotype the entire set of toes is preserved; in the paratype only the toes of the left foot can be seen in their plantar and partly lateral aspect. In the right foot of the holotype and the left one of the paratype, the toes are in a pamprodactyl position. In the left foot of the holotype, the configuration seems to be anisodactyl, but this might be an artifact because the toes are disarticulated from the tarsometatarsus. The most striking feature is in the proportions of the phalanges (p), as shown by the following measurements (in mm).

digit I: p 1, 4.5–5.5; p 2, 4.0–4.5
digit II: p 1, 2.0; p 2, 6.0; p 3, 4.5–5.5
digit III: p 1, 2.5; p 2, 2.5–3.0; p 3, 6.0; p 4, 5.0–6.0
digit IV: p 1, 2.0; p 2, 1.5–2.0; p 3, 1.5–2.0; p 4, 6.0; p 5, 5.5–6.0

Feathers: There are some small remnants of feathers in the holotype (Figure 1), suggesting that the birds had quite long remiges or rectrices.

Contents of the Digestive System: In the holotype at least 25 densely packed seeds are preserved. Surely, this was the bird's last meal. It is difficult, however, to decide whether the seeds were in the stomach or in the crop. The seeds obviously belong to a dicotyledonous plant, but their identity is as yet unknown.

Discussion

Selmes absurdipes shows that not only the distribution but also the morphological range of the Sandcoleiformes is wider than initially presumed. The birds of this order are real taxonomic mosaics, having similarities with many other groups. For this reason it might be worthwhile to reflect on the definition of the Sandcoleiformes. It is my impression that they probably could be combined with the Coliiformes. The taxonomic definition of the latter is founded on the features of a small group of very similar species, and the resultant narrowness of the taxonomic definition makes it unduly difficult to include new taxa with the Coliiformes. There are, however, substantial similarities between sandcoleids and colies, and *Selmes* adds to these similarities (internasal septum, distal end of tarsometatarsus). But because I have not seen the original material of most sandcoleiform species, these considerations should be taken only as suggestions.

The new species undoubtedly was a highly specialized bird. Houde and Olson (1992:143) emphasized that the pedal phalanges in Sandcoleidae are "extremely short" and they figured as an example the foot of *Anneavis anneae* Houde and Olson (1992). In *Selmes* the phalanges are even more shortened. Whereas in *Anneavis* all phalanges are longer than broad, in *Selmes* the proximal phalanges of toes II, III, and IV are broader than long. In the latter the tarsometatarsus is markedly longer than the longest toe, and toes III and IV are of almost equal length. In *Anneavis,* toe III is the longest by far and equals the tarsometatarsus in length. It is hard to imagine how *Selmes* used its feet. Inferring from the construction of the toes, which is closest to that of swifts, it could only cling to more or less sloping surfaces. Perching would seem to have been nearly impossible; but, why are the toes so short and the rest of the leg comparatively long? As yet, there is no answer. Maybe the identification of the seeds will shed some light on the behavior of this remarkable bird.

KURZFASSUNG

Selmes absurdipes, n. gen., n. sp., wird auf der Beschreibung zweier fossiler Vögel von Messel begründet. Das wichtigste Kennzeichen der neuen Gattung ist der pamprodactyle Fuß mit ungewöhnlich kurzen Zehen, aber verhältnismäßig langem Tarsometatarsus und Tibiotarsus. Die Sandcoleiformes waren nicht auf Nordamerika beschränkt und entwickelten eine beachtliche morphologische Radiation. Möglicherweise sollten Sandcoleiformes und Coliiformes vereinigt werden.

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A Fossil Screamer (Anseriformes: Anhimidae) from the Middle Tertiary of Southeastern Brazil

Herculano M.F. Alvarenga

ABSTRACT

A new genus and species of anhimid is described based on 14 fragmentary, partially associated bones collected from the shales of the Tremembé Formation of the Taubaté basin in southeastern Brazil. The age of this formation is either upper Oligocene or lower Miocene. An isolated, almost complete left coracoid was chosen as the holotype. This bird, the first paleospecies described for the family Anhimidae, was smaller and more gracile than *Chauna chavaria* (Linnaeus), the smallest species of living screamers.

Introduction

The screamers (Anseriformes: Anhimidae) are distinguished from the more widespread family Anatidae by the narrow, downwardly hooked bill lacking filtering fringes, long legs, and large, unwebbed feet with strong hind toes. The skeleton of anhimids is very noticeably pneumatized. There are three modern species of screamers in two genera, *Anhima cornuta* (Linnaeus), *Chauna chavaria* (Linnaeus), and *C. torquata* (Oken), all of which are endemic to South America. There are no fossil species described for this family (Olson, 1985), but undescribed fossils of possible screamers are known from the early Eocene of Wyoming and England (S.L. Olson, pers. comm., 1995). In the present study, a new genus and species of anhimid is described, the first record for this family in the Tertiary of South America.

The Tremembé Formation, in the town of the same name in the Taubaté basin of southeastern Brazil (Figure 1), is a lacustrine deposit of small extent. The sediments are composed of alternate layers of thinly foliated bituminous shales, 6 to 10 meters thick, and an almost homogeneous montmorillonitic clay of about the same thickness (Figure 2). Both of these layers have produced a large diversity of fossil vertebrates, including representatives of six families of birds (Alvarenga, 1982, 1985, 1988, 1990, 1995). The age of the Tremembé Formation is either upper Oligocene or lower Miocene, as discussed by Soria and Alvarenga (1989), Alvarenga (1990), and Vucetich et al. (1993).

The presence of flamingos, such as *Palaelodus* and *Agnopterus* (Alvarenga, 1990), a cathartid vulture (Alvarenga, 1985), and a large number of small fossil fishes and crustacea suggest the interpretation of the site as an old lake of shallow, alkaline water. Some large and small mammals (Soria and Alvarenga, 1989; Vucetich et al., 1993) and a large phorusrhacid (Alvarenga, 1982) also are known from these sediments.

MATERIALS AND METHODS.—Among the birds described from the Tremembé Formation, some specimens were found articulated in the shales, whereas others, in the layer of montmorillonitic clay, often occurred as fragmented and dissociated bones, which caused some difficulties in relegating them to a particular taxon. The fossils described herein were collected by the author from the montmorillonitic clay on different occasions from 1978 to 1993. They belong to at least three individuals, all identified as anhimids of a size compatible with that of a single species.

The bones were compared with those of skeletons of almost all families of birds, especially Anhimidae (*Chauna chavaria, C. torquata, Anhima cornuta*), Anatidae (*Anseranas semipalmata* (Latham)), and some Gruidae, including *Grus, Balearica,* and *Anthropoides*. The single skeleton of *Chauna chavaria* used in this study was obtained on loan from the National Museum of Natural History (USNM; collections of the former United States National Museum), Smithsonian Institution, and all others are from the author's collection (HA).

Anatomical terminology follows that of Howard (1929) and Baumel et al. (1979), although I also follow Olson (1987) in using the term "procoracoid foramen" in the description of the coracoid. The fossil specimens herein described are housed in the Vertebrate Paleontology collection of Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), Brazil.

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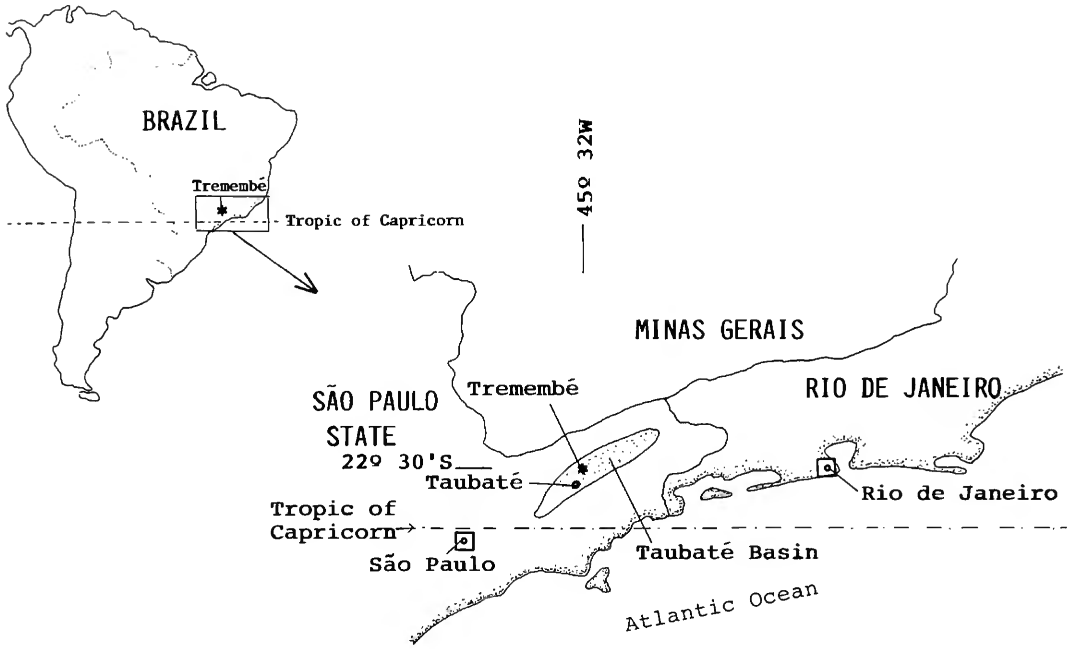

FIGURE 1.—Map of Taubaté basin showing the town of Tremembé, the type locality of *Chaunoides antiquus*, n. gen. n. sp.

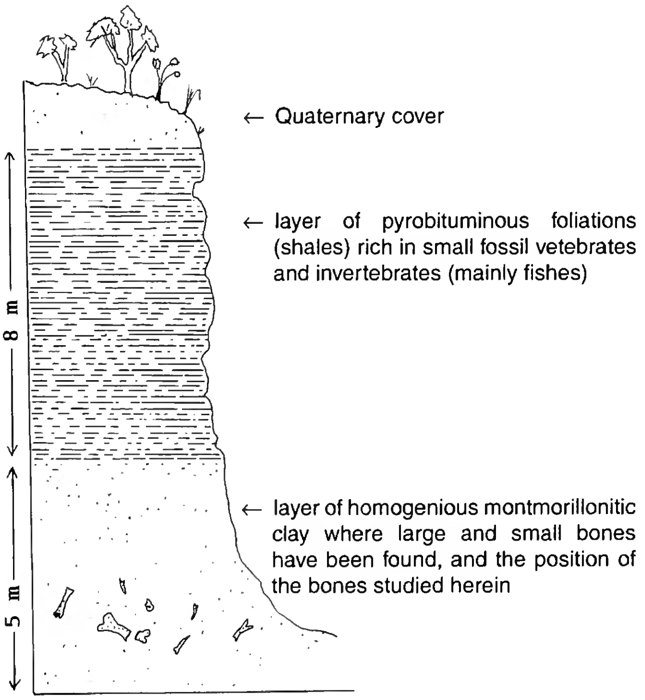

FIGURE 2.—A simplified section of the Tremembé Formation showing the stratigraphic position of the layers of shales, clay, and fossils.

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Order ANSERIFORMES

Family ANHIMIDAE

Chaunoides, new genus

TYPE SPECIES.—*Chaunoides antiquus*, new species.

HORIZON.—Middle Tertiary, late Oligocene or early Miocene, Tremembé Formation.

GEOGRAPHIC DISTRIBUTION.—Taubaté basin, southeastern Brazil.

ETYMOLOGY.—From the Latinized suffix *-oideus*, meaning resembling, like; referring to a bird that was similar to the genus *Chauna*.

DIAGNOSIS.—Coracoid of similar size and form to that of the living species of *Anhima* and *Chauna* (Figures 3–5), including

FIGURE 3.—*Chaunoides antiquus*, n. gen. n. sp., holotype, left coracoid (MNRJ 4619-V), coated with ammonium chloride: A, ventral view; B, dorsal view. (Scale bar=1 cm.)

a large pneumatic foramen in the sterno-coracoidal fossa, a large procoracoid foramen, and a large transverse procoracoid process. The coracoid differs from that of *Anhima* by having a (1) narrower head; (2) glenoid facet with the transverse width greater than the length, also easily observed in ventral view (Figures 3A, 5) because of its lateral expansion (similar to *Chauna*); (3) larger and deeper scapular facet; and (4) larger pneumatic foramen, with rounded borders, in the sterno-coracoidal fossa. The coracoid differs from that of *Chauna torquata* and *C. chavaria* by having (1) a smaller acrocoracoid process; (2) the scapular facet more rounded and deeper; (3) the dorsal surface less swollen; and (4) the large pneumatic foramen in the sterno-coracoidal fossa wider and dorsoventrally more compressed, with a small process in the dorsal border.

***Chaunoides antiquus*, new species**

HOLOTYPE.—Nearly complete left coracoid, lacking only the tip of the head, tip of the procoracoid process, and the sterno-coracoidal process (Figure 3). Vertebrate paleontology collections of Museu Nacional de Historia Natural da Universidade Federal do Rio de Janeiro, MNRJ 4619-V.

TYPE LOCALITY.—Santa Fé Farm, 2 km north of Tremembé, São Paulo State, Brazil (22°30'S, 45°32'W) (Figure 1). Montmorillonitic clay, about 4 m below the most superficial level of shales.

HORIZON AND AGE.—Tremembé Formation, Taubaté basin, upper Oligocene or lower Miocene.

MEASUREMENTS OF HOLOTYPE.—See Table 1.

PARATYPES.—Another left coracoid lacking the sternal end (MNRJ 4620-V), identical in morphology to the holotype, associated with an almost complete left femur (MNRJ 4621-V); the distal end of a left ulna (MNRJ 4622-V); the distal end of a right radius (MNRJ 4623-V); a left radius lacking the proximal end (MNRJ 4624-V); a left ulna lacking the proximal end (MNRJ 4632-V), associated with a segment of distal shaft of a left tibiotarsus (MNRJ 4631-V); and two segments of the distal end of left tibiotarsi (MNRJ 4625-V, MNRJ 4629-V), the last being associated with the proximal end of a left tarsometatarsus

TABLE 1.—Measurements (mm) of *Chaunoides antiquus*, n. gen. n. sp., compared with other Anhimidae.

Measurement	*Chaunoides antiquus*, n. gen. n. sp.		*Chauna chavaria*	*Chauna torquata*			*Anhima cornuta*	
	Holotype, MNRJ 4619-V	Paratypes	USNM 347738 (sex indet.)	HA 41 (female)	HA 389 (sex indet.)	HA 702 (male)	HA 40 (female)	HA 902 (female)
Coracoid		MNRJ-4620-V						
midshaft width	12.3	11.7	11.3	15.4	11.6	15.7	13.9	13.6
acrocoracoid apex to internal angle	66.1	–	65.8	71.1	62.6	68.0	64.8	69.5
Femur		MNRJ 4621-V						
top of head to internal condyle	–	89.7	92.5	97.1	88.6	101.0	93.2	94.3
least width midshaft	–	10.0	11.5	12.9	10.6	13.7	12.0	14.4
Radius	–	MNRJ 4623-V, 4624-V						
greatest width, distal end	–	12.2, 12.5	15.5	17.0	14.0	16.1	15.4	16.4
Tarsometatarsus		MNRJ 4630-V						
width of proximal articular surface	–	21.05	23.1	23.8	22.0	26.1	21.7	23.0
Tibiotarsus		MNRJ 4625–4629-V, 4631-V						
width immediately above tendinal bridge	–	14,2, 14.0, 14.5, 15.0, 13.8, 14.1	15.8	17.8	15.0	17.9	16.1	20.3
Ulna		MNRJ 4622-V, 4632-V						
greatest width of external condyle	–	14.4, 16.1	17.6	19.6	17.2	20.1	18.3	18.1

FIGURE 4.—Dorsal view of the left coracoid of *Chaunoides antiquus*, n. gen. n. sp., compared with those of living anhimids: A, *Chauna torquata* (HA 41); B, *Chaunoides antiquus*, n. gen. n. sp., holotype (MNRJ 4619-V); C, *Chaunoides antiquus*, n. gen. n. sp., paratype (MNRJ 4620-V); D, *Anhima cornuta* (HA 40). The fossil bones (B and C) are coated with ammonium chloride. (Scale bar=1 cm.)

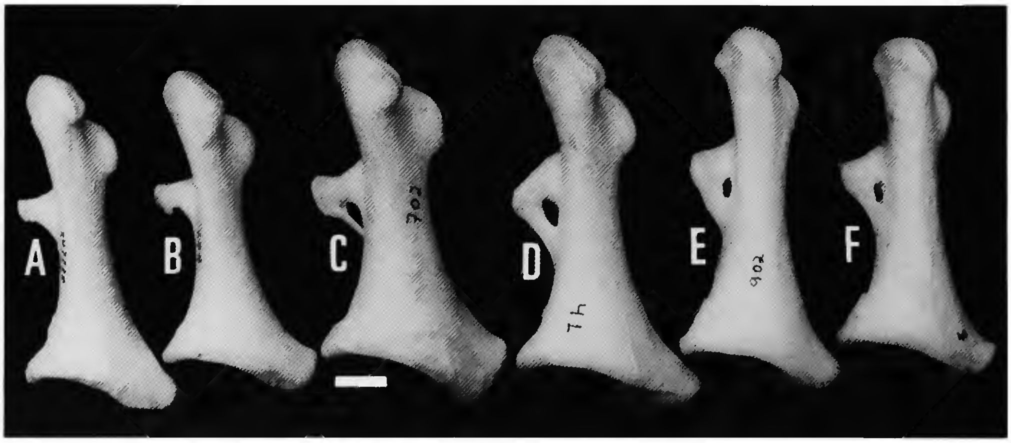

FIGURE 5.—Coracoids of anhimids, in ventral view, showing variation: A, *Chauna chavaria* (USNM 347738); B, *Chauna torquata* (HA 389); C, *Chauna torquata* (HA 702); D, *Chauna torquata* (HA 41); E, *Anhima cornuta* (HA 902); F, *Anhima cornuta* (HA 40). Note the absence of a procoracoid foramen in A and B. (Scale bar=1 cm.)

(MNRJ 4630-V). There also are three unassociated segments of distal, right tibiotarsi shafts (MNRJ 4626-V, MNRJ 4627-V, MNRJ4628-V).

MEASUREMENTS OF PARATYPES.—See Table 1.

ETYMOLOGY.—From the Latin *antiquus*, antique, old, ancient.

DIAGNOSIS.—As for the monotypic genus.

DESCRIPTION AND COMPARISONS.—The coracoid of *Chaunoides* is proportionally more slender than in living anhimids, and the procoracoid process is located slightly more toward the shoulder than in living species of anhimids (see Figures 3–5). The distal end of the ulna has the carpal tuberosity less pronounced than in living anhimids, somewhat similar to *Chauna chavaria* (Figure 6). The distal end of the radius of *Chaunoides*

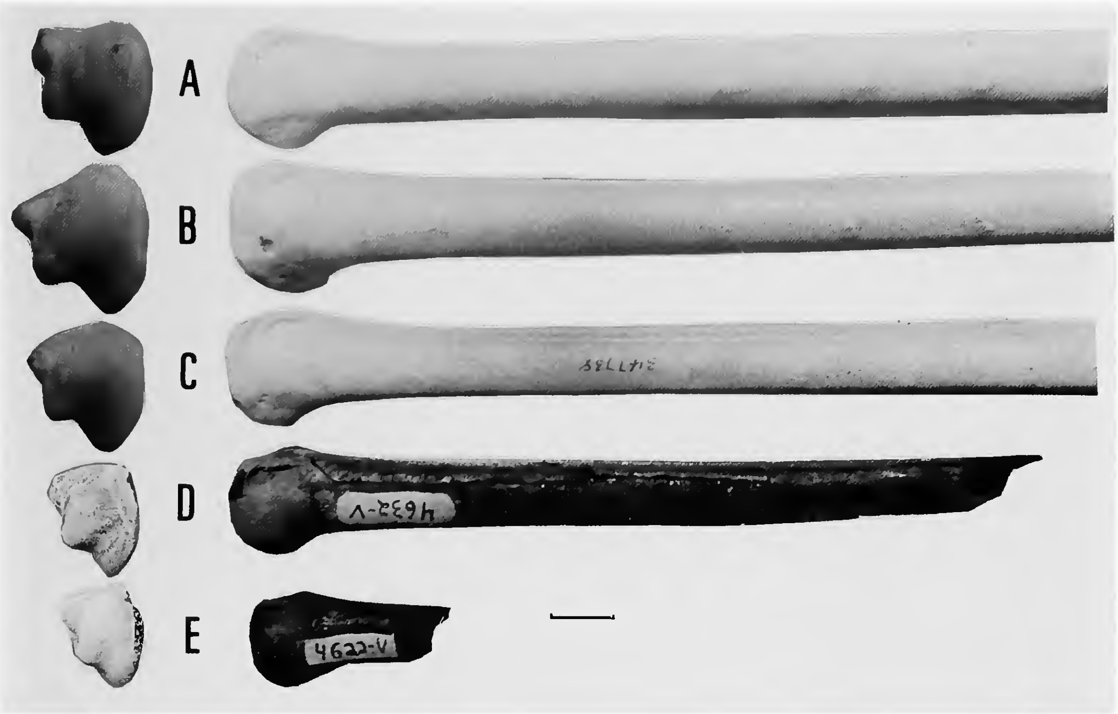

FIGURE 6.—The distal end of left ulna, in distal view (left) and in anconal view (right), of *Chaunoides antiquus*, n. gen. n. sp., compared with other Anhimidae: A, *Anhima cornuta* (HA 902); B, *Chauna torquata* (HA 702); C, *Chauna chavaria* (USNM 347738); D, *Chaunoides antiquus*, n. gen. n. sp., (paratype, MNRJ 4632-V); E, *Chaunoides antiquus*, n. gen. n. sp. (paratype, MNRJ 4622-V). (Scale bar=1 cm.)

has a similar morphology to that in other anhimids, but, in contrast, there is no pneumatic foramen (Figure 7).

The femur (Figure 8) is less robust than in *Anhima* and *Chauna*, with its neck longer and more similar to that in *Anseranas* and other anatids. Its distal end is similar to that of *Anhima* and *Chauna*, with a shallow patellar groove and a flat articular surface of the internal condyle. The prominent crista supracondylaris medialis, being in a posteromedial position, gives a square shape to the distal end of the femur in medial view. The tibiotarsus of *Chaunoides* has the distal end of the shaft slightly bowed toward the midline, and the internal condyle extends far mediad, as is generally the case in Anseriformes (Figure 9). The tendinal groove is not pneumatized, in contrast to that of extant anhimids, and its medial border is very pronounced and extends proximad to the middle of the

FIGURE 7 (right).—The distal end of (A) right radius (paratype, MNRJ 4623-V), and (B) left radius (paratype, MNRJ 4624-V), of *Chaunoides antiquus*, n. gen. n. sp., in palmar view, compared with the left radius, also in palmar view, of other Anhimidae and Anatidae: C, *Chauna chavaria* (USNM 347738); D, *Anhima cornuta* (HA 902); E, *Chauna torquata* (HA 41); F, *Anseranas semipalmata* (HA 1201). (Scale bar=1 cm.)

FIGURE 8.—The left femur of *Chaunoides antiquus*, n. gen. n. sp. (paratype MNRJ 4621-V), coated with ammonium chloride (right) compared with *Chauna chavaria* (USNM 347738) (left): A, anterior view; B, posterior view; C, distal view. (Scale bar=1 cm.)

shaft. In the proximal end of the tarsometatarsus (Figure 10), the intercotylar prominence is higher and sharper than in other Anhimidae; the morphology of the hypotarsus is very similar to that in *Chauna*, especially in *C. chavaria*, but the crista medialis is shorter and higher. Also, there is no pneumatic foramen in the proximal end of the tarsometatarsus, whereas in extant anhimids this region is very pneumatized.

Discussion

The procoracoid foramen in *Chaunoides* is large and perfectly formed, as it is in the available specimens of *Anhima* and some specimens of *Chauna;* however, in certain specimens, such as *Chauna chavaria* (USNM 347738) and *C. torquata* (HA 389), this foramen is not formed (Figure 5), a condition possibly due to immaturity or to intraspecific variation. Olson (1987) commented on this same variation in several genera of Accipitridae as possible intraspecific or intrageneric variation. The pneumatic foramen in the sterno-coracoidal fossa of *Chaunoides* and *Chauna* is a very large opening with rounded borders, being the extreme form of a condition that also is found in *Anhima, Anseranas, Opisthocomus,* gruids, some galliforms, and cathartids. In the three species of living anhimids,

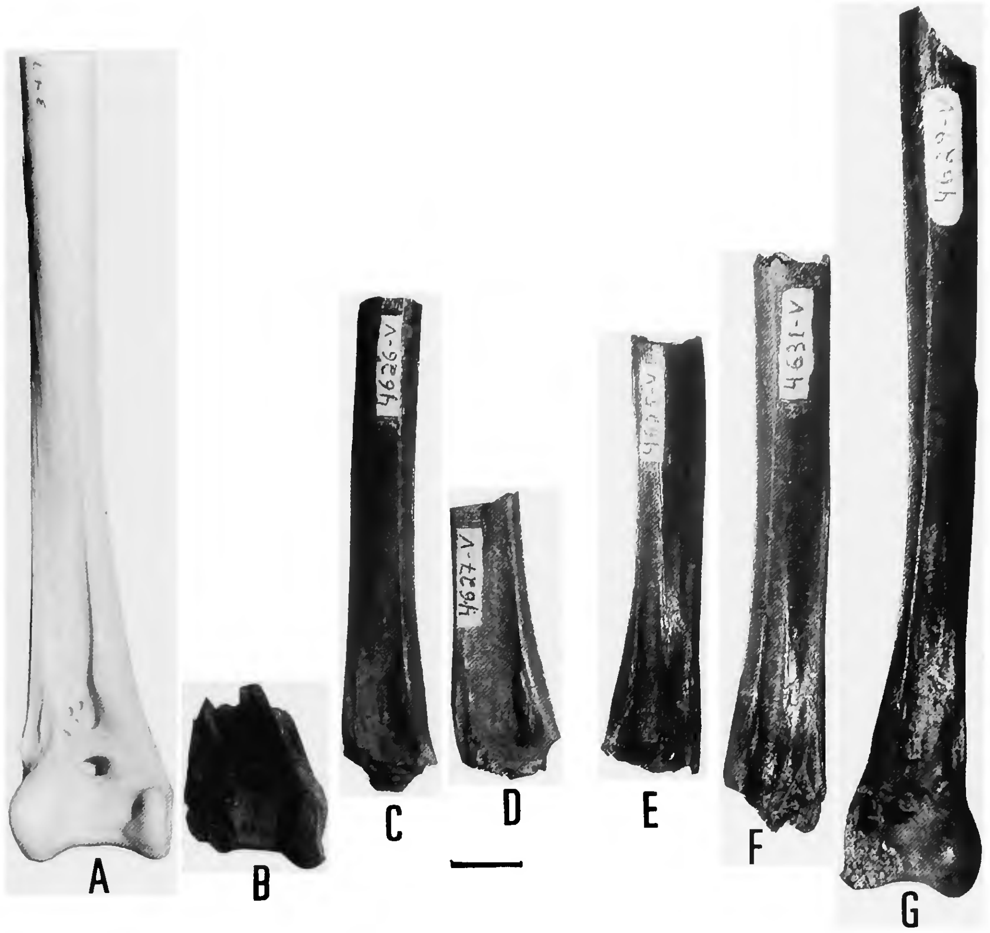

FIGURE 9.—Right tibiotarsus of (A) *Chauna chavaria* (USNM 347738) in anterior view, compared with paratypical tibiotarsi of *Chaunoides antiquus,* n. gen. n. sp.: B, MNRJ 4628-V; C, MNRJ 4626-V; D, MNRJ 4627-V; E, MNRJ 4625-V; F, MNRJ 4631-V; G, MNRJ 4629-V. (Scale bar=1 cm.)

the bones are extremely pneumatized, especially the distal end of the radius, the tendinal groove of the tibiotarsus, and the proximal end of tarsometatarsus. This condition is not observed in *Chaunoides.*

The distal end of the femur of *Chaunoides* is very similar morphologically to that of the other anhimids, but the long neck and the thin shaft give this bone an appearance more like that of anatids, including *Anseranas.* In the tarsometatarsus of *Chaunoides,* the higher intercotylar prominence is quite different from that in extant screamers, but the hypotarsus, with only two calcaneal ridges, is typical of the Anhimidae and also is found in *Paranyroca magna* Miller and Compton, 1939, from the lower Miocene of South Dakota, in contrast to that of the remainder of the Anatidae, which have four calcaneal ridges. The proportions of the femur, tibiotarsus, and tarsometatarsus of *Chaunoides* suggest that it was slightly smaller than *Chauna chavaria,* the smallest living screamer, and also more gracile, with the leg bones more slender and with the skeleton less pneumatized than in the living anhimids.

Conclusion

Chaunoides antiquus is the first fossil species of the family Anhimidae to be recognized. At the Natural History Museum, London (formerly the British Museum (Natural History)), in 1992, I examined the holotype of *Loxornis clivus* Ameghino, 1895 (placed in incertae sedis by Tonni (1980)), which is from the Oligocene (Deseadean) of Argentina. I concluded that this bird may be a representative of the Anhimidae, but because of its poor preservation (only the distal end of a left tibiotarsus, with the medial condyle incomplete), additional material would be required to substantiate this hypothesis.

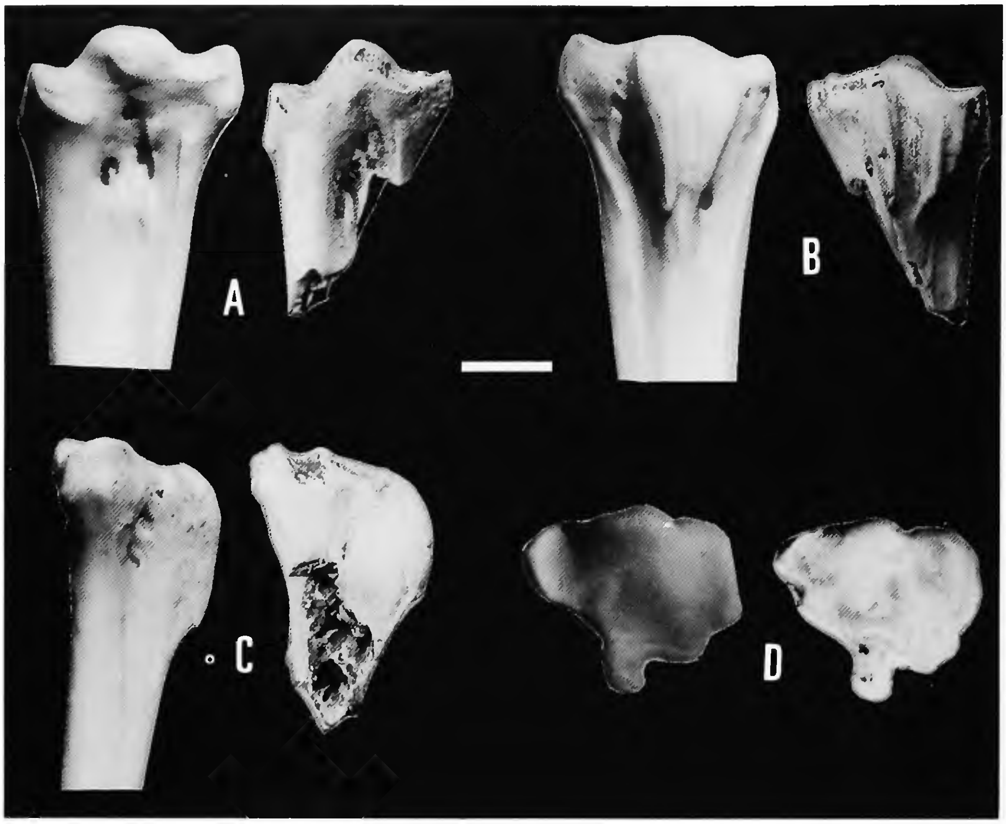

FIGURE 10.—Left tarsometatarsus of *Chaunoides antiquus*, n. gen. n. sp. (paratype, MNRJ 4630-V), coated with ammonium chloride (right) compared with *Chauna chavaria* (USNM 347738) (left): A, anterior view; B, posterior view; C, lateral view; D, proximal view. (Scale bar=1 cm.)

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The Anseriform Relationships of *Anatalavis* Olson and Parris (Anseranatidae), with a New Species from the Lower Eocene London Clay

Storrs L. Olson

ABSTRACT

An associated partial skeleton, including the skull but lacking legs, from the lower Eocene London Clay of Essex, England, possesses derived characters of the coracoid and furcula that show it to belong to the Anseranatidae, which previously had no fossil record. Except for its much larger size, the humerus of this specimen is identical to that of *Anatalavis rex* (Shufeldt) from the late Cretaceous or early Paleocene of New Jersey. The Eocene specimen is described as a new species, *Anatalavis oxfordi*, and the genus *Anatalavis* is transferred from the form-family Graculavidae to a new subfamily, Anatalavinae, of the Anseranatidae. *Anatalavis* is characterized by a very broad duck-like bill, a proportionately very short and robust humerus, and an anterior portion of the pelvis resembling that of ibises and other wading birds more than that of any known anseriform. Other features of its osteology are unique within the order.

Introduction

Waterfowl of the order Anseriformes are among the best known and most distinctive groups of modern birds. Although waterfowl are abundantly represented by Neogene fossils, much of their early evolutionary history has remained obscure. The most informative fossils until now have been the Paleocene and early Eocene remains of *Presbyornis* and its close relatives, which were nearly cosmopolitan in the early Paleogene. *Presbyornis* was shown to have a duck-like skull on the body of a long-legged wading bird and was interpreted as showing a derivation of the Anseriformes from a charadriiform-like ancestor (Olson and Feduccia, 1980b) rather than from the Galliformes, as had been postulated previously. The more recent studies of Ericson (1996, 1997) confirmed the lack of relationship between the Anseriformes and Galliformes, but the ancestry of the Anseriformes was unresolved beyond a complex of various groups of wading birds, including Charadriiformes. *Presbyornis*, however, was determined to have branched off within the order and constitutes the sister group of the Anatidae proper, with the Anhimidae and Anseranatidae being the primitive outliers of the Presbyornithidae/Anatidae clade.

The giant Paleocene and Eocene groundbirds of the genus *Diatryma*, once thought to have been predatory descendants of crane-like birds, also may be part of the anseriform radiation (Andors, 1988, 1992). The dietary habits of *Diatryma*, however, have been equivocated (Andors, 1992; Witmer and Rose, 1991).

Although no fossils of screamers (Anhimidae) had hitherto been reported, a somewhat more primitive genus is now known from the middle Tertiary of Brazil (Alvarenga, this volume), and I have examined excellent fossils, as yet undescribed, from the lower Eocene Willwood Formation of Wyoming and from the contemporaneous London Clay of England. Thus, of the three major lineages of living Anseriformes, the only one with no early Tertiary (or later) fossil representative is the Anseranatidae, with its sole member being the Magpie Goose, *Anseranas semipalmata*, of Australia.

Two bones from the Hornerstown Formation of New Jersey, a deposit of debated Late Cretaceous or early Paleocene age (Olson, 1994; Hope, this volume), were thought to show some similarities to the Anatidae, but in the absence of associated material they were assigned to the form-family Graculavidae, which contains various taxa resembling primitive Charadriiformes (Olson and Parris, 1987). A new fossil from the London Clay consisting of much of a skeleton, although lacking legs, permits positive identification of the New Jersey fossils as not only belonging to the Anseriformes but belonging to the family Anseranatidae. Thus, the New Jersey and London Clay fossils

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provide the first record of this family, as well as the earliest certain occurrence of the entire order.

The present paper is intended to provide a name for the new fossil from the London Clay and to place on record its more salient osteological features. Full analysis of anatomical details and phylogenetic significance will have to await the appearance of information not presently available for certain extant but sequestered fossils, especially those of Eocene Anhimidae.

Nomenclature for species' binomials and English names of modern birds herein follows Sibley and Monroe (1990).

ACKNOWLEDGMENTS.—I must begin by crediting the singular cooperativeness of Andrew Oxford, who collected the specimen that is the primary object of the present study and who, at my first suggestion, donated it to the Natural History Museum, London (formerly the British Museum (Natural History)) (BMNH). In connection with this transaction, I cannot fail to mention that the hospitality shown to me and my family by Mr. and Mrs. Oxford at their domicile at Great Mongeham, Deal, Kent, afforded us some of our most pleasant memories generated during a pleasant year in England. Mr. Oxford and I each owe a debt of gratitude to that veteran collector of fossil birds of the London Clay, Michael Daniels, who separately introduced us to the incredibly productive mudflats at Walton-on-the-Naze, who led me to contact Mr. Oxford about his fossil bird, and whose comments on the manuscript inspired me to delete much that was equivocal. The repeated hospitality of Mr. and Mrs. Daniels at their home in Holland-on-Sea, Clacton, Essex, has been of inestimable benefit to me for my knowledge of early Eocene birds.

At the BMNH, Angela Milner greatly facilitated the present study by making arrangements for the incorporation of the specimen into the collections and having it prepared and photographed. In this connection, there are hardly sufficient words of praise for William Lindsay, whose painstaking removal of an exceedingly fragile and difficult specimen from its envelope of clay and pyrite was undertaken in such a spirit of collaboration and sensitivity that his contribution must rank equal to that of any scientist who studies these bones. Sandra Chapman has repeatedly been of assistance during my study of fossil bird collections at the BMNH. Robert Prys-Jones and Cyril Walker, of the Bird Group at Tring, were instrumental in lending comparative modern skeletons. The photographs are by Phil Crabb, Natural History Museum, London, Photo Unit, except Figure 8C,D, which is by the Smithsonian Photographic Services (SPS). Carl Hansen (SPS) was instrumental in assisting with the electronic composition of the figures.

Order ANSERIFORMES

The primary adaptation of the order Anseriformes is the modification of the bill so that the upper jaw houses an enlarged tongue, which functions as a double-piston pump used in filter-feeding (Olson and Feduccia, 1980a), giving rise to a characteristic "duck-billed" shape that may be modified secondarily for other feeding functions. The following features also are characteristic of the Anseriformes, some being convergent with Galliformes (Olson and Feduccia, 1980b; Ericson, 1996): the configuration of the quadrato-mandibular articulation; the enlarged, deep, curved, blade-like retroarticular process of the mandible; and the enlarged rounded or ovoid "basipterygoid process" on the parasphenoid rostrum, with a corresponding enlarged facet on the pterygoid. These characters are practically all that exist to demonstrate the anseriform relationships of both living and fossil screamers (Anhimidae), in which the bill has either lost or never had the adaptations for filter-feeding. The holotype of the new species described below has a skull with all of the features typical of the order Anseriformes, to which it clearly belongs.

Family ANSERANATIDAE

Recognition of the living Australian Magpie Goose, *Anseranas semipalmata,* as a monotypic family of Anseriformes has been supported by several anatomical studies (e.g., Verheyen, 1953; Woolfenden, 1961; Livezey, 1986), and the distinctiveness of this species is confirmed by DNA sequencing as well (Michael Sorensen, University of Michigan, pers. comm., 1996). Two presumably derived characters group the fossil genus *Anatalavis* in the same family as *Anseranas.* The first is the unique V-shaped furcula with a large, deep symphysis. In other members of the order the furcula is an unelaborated U-shaped structure with a symphysis that is scarcely, if at all, larger than the rami. I interpret the former condition to be a derived character within the Anseriformes. If it is primitive, the only outgroups that show any similarity (and this only in a general way) are storks (Ciconiidae) and, to an even lesser extent, herons (Ardeidae). The second character is the presence of a distinct, large pneumatic foramen in the dorsal surface of the sternal end of the coracoid. Although a similar condition exists in modern Anhimidae, which have one of the most pneumatized skeletons in any group of birds, this foramen is absent in Eocene Anhimidae, which are evidently completely nonpneumatic (pers. obs.). Therefore, the condition in modern screamers is obviously independently derived and is not an indication of relationship with the Anseranatidae.

Subfamily ANSERANATINAE

INCLUDED GENUS.—*Anseranas* Lesson.

DIAGNOSIS.—Subfamilial characters are intended as diagnostic only within the Anseranatidae. Rostrum strong, deep, and hooked; frontal area with a large bony casque; attachment for M. depressor mandibulae not greatly developed. Humerus of normal anseriform proportions. Pelvis with anterior portions of the ilia narrow.

Subfamily ANATALAVINAE, new subfamily

INCLUDED GENUS.—*Anatalavis* Olson and Parris, 1987.

DIAGNOSIS.—Rostrum very broad and shallow, not hooked; frontal area without bony casque; attachment for M. depressor mandibulae greatly enlarged. Humerus proportionately very short and extremely robust. Pelvis with anterior portions of ilia markedly expanded and rounded.

Anatalavis Olson and Parris, 1987

TYPE SPECIES.—*Telmatornis rex* Shufeldt, 1915.

INCLUDED SPECIES.—*Anatalavis rex* (Shufeldt), *Anatalavis oxfordi,* new species.

The genus *Anatalavis* was proposed for the species *Telmatornis rex* from the Hornerstown Formation in New Jersey, which differed from the type species *Telmatornis priscus* Marsh in the proportionately much shorter, more robust, and curved shaft of the humerus (Olson and Parris, 1987). *Anatalavis rex* is known so far only from two humeri lacking the proximal ends and was assigned to the form-family Graculavidae, which was used to include various fragmentary postcranial fossils showing similarities to the Presbyornithidae, Burhinidae, and other families. At the time, it was recognized that if cranial material could ever be associated with any of the genera of Graculavidae, it would probably prove possible to refer them to various other families or orders (Olson and Parris, 1987). The age of the fossil birds from the Hornerstown Formation remains controversial, being either latest Cretaceous or early Paleocene (Olson and Parris, 1987; Olson, 1994).

The fossil from the London Clay is herein assigned to *Anatalavis* because the humerus is identical in proportions and has the same distinctive curvature and robustness as that of *A. rex* (Figure 8), which it matches in all details except size. At the time the genus *Anatalavis* was proposed, it was thought that the humerus appeared somewhat duck-like, hence the name, and this is fully borne out by the associated fossil from the London Clay.

Anatalavis oxfordi, new species

FIGURES 1–9

HOLOTYPE.—Partial, associated skeleton, BMNH Department of Palaeontology registry number A5922. Collected 12 October 1991 by Andrew Oxford and Michael Daniels.

TYPE LOCALITY.—Tidal mudflats and basal cliffs at Walton-on-the-Naze, Essex, England.

HORIZON.—London Clay (Ypresian), lower Eocene.

MEASUREMENTS OF HOLOTYPE (in mm).—*Skull* (measurements taken from ventral aspect): Total length from posterior of cranium to tip of bill as preserved, 100 (measurement longer than it should be due to separation of cranium and rostrum); length from posterior of cranium to apparent nasofrontal hinge, 46.5; length and width of right nostril, 8.6 × 5; length from anterior margin of nostril to bill tip, 34; maximum width of bill as preserved, 27.5.

Skull (measurements taken from dorsal aspect): Width of interorbital bridge, 21.5; width of frontals at nasofrontal hinge, 12.7; dorsal length and width of narial opening, 12.0 × 6.5; width of internarial bar, ~2.5; width of cranium across squamosal protuberances, 25.3; depth (including occipital condyle) and width (across occipital condyle) of area of cervical muscle attachment, 18.5 × 19.3.

Mandible: Length of retroarticular process, 11.0; depth of retroarticular process at midpoint, 6.9.

Pterygoid: Total length, 11.4; greatest diameter of basipterygoid facet, 4.6.

Atlas: Depth, 9.8; width, 8.5.

Axis: Length of centrum, 12.2; depth, 10.8.

Thoracic Vertebra (19th?): Length of centrum, 10.9.

Caudal Vertebra: Width (double the distance from tip of transverse process to midline), 17.8; length of centrum, 6.7.

Furcula: Length from apex of right ramus to farthest extent of symphysis, 53.7; depth of symphysis, 14.4; width and depth of ramus at broadest point, 7.0 × 2.1.

Coracoid: Length from head to internal angle, 48.0; width and depth of shaft at approximate midpoint (narrowest point below procoracoid process), 8.7 × 4.5; depth through head, 9.3; distance from distal margin of procoracoid foramen to internal angle, 29.0; width of sternal articulation, 22.3.

Scapula: Length from acromion to posterior tip, ~79; width of articulation including acromion, 12.5; depth of articular end, 4.4; greatest width of shaft, 7.0.

Sternum: Anterior depth through carina, 39.3; estimated width through third costal facet, 42.5; width of anterior base of carina, 5.6.

Pelvis: Width across antitrochanters (estimated by doubling distance to midline), 46; length from anterior margin of iliac shield to posterior margin of antitrochanter, 52; anterior depth of synsacrum, 24.

Humerus: Length, 119.3; length from head to distal margin of pectoral crest, 41.7; width and depth of shaft at midpoint, 9.7 × 7.8; depth through internal tuberosity, 20; distal width and depth, 22.3 × 11.7; length of radial condyle, 11.6.

Ulna: Width and depth of shaft at approximate midpoint, 6.6 × 6.8; distal depth ~13; distal width, 10.7+.

Ulnare: Greatest diameter, 13.5.

Carpometacarpus: Length, 69.5; length from proximal symphysis to distal end, 43.8; length of intermetacarpal space, 32.8; length of distal symphysis, 11.0; proximal depth, 18.5; width of trochlea, 9.7; distal width, 10.0; greatest width of major metacarpal, 6.9.

Alular Digit: Length, 21.3.

Major Digit, Phalanx 1: Length, 30.2; proximal width, 8.0; distal depth, 7.8.

Major Digit, Phalanx 2: Length, 22.7.

Minor Digit: Length, 15.2.

ETYMOLOGY.—Dedicated to the collector and donor, Andrew Oxford, of Great Mongeham, Kent.

DIAGNOSIS.—Much larger than *Anatalavis rex* (Table 1).

PRESERVATION OF THE HOLOTYPE.—The holotype is essentially an associated, partially articulated skeleton lacking the posterior half of the pelvis, the tail (except one caudal vertebra), and both hindlimbs. The skull, vertebral column, pectoral girdle, and wings are present, although in various states of preservation and with some elements missing (e.g., the right wing is missing except the proximal two-thirds of the humerus and one phalanx).

TABLE 1.—Comparative measurements (mm) of the humerus of the two species of *Anatalavis* (*A. rex*, holotype and paratype, from Olson and Parris, 1987).

Measurement	*A. rex*	*A. oxfordi*
Length from distal end of pectoral crest to ulnar condyle	49.1, 50.7	80.0
Shaft width at midpoint	5.4, 5.6	9.7
Width of shaft at proximal extent of brachial depression	7.2, 7.5	13.2
Depth through radial condyle	7.3, 7.5	12.1
Distal width	3.6, 13.2	22.3

Cranium and Bill (Figures 1, 2): The skull is considerably distorted through compression and by having been pushed into other bones. Although the rostrum and cranium appear to be continuous, they are actually no longer articulated and have bone, mostly of the palatal region, in the intervening space. The cranium is abraded along the left (dorsal) margin, the palatines are crushed and distorted and are pushed over to the right of the midline. The right quadratojugal is present and more or less in place. What may be most of the left quadratojugal was broken off and is present as a separated bone. The left pterygoid is well preserved as a separate bone (Figure 3). The rostrum has portions of the left margin abraded. The entire bill is turned upward through compression, having been pressed into an underlying portion of humerus that has made a great depression in the left dorsal surface, which is seen as a large tumescence in ventral view. As seen in dorsal aspect, crushing has produced a large, somewhat triangular pit in the cranium just anterior to the parietals. The nasal part of the nasofrontal articulation is very badly crushed and distorted on the left side but is somewhat better preserved on the right. The left nostril is crushed and almost obliterated, whereas the right one is almost undistorted.

Lacrimal?: What is possibly a portion of the right lacri-

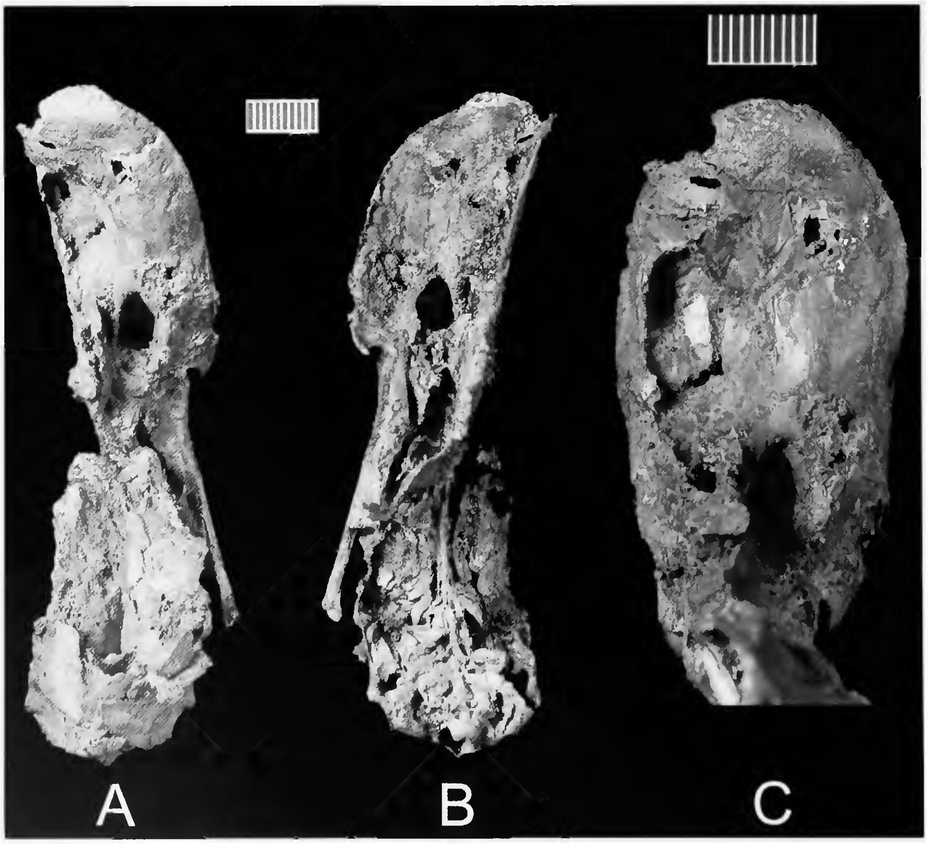

FIGURE 1.—Skull with rostrum of *Anatalavis oxfordi* (holotype, BMNH A5922): A, dorsolateral view; B, ventrolateral view; C, rostrum in direct dorsal view. Scales in mm.

mal was found under the right orbit, but it is so fragmentary that no interpretation can be made of it. Regardless, it is clear from the cranium that the lacrimal was not fused.

Mandible (Figure 4): The mandible appears to have slipped forward during burial, and most of it has been eroded off the original block of matrix. Only the right articular por-

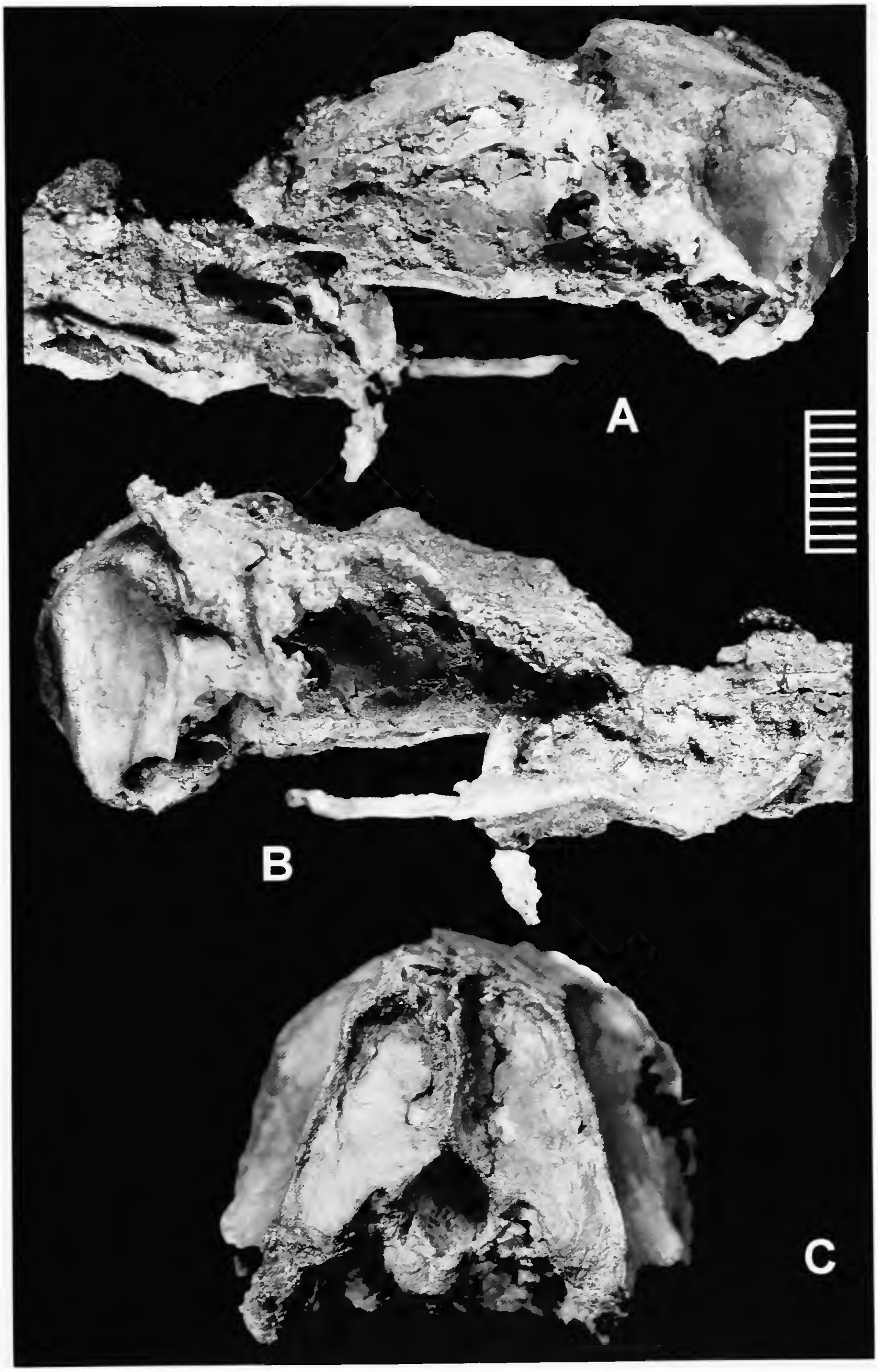

FIGURE 2.—Cranium of *Anatalavis oxfordi* (holotype, BMNH A5922): A, left lateral view; B, right lateral view; C, posterior view. Scale in mm.

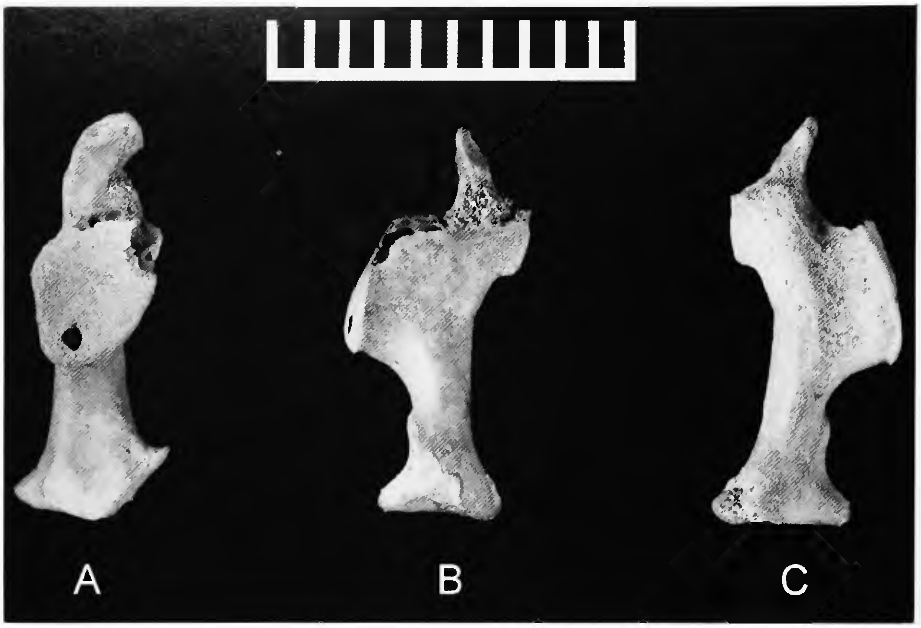

FIGURE 3.—Left pterygoid of *Anatalavis oxfordi* (holotype, BMNH A5922): A, medial (internal) view; B, dorsal view; C, ventral view. Scale in mm.

FIGURE 4.—Right articular portion of the mandible of *Anatalavis oxfordi* (holotype, BMNH A5922): A, lateral (external) view; B, medial (internal) view; C, dorsal view. Scale in mm.

tion, with retroarticular process and an unidentified adherent piece of bone, was preserved with the specimen, lying under the rostrum.

Vertebrae: Vertebrae 1 through 4 are present, as are at least four thoracics, fragments of other vertebrae, and a single caudal lacking most of the right transverse process and neural crest. There also are various fragments of ribs and other pieces of unidentified bone.

Furcula (Figure 5): Complete except lacking the very tip of the left ramus and showing some lateromedial distortion.

Coracoids (Figure 6A–F): The right coracoid lacks the external angle and the tip of the procoracoid process. The left lacks the head and the tip of the external angle.

Scapulae (Figure 6G): Both are present and complete except the left lacks much of the coracoidal articulation.

Sternum (Figure 7): This lacks the posterior one-third or so, with much of the left side being badly damaged. The anterior part of the carina is well preserved. The sternocoracoidal processes are variously damaged or obscured, and the dorsal surface of the anterior portion is obscured by the anterior part of the pelvis and matrix.

Pelvis (Figure 7): This consists of the anterior half or more. The right side is lacking posterior to the anterior iliac shield, and the left side is obscured anteriorly by the sternum but posteriorly preserves the dorsal part of the acetabulum, antitrochanter, and part of the posterior portion of the ilium.

FIGURE 5.—Furcula of *Anatalavis oxfordi* (holotype, BMNH A5922): A, anterior view; B, posterior view; C, right lateral view (rotated slightly clockwise). Scale in mm.

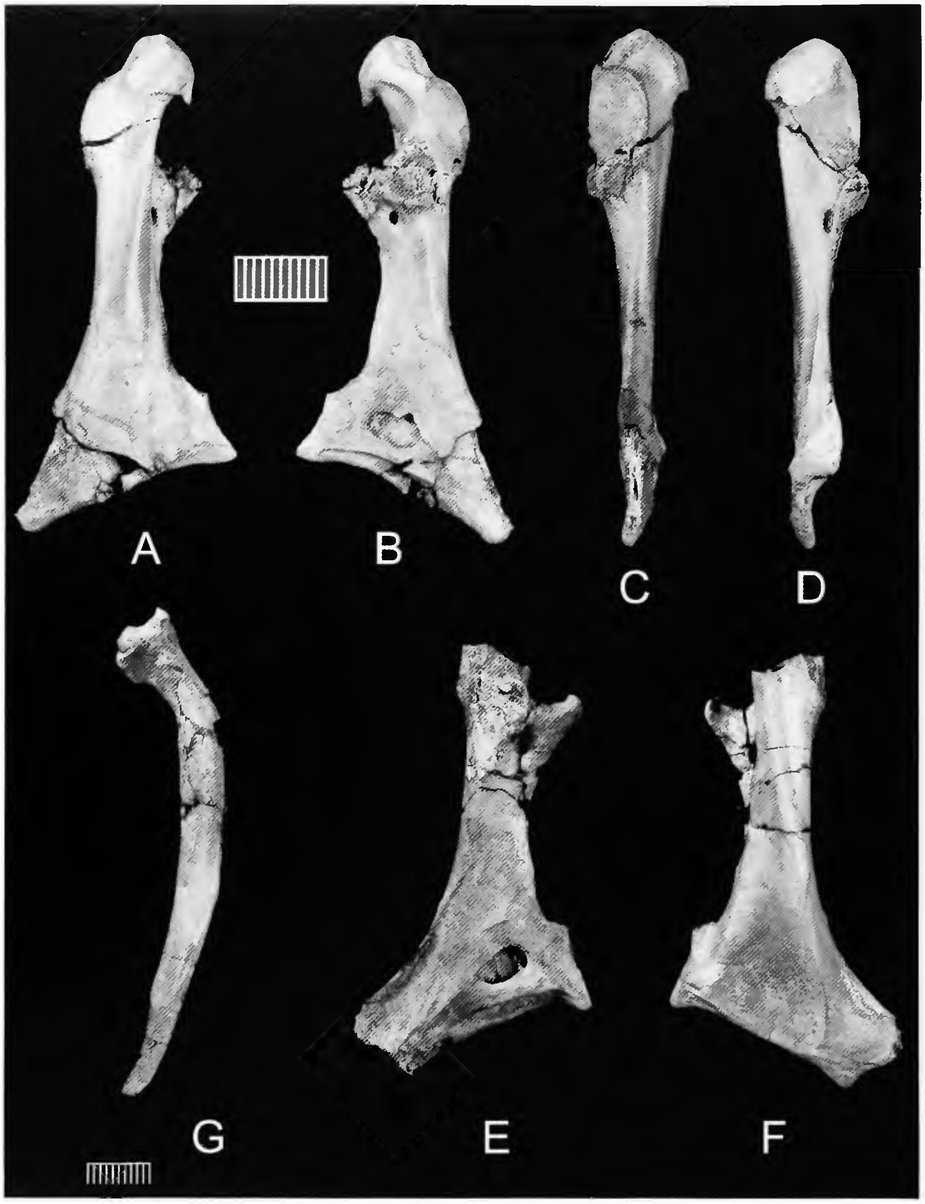

FIGURE 6.—Coracoids and scapula of *Anatalavis oxfordi* (holotype BMNH A5922): A–D, right coracoid in (A) ventral view, (B) dorsal view, (C) lateral (external) view, (D) medial (internal) view; E,F, left coracoid in (E) dorsal view, (F) ventral view; G, right scapula in ventral view. Scales in mm.

Humeri (Figure 8): The left is complete, lacking a bit of the pectoral crest and has the proximal end somewhat crushed and distorted. The right lacks the distal one-third and is much crushed and obscured by adhering matrix and bone.

Radius and Ulna: These are represented only by the distal two-thirds or more of the left radius and ulna. The radius lacks much of the articular end, and the ulna has the internal condyle broken and the distal end obscured by an adhering piece of bone.

Carpal Bones: Only the left ulnare (Figure 9) was located and identified.

Carpometacarpus (Figure 9): The right is lacking. The left is complete, having been broken and repaired, with a small piece of the major metacarpal missing and the whole element showing some compressional distortion.

Alar Phalanges (Figure 9): All phalanges of the major and minor digits of the left wing are present, as is phalanx 1 of the right major digit. The single alular digit is presumably that of the left side as well.

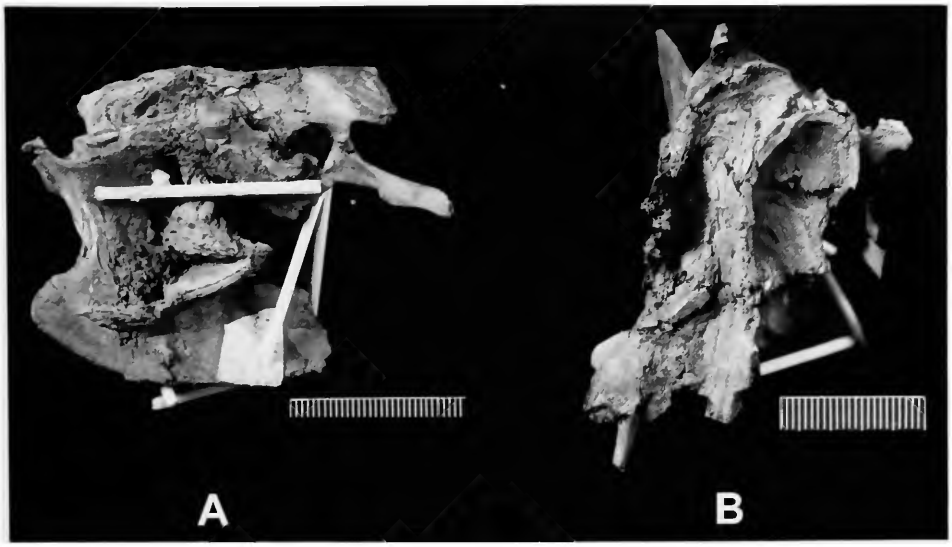

FIGURE 7.—Sternum and pelvis of *Anatalavis oxfordi* (holotype, BMNH A5922): A, left lateral view; B, dorsal view. Scales in mm.

FIGURE 8.—Left humeri of *Anatalavis*. A–C, *A. oxfordi* (cast of holotype, BMNH A5922) in (A) anconal view, (B) palmar view, and (C) palmar view, at lesser magnification. D, *A. rex* (paratype Yale Peabody Museum 948), enlarged for comparison with C. The slight differences are mainly due to slightly different rotation of the specimens. Scale bars=1 cm.

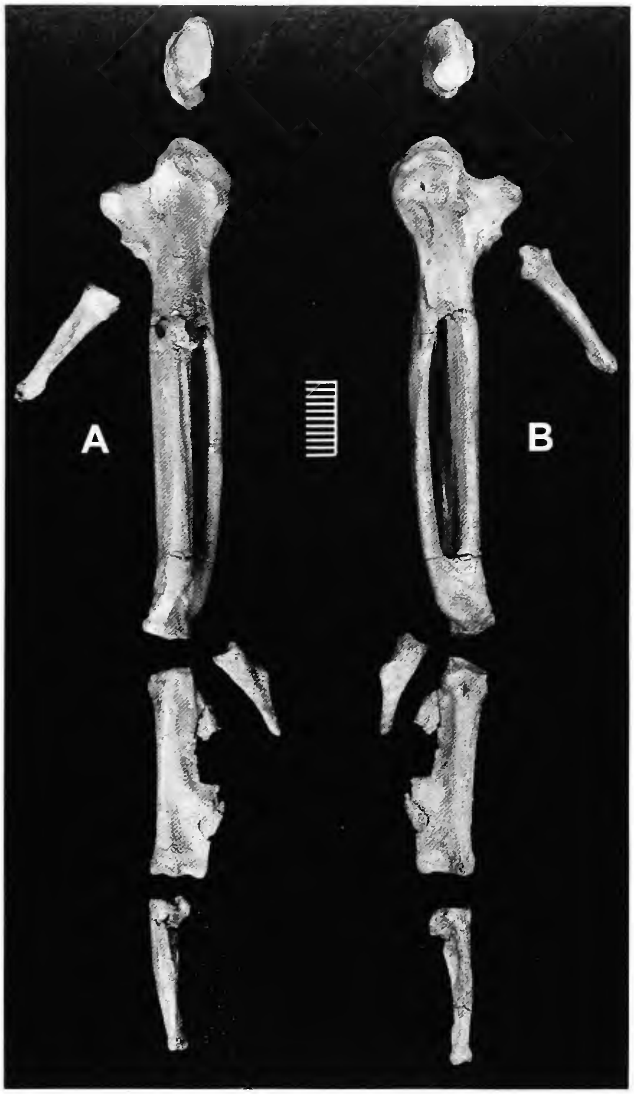

FIGURE 9.—Left manus (ulnare, carpometacarpus, and phalanges) of *Anatalavis oxfordi* (holotype, BMNH A5922) in (A) dorsal view and (B) ventral view (bottom). Scale in mm.

Description and Comparisons

Direct comparisons were made with the three major groups of living Anseriformes. Anhimidae: *Chauna chavaria* male, BMNH S/1954.3.3. Anseranatidae: *Anseranas semipalmata* male (by skull morphology), BMNH 1891.7.20.110; female (by skull), BMNH 1862.7.6.6 (Vellum catalog 441c). Anatidae: *Dendrocygna bicolor* male, BMNH S/1952.1.163; *Anser fabalis*, BMNH 1930.3.24.204.

Using the descriptions and photographs, further comparisons were made with various other taxa of Anseriformes and with Eocene fossils assigned to the Anhimidae and Presbyornithidae, using collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., and of Michael Daniels.

CRANIAL ELEMENTS

SKULL (Figures 1, 2).—There is so much crushing and distortion of the skull that interpretation of many of its aspects is often very difficult. The bill is obviously very different from that of *Anseranas* in being short and very wide, with the bone being quite thin. How concave the ventral surface may have been is now difficult to say, but it cannot have been as deeply excavated as in *Anseranas.* The tip is extremely broad and rounded, quite unlike the pointed, nail-like tip of *Anseranas.* The nostrils are very short, broad, and rounded compared with any other anseriform. The internarial bar is very narrow. As preserved, the nostrils in ventral view are almost completely exposed, there apparently being no roofing over of bone (secondary palate) by the maxillopalatines. If this is not the product of breakage, then the condition is unlike that of *Anseranas* or the Anatidae and is more like that in the Anhimidae. The posterior flange of the rostrum below the anterior articulation of the quadratojugal bar is reasonably well developed, about as in *Dendrocygna,* and is not as large, elongated, and pointed as in *Anseranas.*

The interorbital bridge is much wider than in *Anseranas* and bears no hint of the bony casque of that species. From the appearance of the left side, the lacrimals must have been unfused, as in *Anseranas,* which is the primitive condition shared with *Presbyornis* and Anhimidae, as opposed to the Anatidae, in which the lacrimals are fused.

The postorbital process is quite short and blunt, unlike any of the anseriforms compared (smaller in *Chauna,* but pointed). The posterior portion of the temporal fossa bears extremely broad, nearly rectangular scars indicating great development of M. depressor mandibulae, perhaps more so than in any extant waterfowl. In *Anseranas* these scars are narrow and are much less distinct. The anterior temporal fossa is hardly distinguishable in the fossil, however, indicating lesser development of the mandibular adductors. The combination of the deep scars of the depressor mandibulae and the well-developed area of attachment of the cervical musculature produces very distinct nuchal crests on the occiput (Figure 2C). The occipital area may have been crushed lateromedially, thus reducing the size of the foramen magnum, which seems comparatively small, although the occipital condyle is large relative to that of *Anseranas.* There are two vertically oriented, narrow, elongate foramina situated where the large, oval occipital fontanelles occur in most Anseriformes, the two presumably being homologous. It is not clear whether these are evolutionarily incipient fontanelles or whether the fontanelles have become mostly closed by bone, as occurs in certain modern waterfowl.

PTERYGOID (Figure 3).—By virtue of the distinctive facet for articulation with the basipterygoid process of the parasphenoid rostrum, the pterygoid of *Anatalavis* is recognizably anseriform, yet it differs markedly from modern members of the order. The bone is very short and robust, with the basipterygoid facet proportionately very large but nearly round in shape rather than being an elongate oval as in *Anseranas* and *Anser.* The quadrate articulation is much larger and more expanded, and the palatine articulation is completely offset laterally from the main (long) axis of the bone, rather than being in a line with it as in other anseriforms.

MANDIBLE (Figure 4).—Only the right articular is preserved, and this has a large, blade-like retroarticular process that curves upward at the tip. It is very anseriform in appearance but is shorter, deeper, and thicker than typical forms, looking more like that in *Chauna,* although it is relatively larger. The medial process, although broken, is very small, unlike any modern anatid, and the lateral process is likewise not nearly as well developed. Although partly obscured by an adhering piece of bone, the articular surface looks typically anseriform, perhaps most similar to that in *Chauna.* The ramus seems to rise immediately to a deep coronoid process.

The recessus conicalis is absent. This is a deep conical hollow extending on the medial side from the retroarticular process anteriorly under the articulation. It represents a derived character uniting the Presbyornithidae and Anatidae, but it is lacking in *Anseranas* and the Anhimidae (Ericson, 1997).

AXIAL POSTCRANIAL SKELETON

THORACIC VERTEBRA.—The best-preserved thoracic vertebra appears to be equivalent to the 19th of *Anseranas* (which is the sixth in front of the sacrum and the first with a full thoracic rib, but no sternal attachment, so that technically this would be the last cervical). This is very similar to that in *Anseranas* except that the sides of the centrum are concave, with a small pneumatic foramen that is lacking in *Anseranas.* Evidence from various Eocene waterbirds suggests that the condition of having concavities on the centrum, which is characteristic of the Charadriiformes, for example, may be primitive.

FURCULA (Figure 5).—The furcula is absolutely distinctive in being V-shaped and having a long, broad symphysis, thus resembling only *Anseranas* among the Anseriformes, which otherwise have a simple U-shaped furcula. The fossil differs from *Anseranas* in that most of the symphysis is a thin, nearly translucent sheet of bone with a sharp, low crest running down the midline on the posterior face, whereas in *Anseranas* the symphysis has become thickened and pneumatized, with a pneumatic foramen on the dorsal surface and the posterior crest much less distinct. In lateral view the fossil is wide throughout but is thin and flat lateromedially, whereas in *Anseranas* the rami become narrower toward the symphysis but are much thicker lateromedially than in the fossil. The ramus in the fossil comes to a very sharp point dorsally but is not expanded into an angular flange on the anterodorsal edge as in *Anseranas,* which gives the ramus in the latter a more curved appearance.

The furcula in both *Anatalavis* and *Anseranas* differs from that in the Anatidae in being less curved, with the portion posterior to the articulation not forming an angle and extending posteriorly. The modern Anhimidae are utterly different from any of these in having a furcula that is very broad, flat, and pneumatic posteriorly on both rami.

CORACOID (Figure 6A–F).—The fossil has a narrow, pointed procoracoid process, whereas in *Anseranas* this is much broader, blunter, and extends farther sternally. The procoracoid process in *A. oxfordi* has a distinct circular foramen. This is the primitive condition that in Anseriformes is retained in *Anseranas,* Eocene and modern Anhimidae (in the latter it may sometimes be absent; see Alvarenga, this volume), and the Presbyornithidae. The procoracoid foramen has been lost in all Anatidae. Although a similar structure appears in the New Zealand fossil genus *Cnemiornis* and in some individuals of *Cereopsis* (Livezey, 1989), this probably evolved secondarily through ossification of ligaments.

On the internal dorsal surface of the sternal end of the coracoid of the fossil there is a large, sharply delimited, ovoid pneumatic foramen. This also is found in *Anseranas,* where it may vary from a larger, although less distinctly edged, foramen, to a depression with only a pinhole foramen. A very large pneumatic foramen occurs in about the same place on the coracoid of modern Anhimidae, but this is entirely absent in the Eocene members of the family and must therefore have evolved independently as a result of the extreme pneumatization of the skeleton in modern screamers.

The whole sternal end of the bone in the fossil is more expanded, with the external angle a longer, sweeping wing. There also is a distinct projecting angle on the medial edge just above the internal angle that is not found in *Anseranas.* In sternal view the medial part of the sternal articulation is not nearly as deep and expanded as in *Anseranas.*

SCAPULA (Figure 6G).—This bone appears to be relatively longer than in the Anatidae but is not as narrow as in *Anseranas* and apparently has the acromion narrower and more pointed.

STERNUM (Figure 7).—In lateral view the sternum differs from that of *Anseranas* in having the apex of the carina more rounded and undercut by a broad, rounded notch. The distinctly projecting, blunt, triangular manubrial spine in the fossil is lacking in *Anseranas.* In these respects the sternum in the fossil is more similar to that in *Chauna;* however, in *Chauna* the manubrium is shorter and blunter.

PELVIS (Figure 7).—The remaining portion of the pelvis is very different from that in any known member of the Anseriformes because the preacetabular portion is relatively short and the anterior iliac shield is very broad, rounded, and deeply excavated for the iliotrochantericus muscles, leaving a broad, well-defined dorsal ridge. In overall appearance, the pelvis in the fossil is more like that in certain wading birds, such as ibises (Plataleidae) and other Ciconiiformes, or Charadriiformes, than in any anseriform. The acetabulum in the fossil is relatively larger than in *Anseranas.*

The ilia appear to be fully fused to the sacral vertebrae, as in all living Anseriformes, which makes the unfused innominates of *Presbyornis* seem all the more anomalous.

PECTORAL APPENDAGE

HUMERUS (Figure 8).—The humerus is characterized by the extremely short, robust shaft with markedly sigmoid curvatures both anteroposteriorly and lateromedially. The total length of the bone is 33% shorter than in *Anseranas,* yet the shaft is slightly wider, indicating very different proportions and presumably a much different flight pattern. The pectoral crest is very broad and rounded, unlike *Anseranas* or the Anatidae, but is somewhat similar to *Chauna.* The head and internal tuberosity are massive, and the capital groove is extremely wide and deep, unlike other anseriforms. The orientation of the internal tuberosity may have been distorted by compression and perhaps pushed distally; regardless, it overhangs the tricipital fossa, which is small and may not have been pneumatic (obscured by pyrite). The capital ridge is very well defined.

The distal end is expanded and flattened compared with most Anatidae but is generally similar to that of *Anseranas* except that the brachial depression is longer and narrower, the radial condyle is longer, and the olecranal and tricipital fossae are slightly deeper. The twisting of the shaft is remarkable because it appears as though the distal end has been rotated clockwise about the long axis of the bone by perhaps 15° or more.

RADIUS AND ULNA.—In their incomplete condition there is little to be said about these elements. Compared with *Anser,* the fossil radius agrees with *Anseranas* in the more expanded distal end and more slender shaft, which is more sharply angular in cross section, with more flattened surfaces than in *Anseranas.*

CARPOMETACARPUS (Figure 9).—This element agrees with that of *Anseranas* in being short and stout, although it is more robust even than that in *Anseranas.* It is intermediate in length between the male and female specimens compared. The alular metacarpal is more vertically oriented than in *Anseranas* and is more like that in the Anatidae. It also is much blunter, with a larger digital facet.

ALAR PHALANGES (Figure 9).—Phalanx 1 of the major digit is relatively short and stout, as in *Anseranas,* but the proximal articulation is wider and not as deep. Phalanx 2 of the major digit and the minor digit are each relatively shorter, the former much more so, than in *Anseranas.*

Discussion

The two species of *Anatalavis* provide the only recognized occurrence of the family Anseranatidae in the fossil record. *Anatalavis rex,* from the Hornerstown Formation of New Jersey, whether Late Cretaceous or early Paleocene in age, also provides the earliest certain record of the entire order Anseriformes. The material of *Anatalavis oxfordi,* from the lower Eocene London Clay, is more complete than that of any early Tertiary anseriform yet described, apart from *Presbyornis,* and provides us with a new set of clues regarding early evolution in waterfowl.

The skull in *Anatalavis oxfordi* indicates that it was most likely an obligate filter feeder. The bill is very broad yet is thin and weak. The retroarticular process of the mandible is quite well developed, although not nearly to the extent observable in the more extreme members of the Anatidae, yet the massive development of M. depressor mandibulae shows it to have been more adapted for straining, as opposed to grasping, in which the mandibular adductors play a greater role (Goodman and Fisher, 1962). This is practically the opposite of its nearest presumed relative, the Australian Magpie Goose (*Anseranas semipalmata*), in which the bill is strong, deep, and hooked and is used in digging out tubers and other plant material (Frith, 1967).

Although the palate is very poorly preserved in the holotype of *A. oxfordi,* the fundamentally different morphology of the pterygoid compared with modern Anseriformes suggests that aspects of the organization and function of the skull in *Anatalavis* may have differed considerably from that in living waterfowl.

In the shoulder girdle, the peculiar structure of the furcula and the pneumatic foramen in the dorsal surface of the sternal end of the coracoid are considered to be derived characters uniting *Anatalavis* and *Anseranas* in the family Anseranatidae. The two otherwise have very little else in common that is not generally present in most of the rest of the order.

The proportionately short and very robust, twisted humerus of *Anatalavis* is unique in the order and bespeaks a different mode of flight that probably was very strong and rapid. Many extant waterfowl are strong, fast fliers without having such a robust humerus, however. The overall proportions of the humerus are more like those of a falcon (*Falco,* Falconidae), although why a filter feeder would need such a wing is not easily envisioned.

The pelvis of *Anatalavis* is likewise peculiar for an anseriform in the short, expanded anterior portions of the ilia, whereas in all other waterfowl, including the Anhimidae, the preacetabular part of the pelvis is longer and narrower. From its resemblance to such wading birds as ibises (Plataleidae) and other Ciconiiformes, the pelvis of *Anatalavis* is presumably primitive within the order. The innominate bones, however, are fused to the sacrum, which is a more derived condition also found in Ciconiiformes and other Anseriformes except *Presbyornis.* In the lack of fusion of the innominates, *Presbyornis* more nearly resembles the Charadriiformes.

With the recognition of *Anatalavis* as a member of the Anseranatidae, we can trace each of the three major modern lineages of Anseriformes back to the early Eocene, or earlier in the case of *Anatalavis.* According to the phylogeny developed by Ericson (1997), the Presbyornithidae, which were probably world-wide in distribution in the early Tertiary, are on the lineage leading to the Anatidae proper. As yet unpublished early

Eocene records of the Anhimidae from Wyoming and England establish that this group was in existence at the same time and occurred outside of South America, the modern members of the family evidently being highly derived relicts. *Anseranas* in Australia likewise now appears to be a rather specialized relict of a once more diverse family Anseranatidae.

Although the Anatidae proper probably existed in the Paleogene, they do not appear with any certainty or regularity in the Northern Hemisphere until the Miocene, from which it has been presumed that the family probably originated in the Southern Hemisphere (Olson, 1989). Possibly the Anseranatidae was the more diverse family in the Northern Hemisphere in the Paleogene, and the possible affinities of such taxa as the late Eocene *Romainvillia* Lebedinsky (1927), from France, and *Cygnopterus* Lambrecht (1931), from the early Oligocene of Belgium, with the Anseranatidae should be investigated.

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New Material of *Juncitarsus* (Phoenicopteriformes), with a Guide for Differentiating that Genus from the Presbyornithidae (Anseriformes)

Per G.P. Ericson

ABSTRACT

In many aspects the postcranial skeleton of the early Tertiary *Juncitarsus* (Phoenicopteridae) is very similar to that of *Presbyornis* and *Telmabates* (Presbyornithidae). The phylogenetic positions of the two families indicates that these similarities are due to the retention of morphologies possessed by their most recent ancestor. This paper shows how finds of isolated skeletal elements of either genus can be correctly identified.

Introduction

Despite repeated claims to the contrary, remains of birds are not rare in the fossil record (cf. Olson, 1985); for example, numerous bird bones have been collected from early Tertiary deposits in the United States, Europe, Russia, and China. One of the most abundant taxa in certain Paleocene and Eocene deposits is the Presbyornithidae, a family of long-legged filter feeders that is the sister group to the Anatidae within the order Anseriformes (Ericson, 1997). The Presbyornithidae are normally found in inland freshwater, or possibly saline, environments. This habitat also was occupied by several other long-legged wading birds. Most of these species are represented in the fossil record by isolated bone elements; however, one of these, *Juncitarsus,* is known from several associated elements from at least four individuals, which were described and allocated to the Phoenicopteridae (flamingos) (Olson and Feduccia, 1980).

In the course of a revision of the New World material of the early Tertiary Presbyornithidae (Ericson, in prep.), great similarities in many aspects of the osteology of the Presbyornithidae and *Juncitarsus* were noticed. Nevertheless, many of these elements also exhibit consistent differences that serve to differentiate the two taxa. These differences are pointed out herein with the intention of facilitating the future identification of isolated skeletal elements of the Presbyornithidae and *Juncitarsus.*

Unfortunately, apart from a partial skeleton of *Anatalavis* from the London Clay, now assigned to the Anseranatidae (Olson, this volume), no articulated or otherwise associated specimens exist of the taxa assigned to the form-family Graculavidae (Olson and Parris, 1987), or to any other Late Cretaceous or early Tertiary group of wading birds supposed to be closely related to the Presbyornithidae. It has thus not been possible to extend the comparisons to include these groups.

ACKNOWLEDGMENTS.—Storrs L. Olson kindly put the undescribed material of *Juncitarsus* at my disposal and strongly encouraged the study. Thanks also are directed toward the curators of the following museums, who willingly loaned their material to me: American Museum of Natural History (AMNH), New York; the Buffalo Museum of Science, Buffalo; the Carnegie Museum of Natural History (CM), Pittsburgh; the Geological Museum, University of Wyoming (UW), Laramie; the Museum of Paleontology, University of California (UCMP), Berkeley; and the National Museum of Natural History (USNM; collections of the former United States National Museum), Smithsonian Institution, Washington, D.C. Charlotte Holton provided information on the AMNH specimens, and Storrs L. Olson and David C. Parris reviewed the manuscript; their assistance is greatly acknowledged.

MATERIAL

The Presbyornithidae consists of two genera, *Presbyornis* and *Telmabates,* known from numerous specimens collected from Paleocene and Eocene deposits in Wyoming, Utah, Colorado, Argentina, and Mongolia (Ericson, in prep.). In this

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study, it has been possible to include first-hand observations only for presbyornithids collected in the New World.

Presbyornithidae

Presbyornis pervetus Wetmore: CM 11360 (holotype), 11358, 11359, 11360a, 12032, 12033, 12035–12038; UCMP 119394–119401, 126173–126257; USNM 492550–492552; UW 20593–20600, 20651–20653, 20655–20666.

Telmabates antiquus Howard: AMNH 3170 (holotype), 3166–3187, 3225–3227.

Phoenicopteridae

Juncitarsus gracillimus Olson and Feduccia: USNM 244318 (holotype), 244319–244322, 244324–244338 (paratypes).

Juncitarsus cf. *merkeli* Peters: Buffalo Museum E 25106 (cast in USNM), referred to this taxon by Peters (1987). Only the published description was available of the German holotype of *J. merkeli* Peters (1987).

Previously unrecognized specimens of *Juncitarsus* from Eocene deposits in Wyoming were discovered in the collections of the National Museum of Natural History and the American Museum of Natural History and are described herein. Both were allocated to the genus *Juncitarsus* through comparisons with the type material of *J. gracillimus.* Although they are too large to be conspecific with *J. gracillimus,* they agree well in size with *J. merkeli.* Most skeletal elements present in the new specimens have already been described (forming the foundation for their allocation to *Juncitarsus*). A few previously unknown, or poorly described elements do occur among the new material.

Genus *Juncitarsus* Olson and Feduccia, 1980

Juncitarsus cf. *merkeli* Peters, 1987

REFERRED MATERIAL.—USNM 468466, apparently associated material consisting of symphyseal part of furcula, parts of costal region and manubrium of sternum, anterior part of left scapula, complete right coracoid, sternal part of left coracoid, caput of right humerus, proximal half of left humerus, distal end of right radius, distal end of right carpometacarpus, right phalanx 1 of digit II, right phalanx 2 of digit II, complete right femur, complete left femur, lateral condyle of right tibiotarsus, distal end of right tarsometatarsus, and four pedal phalanges. Collected in Wyoming, Uinta County, Wildcat Butte, section 1, T. 17 N, R. 113 W, 1 mile south of Church Butte, "very low exposures," on 2 August 1959 by C.L. Gazin.

A second lot of material consists of the following: part of manubrial region of sternum, AMNH 16232; anterior part of left scapula, AMNH 6046; distal end of right ulna, AMNH 5956; proximal end of right radius, AMNH 6025; part of proximal end of left carpometacarpus, AMNH 6028; proximal half of right femur, AMNH 16231; part of proximal end of left femur, AMNH 6007; distal ends of right and left femoras, AMNH 5998; and part of shaft of tarsometatarsus, AMNH 7730.

AMNH 5956–7730 were collected in 1906 by Walter Granger in Wyoming, Sweetwater County, Washakie Basin, 100 ft above the brown sandstone north of Haystack Mountain. They were found in the Washakie Formation, which is of Bridgerian age. AMNH 16231–16232 were collected at an unknown date in Wyoming, Sweetwater County, Washakie Basin, north of Haystack Mountain.

DISTRIBUTION.—Early to middle Eocene in Wyoming and Germany.

DIAGNOSIS.—The collections are referred to the genus *Juncitarsus* based on the skeletal characteristics described in "Comparative Osteology," below. The specimens are tentatively referred to *Juncitarsus merkeli* Peters, 1987, based on their overall similarity in size to this species, being markedly larger than *Juncitarsus gracillimus.* Very few measurements can be directly compared, however. The middle trochlea of tarsometatarsus USNM 468466 is 4.4 mm wide (3.9 mm in *Juncitarsus gracillimus*), and the inner trochlea is 6.9 mm deep (6.3 mm in *J. gracillimus*).

REMARKS.—The two collections may consist of remains from a single individual each. The two finds from Wyoming described herein, together with the Buffalo Museum specimen, referred to *J. merkeli* by Peters (1987), corroborate the intercontinental distribution of *Juncitarsus.* The Buffalo Museum specimen from the early Eocene Green River Formation of Wyoming shows that *Juncitarsus* and *Presbyornis* did overlap in time and space, although the latter seems not to have persisted into the middle Eocene, when *Juncitarsus* became more abundant.

Comparative Osteology

The characteristics described herein are only those that show no overlap between *Juncitarsus* and the Presbyornithidae; however, only a very few specimens exist for comparing *Juncitarsus* with the abundant material of the Presbyornithidae. Although the morphological range in the Presbyornithidae is unlikely to change dramatically with the addition of more specimens, the situation could change for *Juncitarsus,* and with more material, additional aspects of its morphology may overlap with the Presbyornithidae.

The most obvious difference between *Presbyornis* and *Juncitarsus* is the typical desmognathous, duck-like head of the former, in contrast to the schizognathous skull as shown in the holotype of *Juncitarsus merkeli* (Olson and Feduccia, 1980; Peters, 1987). The cranium of *Juncitarsus gracillimus* is almost unknown. Despite the striking differences in cranial morphology, the two taxa are very similar postcranially in several respects. Although many of these similarities may be due to symplesiomorphy, i.e., the retention of primitive morphologies, it can be fairly assumed they also bear witness to a common ancestor not too far removed in time. The Presbyornithidae have been demonstrated to have an anseriform affinity (Ericson, 1997), whereas *Juncitarsus* is thought to have its closest living relatives among the flamingos (Phoenicopteridae) (Olson and Feduccia, 1980; Peters, 1987). The observed similarities in these two fossil taxa thus suggest a systematic proximity of Anseriformes and Phoenicopteridae. This corroborates the conclusion drawn in an extensive phylogenetic analysis (Ericson, 1997) of nonpasserine families (Figure 1).

SKULL.—The only cranial element found of *Juncitarsus gracillimus* is an unfused frontal bone that suggests that *Juncitarsus* has a deeper depression for the supraorbital salt gland and a more rounded margo interorbitalis than does *Presbyornis.*

VERTEBRAE.—No direct comparison between supposedly homologous cervical vertebrae in *Juncitarsus* and the Presbyornithidae has been possible. In general, the upper cervicals of *Juncitarsus* seem to be elongated, resembling those of the Phoenicopteridae (Peters, 1987). No such elongated vertebrae have been observed in *Presbyornis.* Olson and Feduccia (1980) described a cervical vertebra of *Juncitarsus* comparable to the 16th of *Phoenicopterus* and the 15th of *Phoeniconaias.* They stressed the similarities between the Phoenicopteridae and *Juncitarsus* and specifically pointed out the flat, elongated ventral surface with two distinct anterior hemapophyses, along with the presence of a large, sloping neural crest. In *Presbyornis* the ventral surface is flat, too, with distinct anterior hemapophyses. The corpus is considerably narrower in ventral aspect in *Presbyornis,* however, and no vertebra with a high neural arch has been observed. The posterior cervical vertebrae in *Presbyornis* closely match the corresponding ones in the Anseranatidae and certain charadriiform birds, such as the Scolopacidae.

The thoracic vertebrae in *Juncitarsus* are most probably not pneumatized, unlike the Presbyornithidae. Otherwise their morphologies are very similar in being laterally compressed and possessing a well-developed neural spine. This morphology is rather different from that of the Phoenicopteridae but agrees with that of the Charadriiformes. Given the phylogenetic relationships of these taxa (Ericson, 1997), this might be symplesiomorphic.

STERNUM.—It was possible to compare only the manubrial region of the sternum, which showed no differences.

CORACOID.—*Juncitarsus* differs from the Presbyornithidae in having processus acrocoracoideus relatively larger and triangular and facies articularis clavicularis excavated (Figure 2).

FURCULA.—Only the symphyseal part is known of *Juncitarsus,* which seems to be more flattened and narrower than in the Presbyornithidae.

SCAPULA.—The craniodorsal margin of the scapula is straight in *Juncitarsus,* whereas it is generally curved in the Presbyornithidae, with the acromion pointing more dorsally (Figure 3).

HUMERUS.—When comparing *Juncitarsus gracillimus* with *Presbyornis pervetus,* which is of similar size, the humerus seems much more slender in *Juncitarsus.* In the proximal end, *Juncitarsus* differs considerably from the Presbyornithidae in having the caput humeri not undercut at all (deeply undercut in

FIGURE 1.—Phylogenetic position of the Presbyornithidae (from Ericson, 1997). Note the anseriform affinity of the Presbyornithidae and the proximity of the unresolved polychotomy that includes the flamingos, Phoenicopteridae, to the anseriforms.

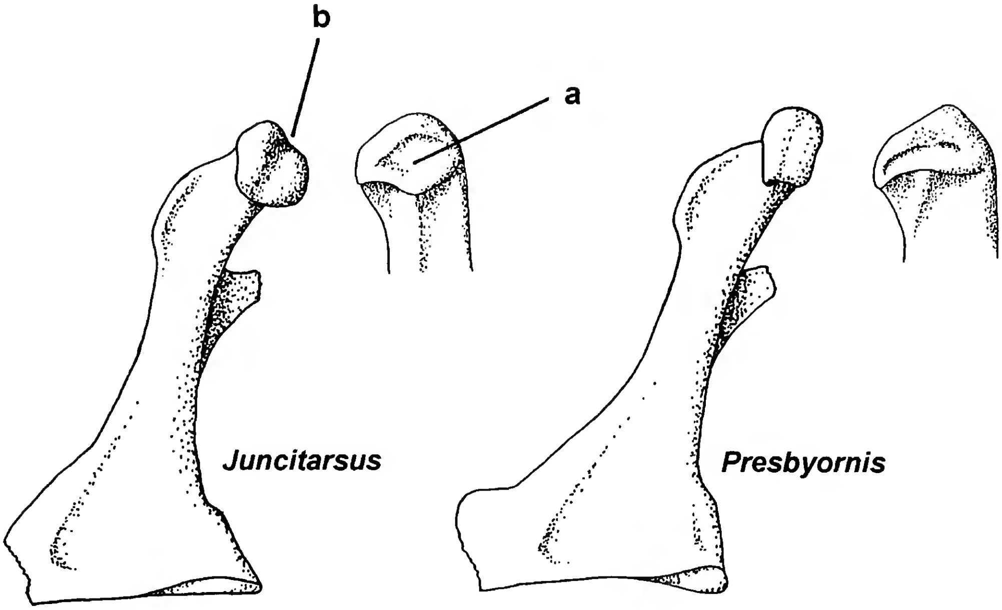

FIGURE 2.—Right coracoid in ventral view, with inset showing the head in medial view. *Juncitarsus gracillimus:* USNM 468466. *Presbyornis pervetus:* UCMP 126194. (*a*=processus acrocoracoideus, *b*=facies articularis clavicularis.)

the Presbyornithidae); the scar for M. scapulohumeralis cranialis forming a shallow to moderately deep, elliptical depression (a narrow, deep scar in the Presbyornithidae); the fossa pneumotricipitalis ventralis small and perhaps pneumatic (a large, deep, nonpneumatic excavation in the Presbyornithidae); the scars for Mm. latissimus dorsi posterioris and anterioris are directed toward a point well distal of where the deltoid crest sets off from the shaft (directed toward where the crest sets off from the shaft in the Presbyornithidae) (Figure 4).

In the distal end of the humerus, *Juncitarsus* differs from the Presbyornithidae in having the attachment area of the anterior articular ligament of Howard (1929) much more elevated and lateromedially narrow; the processus flexorius not as ventrally protruding; probably a well-developed sulcus for M. scapulohumeralis, which is lacking in the Presbyornithidae; and the two scars for M. flexor carpi ulnaris on the processus flexorius distinctly unequal in size (the posterior is considerably larger), whereas these scars are of about equal size in the Presbyornithidae, or the anterior is the larger (Figure 5).

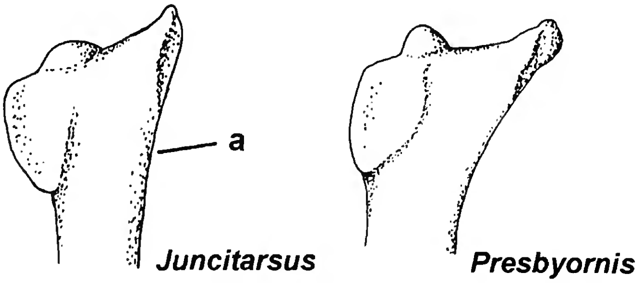

FIGURE 3.—Left scapula in dorsal view. *Juncitarsus gracillimus:* USNM 468466. *Presbyornis pervetus:* UCMP 126193 (in mirror image). (*a*=craniodorsal margin.)

ULNA.—I have found no distinctive differences in the proximal end, maybe due to the poor preservation of the only specimen of *Juncitarsus* available. In the distal end, the tuberculum carpale is short and directed cranially, not clearly craniodistally as in *Presbyornis* (proximodistally much longer and blunter in *Telmabates*).

RADIALE.—Although generally very similar, *Juncitarsus* differs from *Presbyornis* (the only presbyornithid genus in which this bone is known) in lacking the deep excavation of the dorsal side and in having the incisure at the cranial side deeply cut and not as wide (Figure 6).

CARPOMETACARPUS.—The only proximal end known of *Juncitarsus* has the cranial margin of trochlea carpalis (bordering the anterior carpal fossa) convex, not deeply concave as in the Presbyornithidae (Figure 7). No difference has been found in the distal end of the carpometacarpus.

FEMUR.—The femur of *Juncitarsus* seems to be more robust than that in the Presbyornithidae. Furthermore, the femoral neck in *Juncitarsus* is broader in proximal view; the impressiones iliotrochanterici show a very different pattern than in the Presbyornithidae; and the trochlea fibularis is concave, or flat,

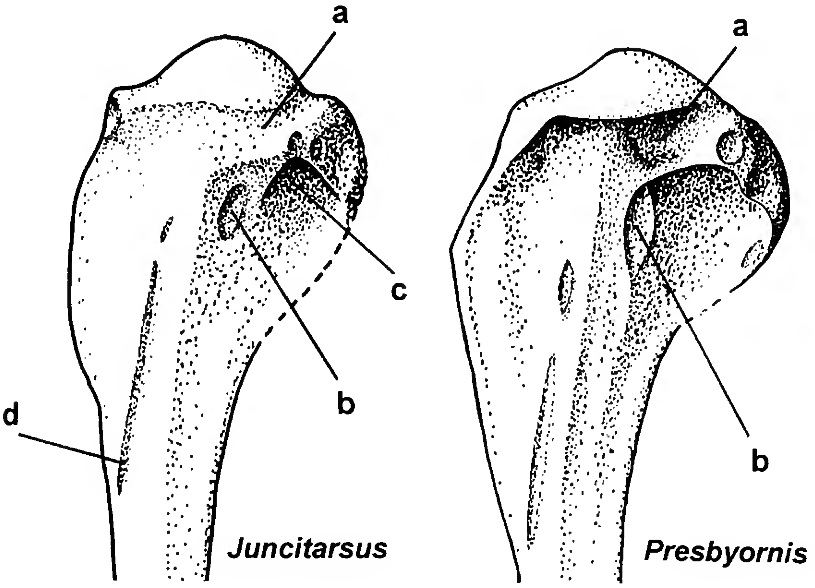

FIGURE 4.—Proximal end of left humerus in anconal view. *Juncitarsus gracillimus:* proximal end USNM 468466. *Presbyornis pervetus:* UCMP 126205; the shape of crista deltoidea, however, is based on USNM 492550 (in mirror image). (*a*=area below caput humeri, *b*=scar for M. scapulohumeralis cranialis, *c*=fossa pneumotricipitalis ventralis, *d*=scars for Mm. latissimus dorsi posterioris and anterioris.)

in lateral view in *Juncitarsus* (most often convex in the Presbyornithidae) (Figure 8).

TIBIOTARSUS.—A part of the distal, lateral condyle is the only adult specimen of *Juncitarsus* available for comparison. It differs from the Presbyornithidae in having the distal margin distinctly concave, not smoothly rounded.

TARSOMETATARSUS.—The tarsometatarsus (Figure 9) is considerably more elongated and slender in *Juncitarsus* than in the Presbyornithidae; the intercotylar knob is much larger; the cotylae are deeper and narrower; the hypotarsus is lateromedially narrower and protrudes more caudally, with the crista lateralis as large as the crista medialis (the crista medialis is very low in the Presbyornithidae); and the shaft is rectangular in both taxa but is laterally very compressed in *Juncitarsus*, not craniocaudally compressed as in *Presbyornis* (insufficiently known in *Telmabates*). The distal end essentially is very similar to the Presbyornithidae but is more laterally compressed; the foramen vasculare is as large as in the Presbyornithidae but is narrower mediolaterally, with its caudal opening situated slightly more proximad; and the scar for the hallux is situated more distally on the shaft.

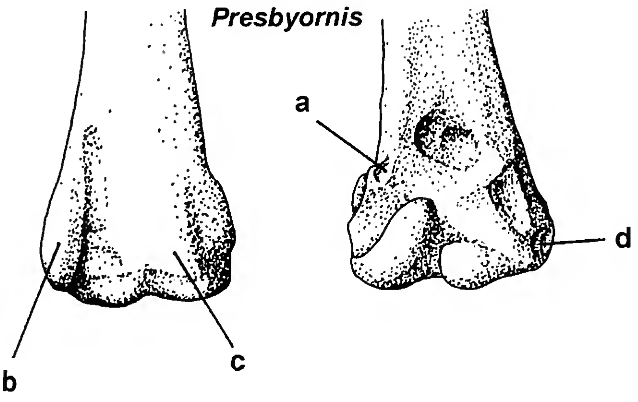

FIGURE 5.—Distal end of right humerus of *Presbyornis pervetus*, UCMP 119399 (in mirror image), in anconal (left) and palmar (right) views. (*a*=attachment for the anterior articular ligament, *b*=processus flexorius, *c*= sulcus M. scapulohumeralis, *d*=scars for M. flexor carpi ulnaris.)

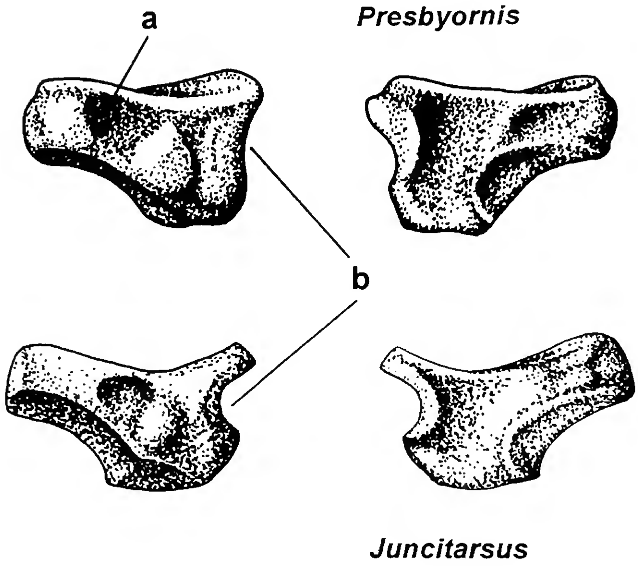

FIGURE 6.—Right radiale in dorsal view (left) and in ventral view (right). *Juncitarsus gracillimus:* USNM 244333 (in mirror image). *Presbyornis pervetus:* USNM 492552. (*a*=excavation of dorsal side, *b*=incisure.)

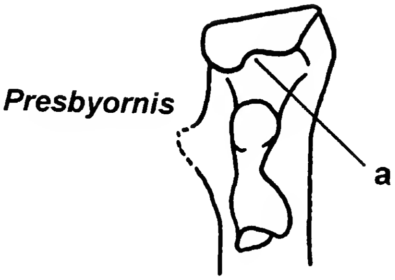

FIGURE 7.—Left carpometacarpus of *Presbyornis pervetus*, UCMP 126228, in dorsal view. (*a*=cranial margin of trochlea carpalis.)

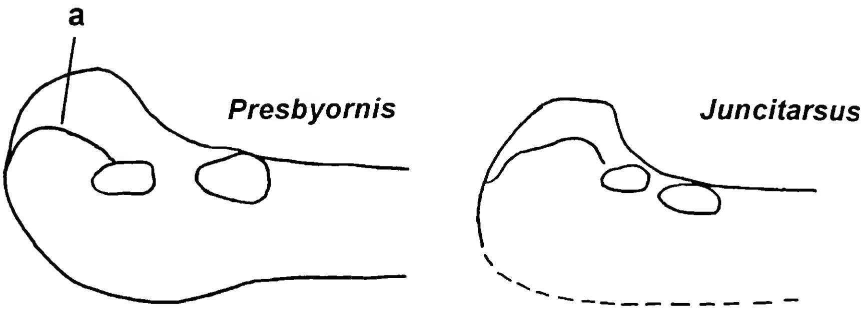

FIGURE 8.—Right femur in external view. *Juncitarsus gracillimus:* USNM 468466 (in mirror image). *Presbyornis pervetus:* UCMP 126244. (*a*=trochlea fibularis.)

Discussion

Despite their close match in general skeletal morphologies, *Juncitarsus* does differ from the Presbyornithidae in several aspects that can be useful in the identification of fragmentary material. Given that *Juncitarsus* is correctly referred to the Phoenicopteridae, it may not be particularly closely related to the Prebyornithidae (Ericson, 1997). Rather, the similarities between the two taxa should be interpreted as symplesiomorphies. Surely, this also is the explanation of the observed morphological similarities between the Presbyornithidae and certain other early Tertiary birds, such as the Graculavidae (Olson and Parris, 1987). Many aspects of the skeletal morphology might thus be less useful in the reconstruction of the phylogenetic relationships between these taxa. The similarities do show, however, that these long-legged forms perhaps share a not much older common ancestor, and that they are parts of a radiation of late Mesozoic "shorebirds," as postulated by Martin (1983).

Martin (1983:320) suggested that the supposed radiation of shorebird-like forms could possibly include "the progenitors of the entire Tertiary radiation" of birds. This seems less likely, however, given that many landbirds, such as galliforms, strigiforms, caprimulgiforms, and cuculiforms, had evolved by the early Tertiary, some already by the Paleocene (Olson, 1985). These birds exhibit skeletal morphologies quite different from the group of "shorebirds" to which *Juncitarsus* and the Presbyornithidae belong. If we allow for the time necessary to evolve these various adaptations, it seems justified to assume that a few different phylogenetic lineages leading to subclades of modern neognaths were established by the late Mesozoic. It would not be very surprising if these lineages eventually prove to correspond to Olson's (1985:84) tentative division of the modern birds into the palaeognathous birds, "basal land bird assemblage," "higher land bird assemblage," and "water bird assemblage."

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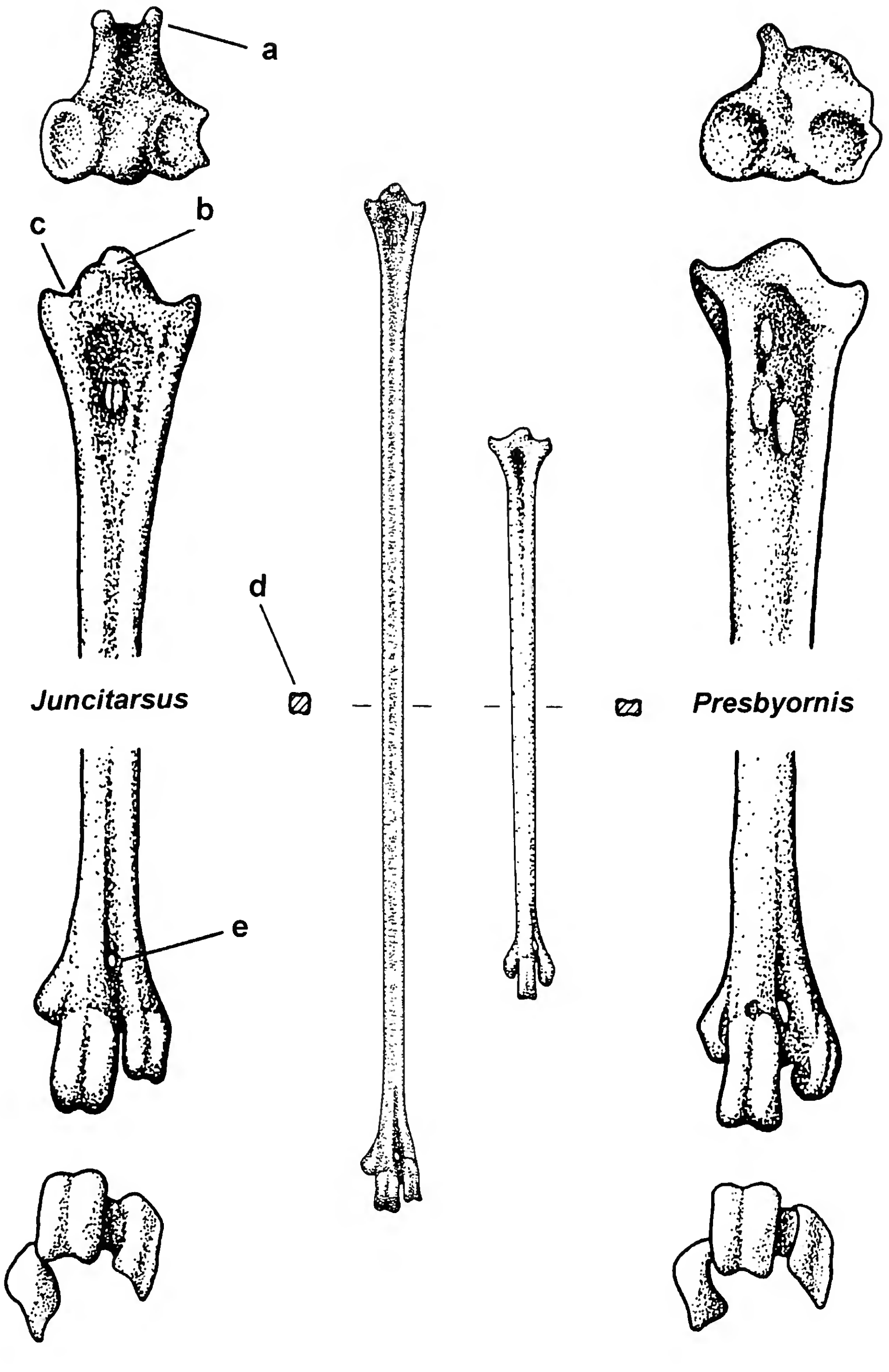

FIGURE 9.—Left tarsometatarsus. Different aspects of *Juncitarsus gracillimus* (left, based on USNM 244318 (holotype), except top left figure, which is the mirror image of USNM 244322) shown with the corresponding aspects of *Presbyornis pervetus* (right, based on USNM 492551, in mirror image, for complete bone; UCMP 126173, in mirror image, for proximal view; UCMP 126177, in mirror image, for anterior view of proximal end; UCMP 126178 for anterior view of distal end; UCMP 126182 for distal view). (*a*=hypotarsus, *b*=intercotylar knob, *c*=cotyla, *d*=cross section of shaft, *e*=foramen vasculare.)

Presbyornis isoni and Other Late Paleocene Birds from North Dakota

Richard D. Benson

ABSTRACT

Paleocene fossil birds from North Dakota in the collections of the Science Museum of Minnesota range in age from Tiffanian 3 to Tiffanian 4 and seem to represent five taxa. A humerus is referred to the anseriform *Presbyornis isoni* Olson, previously known from a less complete humerus from the late Paleocene of Maryland. All known specimens of *Dakotornis cooperi* Erickson, referable to the extinct charadriiform form-family Graculavidae, are reviewed. A cervical vertebra and a tarsometatarsal fragment, both within the probable body-size range of *Dakotornis cooperi* but probably representing different taxa, are referred to the Graculavidae. Another distal end of a tarsometatarsus, from perhaps the smallest currently known Paleocene bird, also is referred to the Graculavidae. These two tarsometatarsi exhibit a mosaic of charadriiform characters. Together with the tarsometatarsus of *Telmatornis priscus* Marsh, three size classes of North American Paleocene graculavid tarsometatarsi are now known.

Introduction

A new Paleocene species of the fossil anseriform genus *Presbyornis, P. isoni,* was established by Olson (1994) on the basis of two bones, an incomplete humerus and a manual phalanx 1 of the major digit, discovered in Maryland. This is the largest known presbyornithid. The purpose of this paper is to describe an additional, more complete humerus of *P. isoni* as well as other avian fossils from three late Paleocene sites in North Dakota: the Wannagan Creek Quarry, the Judson Locality, and the Brisbane Locality.

The Wannagan Creek Quarry of western North Dakota occurs in the Bullion Creek (formerly "Tongue River") Formation, consisting of riverine and lacustrine deposits. The Wannagan Creek fossil flora and fauna indicate a subtropical swamp environment: the most abundant large vertebrate is the 15-ft (4.5-m) crocodile *Leidyosuchus formidabilis* Erickson; the flora is dominated by bald cypress (*Taxodium olriki* (Heer) Brown), fig (*Ficus* spp.), magnolia (*Magnolia* spp.), and sycamore (*Platanus* spp.) (Erickson, 1991). About 110 mi (175 km) east of the Wannagan Creek Quarry, the Judson Locality also occurs in the Bullion Creek Formation, in deltaic sediments (Holtzman, 1978). The Brisbane Locality occurs in the underlying Slope Formation (Kihm, 1993) near the contemporary marine Cannonball Formation. The paleontology of these two near-shore localities indicates warm-temperate cedar swamps, the faunas of which also included crocodilians (Holtzman, 1978). Fossil footprints of probable shorebirds have been reported from another late Paleocene site (Locality L6421) near Wannagan Creek Quarry (Kihm and Hartman, 1995).

Nomenclature for species' binomials and English names of modern birds follows Sibley and Monroe (1990).

AGE AND CORRELATION.—The age of the avian fossils from Maryland reported by Olson (1994:429) is "near the base of the Upper Paleocene (Landenian), Aquia Formation, Piscataway Member... probably upper nannoplankton zone NP5, but possibly lower NP6.... On the scale of Berggren et al. (1985), the age would be somewhere between 61 and 62 million years." This falls within the Tiffanian North American Land Mammal Age, the Landenian of Europe being more or less coterminous with the Tiffanian of North America (Berggren et al., 1985). The Wannagan Creek Quarry dates to early Tiffanian 4 (=*Plesiadapis churchilli* zone), within the earlier half of paleomagnetic chron 25 Reversed (Sloan, 1987), whereas the Maryland locality that yielded the type specimens of *P. isoni* dates to the middle of chron 26 Reversed (Berggren et al., 1985), seemingly to Tiffanian 1. The Wannagan Creek beds of North Dakota would correlate, in the notation used in Olson (1994), to nannoplankton zone NP7 or NP8, with an age of about 60 million years according to the scales of both Berggren et al. (1985) and Meehan and Martin (1994). The Judson Locality is within the later half of paleomagnetic chron 26 Normal, in early Tiffanian 4 (Kihm, 1993, and pers. comm., 1996), probably less than 100,000 years earlier than Wannagan Creek. The Brisbane Locality dates to early Tiffanian 3A (=*Plesiadapis rex* zone: *Neo-*

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plagiaulax hunteri subzone) at the late part of chron 26 Reversed (Sloan, 1987), with an age of about 61 million years.

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Systematic Paleontology

Class AVES

Order ANSERIFORMES

Family PRESBYORNITHIDAE

Presbyornis isoni Olson, 1994

FIGURE 1

REFERRED MATERIAL.—A badly crushed but mostly complete right humerus, lacking the external tuberosity, the proximal half of the pectoral crest, and the central portion of the bicipital area; SMM P96.9.2; collected by Michael P. Ryan, 28 June 1989. For measurements, see Table 1.

LOCALITY.—North Dakota, Billings County, ~10 mi (16 km) NW of Medora; Wannagan Creek Quarry, field map quadrant P-6.

HORIZON AND AGE.—Late Paleocene, early Tiffanian 4, Bullion Creek Formation, Wannagan Creek Quarry, Bed 2 (lignitic shale); absolute age, ~60 Ma.

COMPARISONS.—Specimen SMM P96.9.2 agrees in all characters with the holotype of *Presbyornis isoni* (USNM 294116), the distal two-thirds of a humerus from the Aquia Formation of Maryland, and confirms that *P. isoni* is an equally good *Presbyornis* at both ends of its humerus by comparison with the type species *Presbyornis pervetus* Wetmore of the early Eocene. The proximal end of the humerus of *P. isoni* agrees with that of the smaller-bodied *P. pervetus* in the following characters: the head is undercut by a deep, arc-shaped extension of the capital groove; the pectoral crest is gently curved and long, about twice the length of the widely curved bicipital crest; the attachment of M. scapulohumeralis posterior is a wide, but elongated, kidney-shaped pit in the distal rim of the bicipital crest; the median crest is continuous with the extremely prominent central ridge of the shaft; and the attachment of M. latissimus dorsi posterior is a prominent oval structure very close to the central ridge. The proximal end of the humerus of *P. isoni* differs from that of *P. pervetus* in lacking a prominent muscle-scar line distal to the attachment of M. latissimus dorsi posterior. In the South American presbyornithid *Telmabates antiquus* Howard, the humeral head and internal tuberosity are both undercut by an extension of the capital groove (P.G.P. Ericson, pers. comm., 1996), whereas in the North Dakota specimen of *Presbyornis isoni,* only the head is undercut, as is the case in *Presbyornis pervetus;* this is further indication that *P. isoni* was correctly assigned to genus.

TABLE 1.—Measurements (in mm) of the two known humeri of *Presbyornis isoni*

Measurement	SMM P96.9.2	USNM 294116 (from Olson, 1994)
Length from head to internal condyle	194.9	–
Distal width	~27	23.3
Depth through external (radial) condyle	13.5	12.9
Greatest diameter of brachial depression	10.0	8.8

As in *P. pervetus,* the humerus of *P. isoni* lacks the stoutness typical of most of the modern anseriforms, although without being very slender. The length/distal-width ratio of the humerus of *P. isoni* is about 7.2, in contrast to 7.6 for the slightly more gracile *P. pervetus,* 6.5 for the stout-winged Snow Goose (*Anser caerulescens*), and 9.4 for the slender-winged Northern Gannet (*Morus bassanus*). The ratios for *Presbyornis* spp. are in general agreement with those of charadriiforms: American Oystercatcher (*Haematopus palliatus*), 6.7; Double-striped Thick-knee (*Burhinus bistriatus*), 6.8; American Avocet (*Recurvirostra americana*), 7.0; Marbled Godwit (*Limosa fedoa*), 7.1; Black Skimmer (*Rynchops niger*), 7.2; South Polar Skua (*Catharacta maccormicki*), 7.3; Franklin's Gull (*Larus pipixcan*), 7.5; and Common Murre (*Uria aalge*), 7.7. Similar values obtain for primitive ducks, such as the Fulvous Whistling-duck (*Dendocygna bicolor*), 7.2.

DISCUSSION.—The Presbyornithidae are primitive anseriforms that share numerous character states with charadriiform birds. For example, the proximal end of the humerus of *Presbyornis* is shallow, as in most charadriiforms and unlike modern anseriforms. Postcranially, presbyornithids resemble the "transitional charadriiform" Graculavidae, a group known from the Late Cretaceous and the Paleocene of North America, from the Paleocene of Sweden ("Scaniornithidae"; Olson and Parris, 1987) and France (Mourer-Chauviré, 1994), and apparently from the earliest Eocene of Australia (Boles et al., 1994). Recently, one genus formerly classified as graculavid, *Anatalavis,* has been shown to be anseriform (Olson, this volume). Similarly, Wetmore (1926), in describing *Presbyornis pervetus,* placed the new family Presbyornithidae in the same suborder as the Recurvirostridae. Feduccia and McGrew (1974) repeatedly called *P. pervetus* "the Green River flamingo," although they noted its duck-like appearance. The Recurvirostridae (avocets),

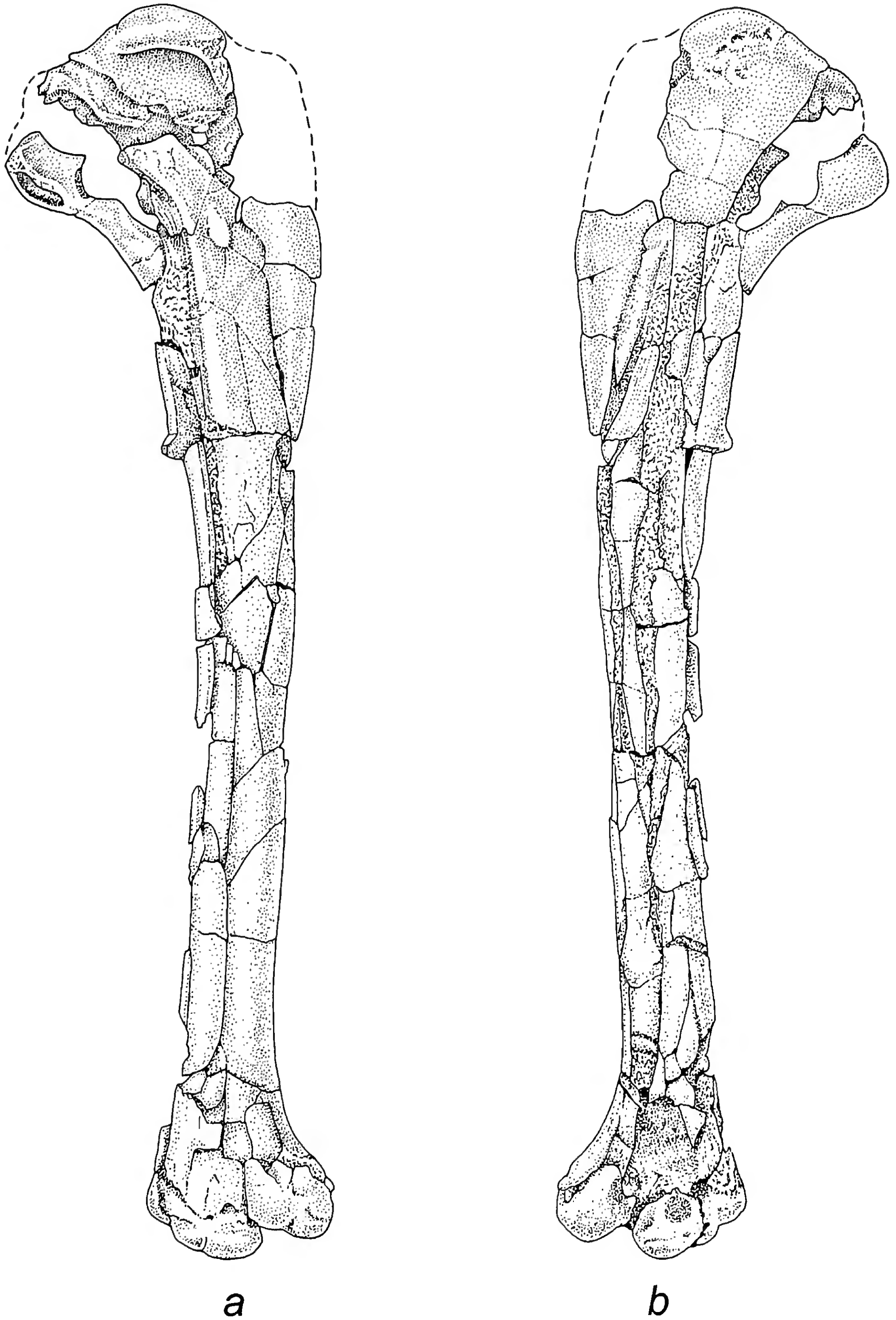

FIGURE 1.—Referred right humerus of *Presbyornis isoni,* SMM P96.9.2 (×1): *a,* anconal view; *b,* palmar view.

which are flamingo-like charadriiforms (Olson, 1985), have the oldest known fossil record of the extant charadriiform families (Eocene of Europe; Olson, 1985; Unwin, 1993). *Presbyornis* is the only presbyornithid genus yet recognized in North America, although Olson (1994) noted that the large-bodied *P. isoni* might well be assignable to a different genus were more of its skeleton known. The individual represented by SMM P96.9.2 was slightly larger than the one represented by the holotype of *Presbyornis isoni* (see Table 1). Their relative difference in size is not greater than that often seen within avian species (pers. obs.), including *Presbyornis pervetus* (P.G.P. Ericson, pers. comm., 1996).

Order CHARADRIIFORMES

Form-Family GRACULAVIDAE

Dakotornis cooperi Erickson, 1975

FIGURE 2

MATERIAL.—*Holotype:* A complete right humerus, SMM P74.24.106 (figured in Erickson, 1975), collected by Bruce R. Erickson and field crew, July 1974. *Referred Material:* A complete right humerus, SMM P75.22.7 (Figure 2), collected by Bruce R. Erickson, summer 1975; a mostly complete left tibiotarsus, SMM P75.22.25 (not figured), collected by Tim McCutcheon, 6 July 1975.

LOCALITY.—North Dakota, Billings County, ~10 mi (16 km) NW of Medora, Wannagan Creek Quarry. Field map quadrants: holotype humerus, G-5; other humerus, G-2; tibiotarsus, K-6 (quadrants are 5 ft (1.5 m) on a side).

HORIZON AND AGE.—Late Paleocene, early Tiffanian 4, Bullion Creek Formation, Wannagan Creek Quarry, Bed 2 (lignitic shale); absolute age, ~60 Ma.

DISCUSSION.—*Dakotornis cooperi* Erickson is the only bird from Wannagan Creek to have been previously published. It was originally described as a "primitive ibis-like bird" representing the extinct family Dakotornithidae within the suborder Plataleae, although its resemblance to thick-knees was mentioned (Erickson, 1975). Although the humerus of *Dakotornis* shares numerous characters with the Plataleidae (ibises), especially in its stoutness and general outline, *Dakotornis* more closely resembles the Graculavidae, as Olson and Parris (1987) pointed out, and even some of the modern charadriiforms such as Burhinidae (thick-knees), Haematopodidae (oystercatchers), Recurvirostridae (avocets), Laridae (gulls), and Scolopacidae (godwits, phalaropes, etc.). These charadriiforms resemble *Dakotornis* in having a shallow proximal end of the humerus that is not pneumatic, a median crest at a nearly right angle to the shaft, and a well-developed central ridge. In all of these characters these modern charadriiforms and *Dakotornis* differ from ibises. In two other characters of the humerus—the proximally produced external tuberosity and the lack of a typically charadriiform ectepicondylar spur—*Dakotornis* is as similar to thick-knees as to ibises. The rounded ectepicondylar prominence of *Dakotornis* closely resembles that of *Burhinus*, whereas in other charadriiforms a spur extends from the proximal rim of this prominence. *Dakotornis* would thus seem to be a good charadriiform. Peters (1983) and Olson (1985) noted the similarities between ibises and charadriiforms (and gruiforms).

The two known humeri of *Dakotornis cooperi*, holotype and referred, discovered in different field seasons, have until now been separated from each other through loans to different persons; I am the first person to see both original specimens side by side. The referred humerus (Figure 2) agrees in all characters with the holotype. The only apparent difference is that the external tuberosity of the holotype (as figured in Erickson, 1975) appears much narrower and sharper than the broad, rounded external tuberosity of the referred humerus. The apparent narrowness of the tuberosity in the holotype, however, is due only to breakage. These two right humeri of *Dakotornis cooperi* are of nearly identical size; the holotype is 87.1 mm long, and the other is 89.0 mm long.

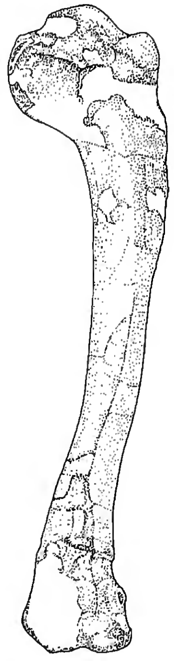

FIGURE 2.—Referred right humerus of *Dakotornis cooperi*, SMM P75.22.7 (×1), anconal view.

The tibiotarsus (SMM P75.22.25) was tentatively assigned to *Dakotornis cooperi* on the basis of size and provenance. Olson and Parris (1987) have noted the graculavid nature of this specimen.

GRACULAVIDAE, gen. et sp. probabiliter indescript.

MATERIAL.—A mostly complete third cervical vertebra, 18.5 mm long, ~15 mm wide (both anteriorly and posteriorly), SMM P77.7.159 (not figured); collected by Richard C. Holtzman, summer 1977.

LOCALITY.—North Dakota, Morton County, ~8 mi (13 km) S of Judson; Judson Locality.

HORIZON AND AGE.—Late Paleocene, early Tiffanian 4, Bullion Creek Formation, Judson Locality; absolute age, ~60 Ma.

COMPARISONS.—This specimen is referred to the Graculavidae due to its Paleocene age and its close resemblance to modern charadriiform cervical vertebrae. This cervical vertebra is identified as the third on the grounds of its caudally oriented, long-bottomed cariniform hypapophysis, gracile neural spine, and reduced pleurapophyses. The third cervical is typically a short vertebra, unlike this specimen, which is 1.2 times longer than its width, although this degree of elongation is common among charadriiforms. In its general outline and proportions between its parts, the specimen most closely resembles the cervical vertebrae of the Charadriiformes. The shapes of the facets of the zygapophyses, of the articulations of the centrum, of the ventral pit anterior to the keel, and of other features are like those of most Charadriiformes but are more like recurvirostrids than like burhinids. The unusual feature of its relatively narrow posterior width (which is not appreciably greater than its anterior width) also is found in oystercatchers (Haematopodidae). Another striking feature is the transverse perforation of the centrum. This condition is observed in some of the more caudad cervical vertebrae (but not necessarily in the craniad vertebrae, such as the third) in avocets (Recurvirostridae), gulls (Laridae), skimmers (Rynchopidae), and sandpipers (Scolopacidae). Transverse perforation of the centrum is fairly common in Anseriformes, and in *Dendrocygna bicolor* even the third cervical is perforated; however, the specimen does not otherwise appear anseriform.

DISCUSSION.—Although this specimen most likely represents an unknown species, the size of the vertebra would seem to fall within the upper limits of probable size for *Dakotornis cooperi,* even if it is somewhat large for a charadriiform body plan. A possible model for the body proportions of the very stout-winged *Dakotornis* might be the Canvasback (*Aythya valisineria*), in which the absolute and relative sizes of the humerus, vertebrae, tibiotarsus, and tarsometatarsus are very similar to those of the humerus of *Dakotornis,* the present vertebra, the Wannagan Creek tibiotarsus, and the tarsometatarsus described below.

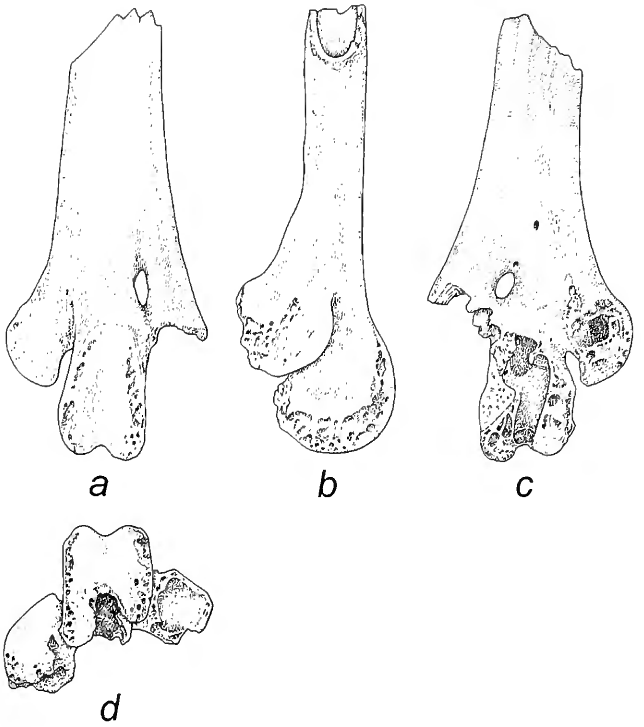

FIGURE 3.—Distal end of left tarsometatarsus of Graculavidae gen. et sp. prob. indescript., SMM P77.8.210 (×3): *a,* anterior view; *b,* medial view; *c,* posterior view; *d,* distal view.

GRACULAVIDAE, gen. et sp. probabiliter indescript.

FIGURE 3

MATERIAL.—Distal 20 mm of a left tarsometatarsus, lacking most of the outer trochlea, SMM P77.8.210 (Figure 3); collected by Richard C. Holtzman, summer 1977.

LOCALITY.—North Dakota, Grant County, ~5 mi (8 km) W of Raleigh; Brisbane Locality.

HORIZON AND AGE.—Late Paleocene, early Tiffanian 3A, Slope Formation, Brisbane Locality; absolute age, ~61 Ma.

COMPARISONS.—This specimen is referred to the Graculavidae on the basis of its general resemblance to the tarsometatarsus of charadriiforms, including that of *Telmatornis priscus,* the only North American graculavid for which the tarsometatarsus was previously known (although *T. priscus* was a much smaller bird). The posterior surface of the specimen displays what might be called a typical "charadriiform basin," i.e., a deep, fairly symmetrical depression bounded by the longitudinal ridges of the inner and outer trochleae and by the proximal rim of the middle trochlea. The specimen resembles *Telmatornis* in the following: the distal foramen is moderately large and oval, the metatarsal facet is well developed, the inner trochlea is oriented distomedially, and the inner trochlea is elevated so that its distalmost extent is just proximal to the half-height of the middle trochlea's digital groove. The inner and outer trochleae, however, are considerably more posteriorly retracted than in *Telmatornis,* so that the tarsometatarsus has a greater arch in distal view. The present specimen differs from the Presbyornithidae in having the metatarsal facet oval and distinct rather than long and weak, a relatively smaller distal foramen, and a lesser trochlear arch in distal view.

Characters of SMM P77.8.210 resemble those of a number of extant charadriiform families in a mosaic manner. Olson and Parris (1987) noted skua-like (and presbyornithid-like) features in the tibiotarsus of another Paleocene graculavid, *Laornis edvardsianus* Marsh. SMM P77.8.210 combines tarsometatarsal characters especially of gulls (Laridae), skuas (Stercorariidae), and oystercatchers (Haematopodidae), among others. The general outline of the bone is oystercatcher-like, except that the orientation of the inner trochlea is gull-like, being neither as distally oriented as in oystercatchers nor as medially oriented as in skuas. Its moderately large distal foramen matches that of oystercatchers, unlike the larger foramen in gulls and skuas. The metatarsal facet is skua-like (as seen in *Catharacta maccormicki*) in both configuration and position (rather than lacking a hind toe as in oystercatchers). The degree of trochlear arch in distal view matches that of gulls or skuas, unlike the very highly arched tarsometatarsus of oystercatchers. The lower elevation of the inner trochlea, unlike that in most of the modern charadriiforms, is similar to that seen in *Telmatornis,* thick-knees (Burhinidae), or skimmers (Rynchopidae).

DISCUSSION.—Considering that the distal end of this tarsometatarsus seems a strange mosaic, had the proximal end been preserved, it might well have resembled that of some other bird altogether, not to mention what the rest of the skeleton may have resembled. Because the preserved part of this bone is, however, a mosaic of exclusively charadriiform characters, the Graculavidae is the best present assignment for this specimen. This fragment would seem, at least in the absence of other Paleocene fossils of more modern aspect, to represent a bird older than the divergence time of any of the extant charadriiform families, as does *Dakotornis.* On body size, the present specimen could be referable to either of the monotypic genera *Dakotornis* or *Graculavus.* The specimens of *Dakotornis cooperi* are about one million years younger than this specimen, and those of *Graculavus velox* Marsh are about four million years older (see Olson, 1994, for the probable early Paleocene age of *G. velox* and the other New Jersey graculavids).

GRACULAVIDAE, gen. et sp. indescript.

FIGURE 4

MATERIAL.—Distal 6 mm of a right tarsometatarsus, with the outer trochlea broken away, SMM P96.9.3; collected by Bruce R. Erickson and field crew, summer 1976.

LOCALITY.—North Dakota, Billings County, ~10 mi (16 km) NW of Medora; Wannagan Creek Quarry, field map quadrant O-19.

HORIZON AND AGE.—Late Paleocene, early Tiffanian 4, Bullion Creek Formation, Wannagan Creek Quarry, Bed 2 (lignitic shale); absolute age, ~60 Ma.

DESCRIPTION.—This tarsometatarsal fragment is from a bird about the size of a Wilson's Plover (*Charadrius wilsonia*) and has the following characters: (1) the distal foramen is moderately large and oval and occupies the distal end of a shallow anterior tendinal groove; (2) in posterior view, two tiny foramina occur just proximal to the distal foramen; (3) the metatarsal facet is shallow and oval; (4) the trochlear arch in distal view is relatively low, with the outer trochlea not posteriorly retracted, but with the inner trochlea retracted so that its central point is posterior to the posteriormost extent of the middle trochlea; the trochlear arch in posterior view (as is common in Charadriiformes) forms a subsymmetrical basin between the three trochleae; (5) the inner trochlea is bulbous (as in most Charadriiformes) and is oriented distomedially; (6) the inner trochlea in distal view bears a very slight, posteriorly oriented wing on its medial side (a smaller wing than in modern Charadriiformes); (7) the inner trochlea is elevated so that its distal extent is about level with the proximal extent of the middle trochlea's digital groove; (8) the middle trochlea extends considerably farther distally than the other two; its lateral rim is slightly greater in distal extent and in anterior extent than is the medial rim; and (9) the outer trochlea would seem to have a slightly greater distal extent than the inner trochlea (the broken-off outer trochlea is preserved, but its contact with the adjacent part of the bone at the breakage is lost).

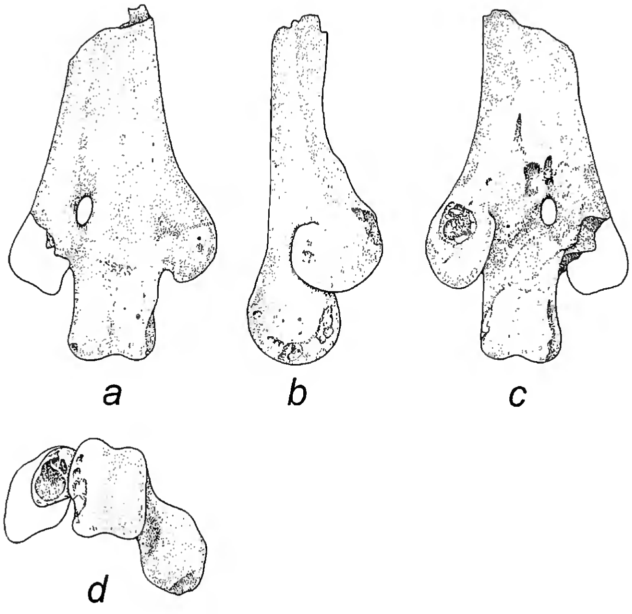

FIGURE 4.—Distal end of right tarsometatarsus of Graculavidae gen. et sp. indescript., SMM P96.9.3 (×8): *a,* anterior view; *b,* medial view; *c,* posterior view; *d,* distal view.

COMPARISONS.—Fossil tarsometatarsi of small, spurless galliforms can be easily mistaken for those of charadriiforms (Olson and Farrand, 1974). Indeed, none of the nine characters listed in the previous paragraph would necessarily be inconsistent with an assignment of the specimen to Galliformes. Olson and Farrand (1974), however, list 10 other tarsometatarsal characters, all relating to the trochleae, that distinguish galliforms from charadriiforms. The present specimen differs from the Galliformes in all 10 of these trochlear characters.

Specimen SMM P96.9.3 shares seven of the nine characters listed above (1–5, 8, 9) with the plover family, Charadriidae, a family not known in the fossil record earlier than the early Miocene (Unwin, 1993). The specimen differs from Charadriidae in two characters of the inner trochlea (6, 7), in which it more closely resembles the Paleocene *Telmatornis* and modern avocets (Recurvirostridae), respectively. It also resembles the Recurvirostridae in characters 3 and 9.

DISCUSSION.—There is no evidence that the families Charadriidae and Recurvirostridae had diverged prior to the date of this fossil (Unwin, 1993), which may represent part of the "graculavid" stock prior to the divergence of these families. Of course, the presence of primitive charadriiform characters in this specimen (and in the Brisbane tarsometatarsus described above), perhaps by retention from much earlier forms, can tell us nothing certain about the divergence times of the extant charadriiform families.

The very small body size of the bird represented by specimen P96.9.3, perhaps the smallest currently known Paleocene bird, need not exclude it from the Graculavidae (which are otherwise much larger birds), as this is only a form-family in any case

(Olson and Parris, 1987). The relative difference in size between *Graculavus velox* and the species represented by P96.9.3 is comparable to that between the largest and smallest modern members of the sandpiper family, Scolopacidae.

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A New Species of *Graculavus* from the Cretaceous of Wyoming (Aves: Neornithes)

Sylvia Hope

ABSTRACT

A new species of *Graculavus* from the Lance Formation, Wyoming, extends the range of the genus from the Atlantic paleocoastline to the near-shore of the Cretaceous inland sea. The type and referred species were nearly contemporaneous in the late Maastrichtian. The new species was a very large flying bird with the proximal end of the humerus in the size range of the largest modern gulls or geese. The systematic and biogeographic significance of *Graculavus*-like birds is discussed.

Introduction

Graculavus velox Marsh, 1872, was described as a cormorant, but since then it has been diagnosed as a shorebird (Shufeldt, 1915) and characterized as "transitional," referring to intermediacy between charadriiforms and gruiforms (Olson, 1985:171). The genus has been monotypic since Olson and Parris (1987) synonymized *G. pumilus* Marsh, 1872, with *Telmatornis priscus* Marsh, 1870. The changing taxonomic treatments reflect the difficulty of identifying isolated fragments of unknown birds.

The discovery of a very large new species of *Graculavus* provides an opportunity to review the significance of this genus of early neornithine birds. The two known species of *Graculavus* are approximately contemporaneous representatives of widely separated, near-shore environments in the Late Cretaceous. Both species are known only from the proximal end of the humerus, which, interestingly, is very similar to that of the early anseriform *Presbyornis*. Because the phylogenetic position of the Anseriformes remains a key problem in avian taxonomy (Ericson, 1996), the resemblance of *Graculavus* to both *Presbyornis* and the Charadriiformes takes on systematic interest. This paper describes the new species and provides a brief perspective on the characters and biogeography of *Graculavus*-like birds.

METHODS

CHARACTER ANALYSIS.—Polarity of osteologic characters was judged from comparison of a broad selection of neornithine birds with other Ornithurae and with Enantiornithes (Hope, unpublished data). Because uncertainties surround the basal phylogeny of Neornithes, the definition and phylogenetic diagnosis of higher groupings within it is uncertain. Principal comparisons herein are to "waterbirds" as defined below. Characters cited for waterbirds occur in most of them, and some characters occur elsewhere among Neornithes as isolated instances but not as a concerted complex. At the genus and species levels, diagnosis of fragments by synapomorphy is rarely possible, so identification at these levels is based on a unique combination of attributes.

NAMES.—Higher taxon names are used in the sense of Wetmore (1960), except that these names are used herein in the node-based sense (de Queiroz and Gauthier, 1992) to include fossil forms sharing a most recent common ancestor with the extant crown taxon. The name "Ciconiiformes" is avoided because of gross disparity in usage, both historical and recent. English vernacular names are used for groups of birds with equivocal systematic status. Such names do not necessarily imply monophyly and are as follows: "waterbirds," refers to all "seabirds," "shorebirds," and the Anseriformes; "seabirds" refers to the Procellariiformes, Pelecaniformes, penguins, loons, and grebes; "shorebirds" refers to the Charadriiformes, ibises and flamingos, storks, and herons.

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Fossil Localities and Stratigraphy

Graculavus velox was recovered from greensand marl of the Navesink or overlying Hornerstown Formation of New Jersey during the last century in the course of commercial mining for the marl. The greensands were formed along the quiet margin of what was then the Atlantic coastline during the middle Maastrichtian through the earliest Paleocene. The phosphatic sediments provided ideal conditions for preservation. Birds from the Hornerstown and Navesink were reported earlier by Marsh (1870, 1872), Shufeldt (1915), and by Olson and Parris (1987). The new specimen represents a larger species of *Graculavus* from the late Maastrichtian Lance Formation, Wyoming. The first bird discoveries in this area resulted from early exploration of the dinosaur fields in the North American West. The University of California began newer expeditions about 1955, and the American Museum of Natural History has been collecting in the Lance since 1960. Birds from the Lance were reported by Marsh (1889:83, footnote; 1892) and by Brodkorb (1963).

The depositional setting and history of exploration in the New Jersey marls is summarized by Olson and Parris (1987). The Navesink Formation is entirely Maastrichtian. The age of the birds from the overlying Hornerstown Formation, whether Cretaceous or early Tertiary, was long debated because of the complexity of the sedimentation patterns and the enigmatic composition of the basal Main Fossiliferous Layer (MFL). This very narrow, densely fossiliferous zone lies directly over the Navesink Formation at the Inversand marl pit in Gloucester County, New Jersey. The MFL in this area includes Maastrichtian macrofossils, with ammonites, mosasaurs, and *Enchodus*. Typically Paleocene foraminifera occur in lower Hornerstown Formation levels at other localities. Vertebrates have not been recovered in the Hornerstown immediately above the MFL, but a Danian (Paleocene) fauna is found approximately 3 m higher (Gallagher and Parris, 1985). Very recent studies interpret the MFL as a Cretaceous lag deposit infilled with a Paleocene matrix, possibly by burrowing arthropods (Gallagher, 1993; Kennedy and Cobban, 1996; other studies cited in both). There is iridium elevation within the MFL but not in a sharply defined high peak. Thus, the Cretaceous/Tertiary boundary probably is within the MFL but is blurred and attenuated by reworking of the sediments (Gallagher, 1992).

The Lance Formation in the southeastern corner of the Powder River basin, Wyoming, consists of massive, loosely consolidated sandstones with lenses of lignites and lignitic shales throughout. The Lance lies conformably directly under the entirely Paleocene Fort Union Formation. The Lance sediments were deposited near the western margin of the North American interior seaway during its final retreat in the latest Cretaceous (Maastrichtian). Plant remains indicate a humid, subtropical environment. An abundant vertebrate fauna including sharks, lizards, mammals, and birds is preserved in channel fill of the ancient, meandering, near-shore streams. Faunal correlation shows a late Maastrichtian age for the fossiliferous sediments. The indurated streambeds have survived erosion better than the surrounding terrain has, and they are exposed now as "blowouts," or elevated sandstone outcrops (Dorf, 1942; Estes, 1964; Clemens, 1960, 1963; Lillegraven and McKenna, 1986).

Systematic Paleontology

NEORNITHES

GRACULAVIDAE

TYPE GENUS.—*Graculavus* Marsh, 1872:363.

REMARKS.—The name Graculavidae is used herein in the sense of Olson and Parris (1987), except that Olson (this volume) has since referred *Anatalavis* to Anseriformes.

Graculavus Marsh, 1872

Limosavis Shufeldt, 1915:19.

TYPE SPECIES.—*Graculavus velox* Marsh, 1872.

INCLUDED SPECIES.—*Graculavus velox, Graculavus augustus*, new species.

Graculavus augustus, new species

FIGURE 1

HOLOTYPE.—AMNH 25223; proximal end of left humerus.

TYPE LOCALITY.—From near Lance Creek, Niobrara County, Wyoming, University of California Museum of Paleontology Locality V-5711 (Bushy Tailed Blowout), on the southern rim of a large valley that empties into Lance Creek, grid coordinates 23,860–23,350 on reconnaissance map of Clemens (1963). Collected by Malcolm C. McKenna and party, August, 1985.

HORIZON.—Upper part of the Lance Formation (late Maastrichtian).

MEASUREMENTS.—Maximum depth of articular head, cranial to caudal, 6.8 mm; width of shaft through dorsal tubercle and

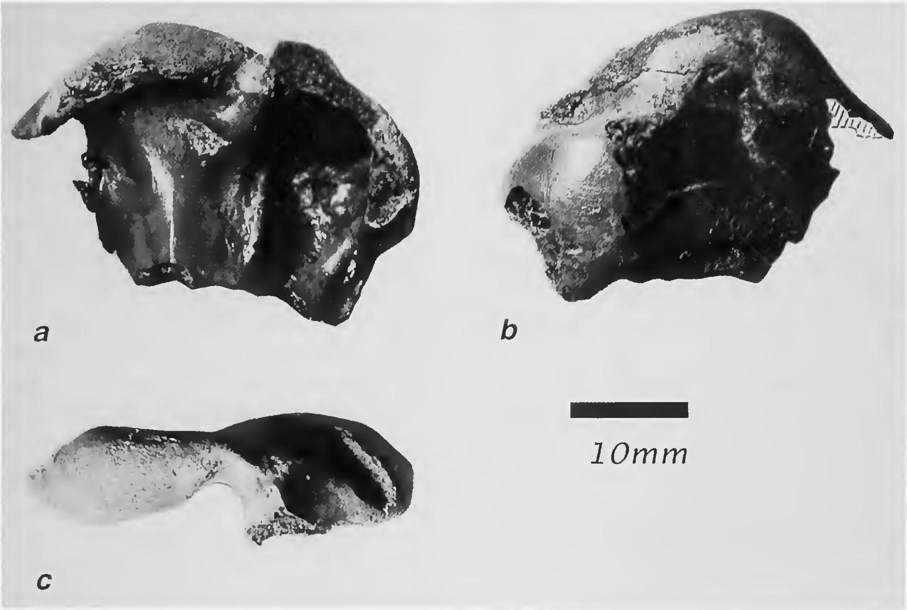

FIGURE 1.—Proximal end of the left humerus of *Graculavus augustus*, new species (holotype, AMNH 25223): *a*, cranial view; *b*, caudal view; *c*, medial view.

base of ventral tubercle, 28.5 mm; internal width of tricipital fossa through base of ventral tubercle and distal border of impression for M. scapulohumeralis caudalis, 9.5 mm; distance from capital incisure to dorsal tubercle, 17.3 mm

ETYMOLOGY.—From the Latin *augustus*, majestic, for the large size of the bird, as well as the month of collection.

DIAGNOSIS.—Derived characters of the Neornithes: moderate enlargement of the articular head of the humerus. Derived characters within the Neornithes: very large bicipital crest and prominence; thin, erect ventral tubercle; large dorsal tubercle; and well-defined caudal margin of the humerus.

The diagnosis of *Graculavus* is based on the differential diagnosis for *Graculavus velox* (Shufeldt, 1915; Olson and Parris, 1987). *Graculavus augustus* is very similar to *G. velox* but is about one-third larger, and the area between the ventral and dorsal tubercles is relatively wider and flatter.

DESCRIPTION.—The new specimen comes from a very large bird with the proximal end of the humerus in the size range of the largest gulls or geese. Surface preservation is excellent. The tips of the dorsal and ventral tubercles are missing, but the shape of the remaining base of each is consistent with the morphology of *Graculavus velox*. The pectoral crest is missing (as it is in *G. velox*). The bicipital crest is broken off just distal to the impression for M. scapulohumeralis caudalis. The shaft is broken off slightly distal to the tricipital fossa.

The bone is delicately sculpted. The proximal end of the humerus is very flat and broad. The articular head is small. On the cranial surface of the humerus, the bicipital prominence is large, slightly raised, and rounded. The sulcus for the transverse ligament is deep and well defined but short, extending from the border of the bicipital crest only as far as the ventral tubercle. The impression for M. coracobrachialis cranialis is shallow and indistinct. In caudal view, the preserved base of the dorsal tubercle shows that it was moderately large and strongly protrudent from the shaft and was very far from the articular head. The head of the humerus does not overhang the capital incisure, which is deep and well defined. The caudal end of the incisure is excavated into a sulcus continuous with the deep sulcus undercutting the articular head. Distally this sulcus is bordered by a large, well-defined transverse scar extending from the base of the ventral tubercle diagonally toward the articular head. Evidently the dorsal tubercle also was deeply undercut, but breakage obscures detail.

The bicipital crest is broad and appears to have been rounded rather than sharply angular. The impression for M. scapulohumeralis caudalis is extremely large and well defined. The ventral tubercle is slender and erect, but breakage prevents seeing its total length. The tricipital fossa is very large and wide and is without a pneumatic foramen. There is a central tumescence in the fossa, separating it into proximal and distal basins. The tumescence is the obverse side of the deep sulcus for the transverse ligament, visible because the cranial wall of the fossa is very thin, and the fossa lacks the bony struts and velum usually associated with pneumaticity. The more proximal of the two resulting basins is small in *Graculavus*.

The surface of the fossa distal to the tumescence shows a series of narrow, shallow transverse ridges and sulci that appear to be impressions of parallel muscle fibers. The striations terminate on a prominent, raised linear scar 7 mm long, extending from within the tricipital fossa near the base of the ventral tubercle distally in the axis of the shaft. The scar may be the central vane of a partly pinnate M. humerotriceps. Similar, although shallower, striations occur in the tricipital fossa of the Western Gull, *Larus occidentalis*. A similar long scar is present in a slightly different position in several modern larids examined and in the Burhinidae. A short, lower crest or ridge extends from close to the proximal end of the long scar proximad and deeper into the triceps fossa. Dorsal to the longer scar there is a small, rough, irregular surface that may be the impression for M. scapulohumeralis cranialis.

The caudal margin of the humerus is very robust and distinct. It is far dorsal to the ventral tubercle. At the level of the base of the ventral tubercle the caudal margin bends abruptly dorsad to terminate at the proximal articular surface of the humerus about halfway between the apex and the dorsal tubercle. The area between the ventral tubercle and the caudal margin of the humerus is broader than that in *Graculavus velox*.

Discussion

Cretaceous and Paleogene neornithines with the proximal end of the humerus similar to that of *Graculavus* are *Telmatornis, Presbyornis, Telmabates,* and *Zhylgaia.* Olson and Parris (1987) compared *Graculavus* most closely to the Burhinidae in the Charadriiformes. *Telmatornis* Marsh, 1870, has been referred to the Charadriiformes (Shufeldt, 1915; Cracraft, 1972; Olson and Parris, 1987) and is most similar to the Scolopacidae. *Presbyornis* Wetmore, 1926, is referable to the Anseriformes based on associated cranial material (Olson and Feduccia, 1980). *Telmabates* Howard, 1955, evidently is referable to the Presbyornithidae (Feduccia and McGrew, 1974). *Zhylgaia* Nesov, 1988, was referred originally to the Presbyornithidae in Charadriiformes but later (Nesov, 1992) was referred, only tentatively, to the Presbyornithidae. *Zhylgaia* has a very steeply angled ventral tubercle (almost 90° to the axis of the shaft), a distinct although shallow impression for M. coracobrachialis cranialis, the head not much undercut, the capital incisure broad and shallow, and the caudal margin of the humerus well defined but not dorsal to the ventral tubercle. These conditions suggest that it does not belong with either the Anseriformes or the Charadriiformes. Thus, the humerus in all of these early waterbirds is very similar, but the birds are not all referable to the same modern higher-level taxon.

In general, the proximal end of the humerus in these birds differs from that of most modern Charadriiformes as follows:

1. Among the articular head and associated structures, the head is smaller, and the dorsal tubercle is farther from the head and is smaller but more protrudent.
2. Impressions for ligaments and muscles on the cranial surface are much less pronounced, including a shallow impression for M. coracobrachialis cranialis and a short sulcus for the transverse ligament.
3. Attachments of the muscles in and around the tricipital fossa are more robust, especially in *Graculavus* itself, but there is no dorsal (second) tricipital fossa.

These differences suggest a distinctive flight mechanism.

Graculavus, Telmatornis, Presbyornis, Telmabates, and *Zhylgaia* from the Late Cretaceous and the Paleogene are more similar to each other than to any modern bird. Many of the characters of *Graculavus* are not unique to the Charadriiformes but occur also among extant waterbirds in a mosaic pattern. The double-basined tricipital fossa occurs in virtually identical form in the Charadriiformes and the Oceanitidae (Procellariiformes). Extreme elongation of the ventral tubercle, very deeply undercut articular head, and very prominent caudal margin of the humerus are present in many Charadriiformes and in most Procellariiformes. A small articular head occurs in many Procellariiformes and in the Pelecaniformes. A small articular head, wide distance between the dorsal and ventral tubercles, and strong protrusion of the dorsal tubercle occur in some petrels, especially *Calonectris* (Procellariiformes), in *Phaethon,* and in some other pelecaniforms (see comparisons in Olson, 1977, figs. 18–20). Judged on varied morphological and behavioral grounds, *Phaethon* is highly plesiomorphic among Pelecaniformes (Cracraft, 1985; Elzanowski, 1995).

This mosaic pattern of sharing characters with *Graculavus* suggests that the various extant groups of waterbirds have retained different suites of characters that were present in a common ancestor. The occurrence of many characters of *Graculavus* in the overall very plesiomorphic *Phaethon* supports this suggestion.

Conclusions

The new, very large species extends the Cretaceous range of *Graculavus* from eastern to western North America. Presbyornithids are now reported from the Late Cretaceous through the early Eocene in North and South America, Antarctica, and Mongolia (Howard, 1955; Feduccia and McGrew, 1974; Olson, 1994; Noriega and Tambussi, 1995). *Zhylgaia* comes from an estuarine habitat in the late Paleocene of Kazakhstan (Nesov, 1988). *Graculavus, Telmatornis, Zhylgaia,* and the Presbyornithidae show that similar graculavid-like birds were widespread in the Late Cretaceous through the early Tertiary. Reports of graculavid-like birds represented only by other parts of the skeleton are harder to evaluate in this context (e.g., Olson and Parris, 1987; Kurochkin, 1988; Nesov and Jarkov, 1989; Elzanowski and Brett-Surman, 1995).

Graculavus augustus was a very large bird and a strong flyer. The bones were delicately sculpted and were not highly pneumatic, resembling contours in flying swimmers and divers; they lacked the extreme inflation of soaring birds. Impressions for tendons and muscles differ sufficiently from those of modern Charadriiformes to suggest distinctive flight mechanics. *Graculavus* is most similar to the Charadriiformes, but it shows a high proportion of characters that may be plesiomorphic among them. Whatever their subsidiary affiliations, the similarity of the humerus among these Late Cretaceous and Paleogene waterbirds probably is due to recent common ancestry.

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Implications of the Cranial Morphology of Paleognaths for Avian Evolution

Felix Y. Dzerzhinsky

ABSTRACT

In the early evolution of birds, bill formation produced a problem for muscular control of the thin, elongated upper jaw. In particular, it required a relatively high retracting force. Three sources of this force evolved. (1) A powerful M. retractor palatini (especially in Tinamiformes and *Apteryx*), originating primarily on the vomer and pterygoid, developed to provide direct muscular connection between the dermal palate and the cranial base. It apparently evolved due to a joining of the medial portions of the pterygoid and mandibular depressor muscles, which were aligned by development of the proc. mandibulae medialis (a character unique to birds). (2) The ancestral pseudotemporalis muscle developed into two portions, a large postorbital portion and an almost horizontally oriented intramandibular portion. Each portion seves to increase the retraction ability of the muscle as a whole. (3) The external mandibular adductor muscle developed, which, in neognaths, is larger than either muscle previously mentioned. Its evolutionary development was temporarily retarded by reduction of one of its places of origin—the upper temporal arch.

Introduction

For more than a century, paleognaths have been subjected to morphological studies in order to ascertain their apparently primitive nature and to discover their position in avian phylogeny (W.K. Parker, 1866; T.J. Parker, 1891; Pycraft, 1900; McDowell, 1948; Hofer, 1945, 1950, 1955; de Beer, 1956; Webb, 1957; Müller, 1963; Bock, 1963; Cracraft, 1974; Yudin, 1970, 1978). I shall try to extract information on avian ancestry from the comparative and functional morphology of the feeding apparatus in paleognaths.

Nomenclature for species' binomials and English names of modern birds follows Sibley and Monroe (1990).

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Skeleto-muscular Consequences of Bill Formation

The adductory force of the mandible is transferred to the upper jaw through a food object. Resistance of the upper jaw to this force is produced (Figure 1) by a combination of tension on the ventral stalk (premaxillary and maxillary bones with palate caudally) and longitudinal compression of the dorsal stalk (frontal projection of premaxillary and premaxillary processes of the nasal bones). The longer the jaw grew, the greater the forces became, and, due to jaw lightening, the stresses became ever greater.

The active forces necessary for normal grasping of food items must be supplied by muscles. The muscular force that creates tension in the palate and upper-bill floor also can accomplish ventral movement of the upper jaw by means of re-

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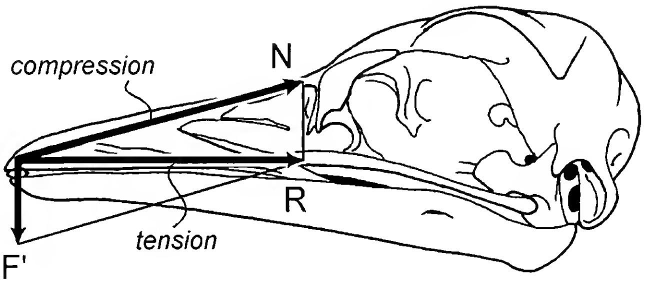

FIGURE 1.—Lateral view depicting the combination of forces in the upper bill of a bird (*Struthio* sp.) that produce resistance against the push from the mandible when grasping food. Lateral view. F'=useful force applied to object, R=rectractory (active muscular) force, N=push transferred to the braincase via dorsal upper-bill stalk.

traction (backward shift) of the palate. Therefore, it is called the retracting or retractory force. The ancestors of birds apparently had no obvious source of such a force. Birds, however, have evolved the following three sources of retracting force.

1. M. retractor palatini (Figure 2) is the ventromedial part of the pterygoid muscle (of Moller, 1930, 1931), which is rather large in tinamous (Figure 2 A,B; Dzerzhinsky, 1983; Elzanowski, 1987), ostriches (Figure 2 D,E), and especially in *Apteryx* (Figure 2 C). In paleognaths (sensu Pycraft, 1900) this muscle usually originates on the pterygoid and on the rear end of the vomer. Its caudal attachment is not situated at the midline on the base of the braincase, as in many neognaths (sensu Pycraft, 1900), but more laterally, near the caudal attachment of the occipito-mandibular ligament, i.e., on the medial part of ala tym-

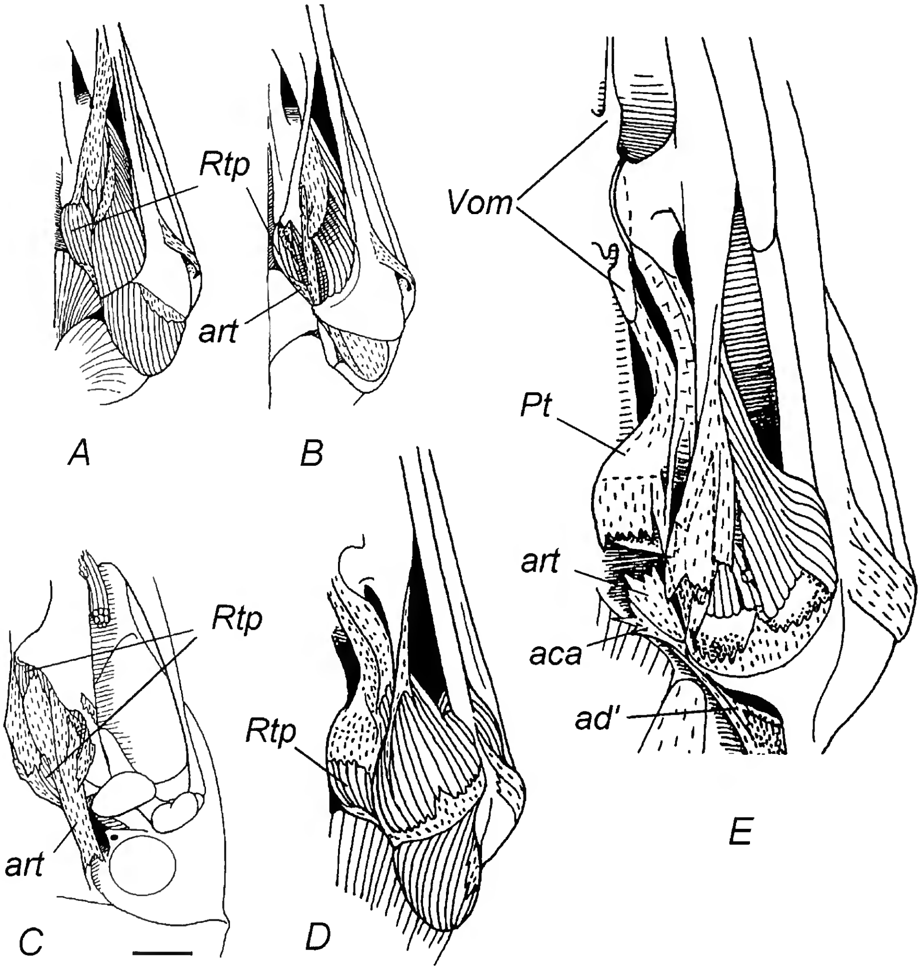

FIGURE 2.—Retractor palatini muscle in ventral view: A,B, tinamou, *Eudromia elegans;* C, Kiwi, *Apteryx* sp. (scale=5 mm); D,E, Ostrich, *Struthio camelus.* aca=aponeurosis of insertion of M. pterygoideus caudalis; ad'=aponeurose of insertion of M. depressor mandibulae that is related to M. retractor palatini; art=aponeurosis of insertion of M. retractor palatini; Pt=pterygoid; Rtp=M. retractor palatini; Vom=vomer (A,C,D, superficial layer; B,E, deeper layers) (A,B, after Dzerzhinsky, 1983.)

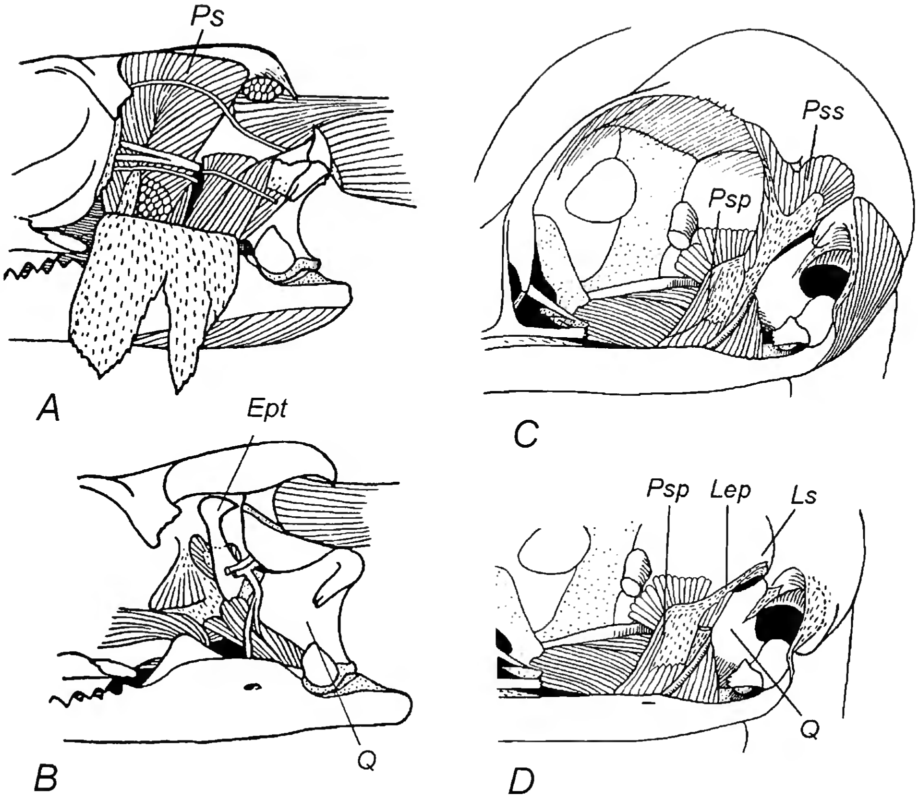

FIGURE 3.—Interrelationship of parts of the pseudotemporalis muscle and epipterygoid or its apparent remainder (lig. epipterygoideum): A,B, Tuatara, *Sphenodon punctatus* (Gray); C,D, tinamou, *Eudromia elegans*. Ept=epipterygoid; Lep=ligamentum epipterygoideum; Ls=laterosphenoid; Ps=undivided M. pseudotemporalis; Psp=M. pseudotemporalis profundus; Pss=M. pseudotemporalis superficialis; Q=quadrate. (A,B, after Dzerzhinsky and Yudin, 1979; C,D, after Dzerzhinsky, 1983.)

panica. In adult Tinamiformes (e.g., *Rhynchotus*) these relations are obscured by later ossification, but they are quite clear in young *Eudromia elegans* Geoffroy Saint-Hilaire (Dzerzhinsky, 1983). Due to the occipito-mandibular ligament, the pterygoid muscle as a whole can act similarly to the retractor, but in contrast to it, via the mandible.

2. M. pseudotemporalis (part of the internal mandibular adductor) applies a retractory force to the mandible, and the force is transferred to the palate via the pterygoid muscle. In *Sphenodon* and lizards (Figure 3A,B), M. pseudotemporalis is undivided and originates mainly from the epipterygoid. In birds, the epipterygoid would limit the mobility of the quadrate, so it either has been replaced by a flexible ligament, as in tinamous (Figure 3 C,D; Dzerzhinsky, 1983), or has been completely reduced. Consequently, the pseudotemporalis muscle has been divided into two portions, originating from two ends of the former epipterygoid. M. pseudotemporalis profundus originates on the tip of proc. orbitalis quadrati, and M. pseudotemporalis superficialis originates on the front wall of the braincase. M. pseudotemporalis profundus produces a retracting force rather effectively, irrespective of the particular direction of its fibers, because the resulting force is transferred to the braincase very caudally, through the quadrato-cranial joint (Figure 4). The main part of M. pseudotemporalis superficialis is well developed in paleognaths and occupies a considerable area of the temporal surface of the braincase (Figure 6A). But even here it passes rather

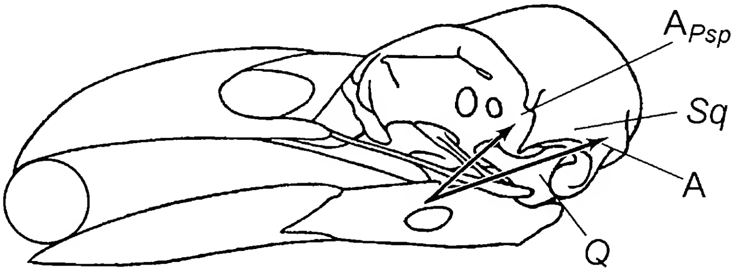

FIGURE 4 (right).—Contraction effect of the pseudotemporalis profundus muscle in the skull of the Common Raven, *Corvus corax* Linnaeus. A_{Psp}=immediate force; A=final force transferred to the braincase via the quadrate bone; Q=quadrate; Sq=squamosum.

steeply, i.e., at a great angle to the jugal bar, and so produces a small retractory effect. It may, however, include (e.g., in *Rhea*) a very inclined portion, the so-called intramandibularis muscle (Figure 5B).

In some birds another inclined portion of this muscle has evolved. The so-called caput absconditum (Hofer, 1950) apparently is a derivative of the main part of M. pseudotemporalis superficialis that is situated in the posterior temporal fossa of a typically diapsid ancestor (Figure 5A; Dzerzhinsky and Yudin, 1979). It is found in Sphenisciformes, Procellariiformes (Figure 5B), and Pelecaniformes but never in recent paleognathous birds.

3. M. adductor mandibulae externus (Figure 6) acting on the upper jaw via the pterygoid muscle is a very important retractor in most birds (e.g., cranes). In paleognaths, however, it shows a rather modest development and, except *Apteryx*, does not spread up over the temporal wall of the braincase. Thus, its origin is limited to the zygomatic process of the squamosal. This restriction might have resulted from a reduction of the main ancestral origin of the muscle, the upper jugal arch. Otherwise, it might be a result of the change of functional requirements in the muscle during the course of development of the long bill and the cranial kinesis.

I presume that the immediate ancestors of birds had an akinetic skull that possessed some prerequisites of cranial kinesis, such as a loose basipterygoid articulation (Yudin, 1970). It seems likely that kinetic mobility appeared first in the most loaded zone, i.e., within the slender upper jaw (Figure 1), and thus resulted in an archaic rhynchokinesis (Yudin, 1970, 1978).

One of the questions about the functional morphology of the avian skull is the influence of sharp strokes, such as are associated with pecking or with accidental strokes against hard substrates while gathering grain or catching small, agile prey. In tinamous, the loose articulation of the frontal bone with the adjacent parietal and laterosphenoid (Figure 7) is equivalent to the so-called "articulating frontoparietal joint" described by Houde (1981) in early Tertiary North American carinates. It does not allow significant rotary movements of any cranial part, so in my opinion it is not associated with ancient mesokinetic mobility. Rather it is for damping shocks received along the dorsal bill stalk while pecking.

The ventral stalk of the upper jaw was initially compliant, and it had to be supported by some solid framework able to transfer to the braincase large, but not dangerous, forces. This framework is formed by the bony palate, and among recent paleognaths it is strongest in *Apteryx* (Figure 8A), doubtless due to its specialization for probing.

In tinamous, *Rhea* (Figure 8B), and, apparently, recent Casuariiformes, the main trajectory of compression stresses runs from the palatine process of the premaxillary bone to the vomer, then to the pterygoid, the quadrate, and finally via the quadrate's otic process to the braincase (Dzerzhinsky, 1983). In ostriches (Figure 8C), where the palatal processes of the premaxillary are missing and the vomer is partly reduced, com-

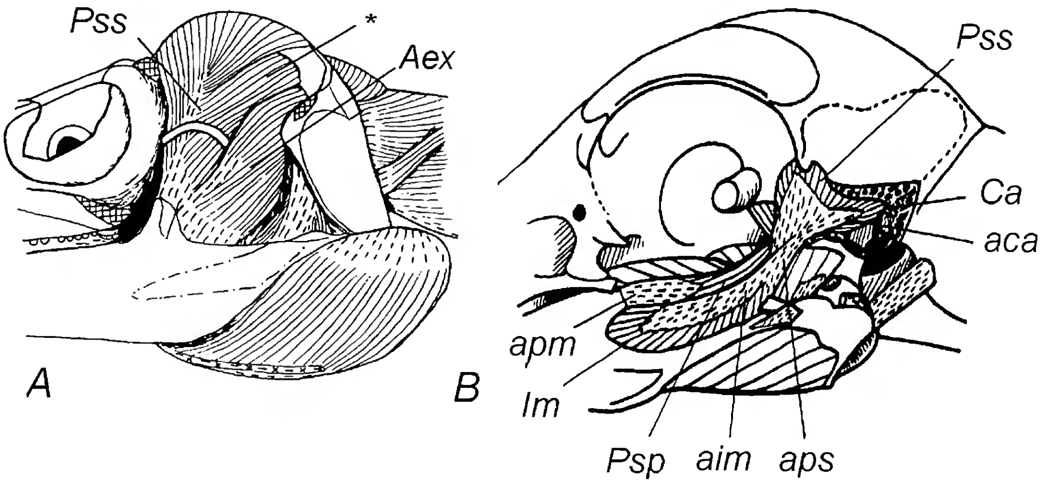

FIGURE 5.—Comparison of the pseudotemporalis muscle in lateral view: A, lizard, *Cyclura nubilis* Gray; B, procellariiform bird, Northern Fulmar, *Fulmarus glacialis* (Linnaeus) (mandible and side wall of braincase partly destroyed and removed). aca=aponeurotic insertion lobe of the caput absconditum of the pseudotemporalis superficialis muscle; Aex=M. adductor mandibulae externus; aim= aponeurotical lobe of origin of the M. intramandibularis; apm=aponeurosis of insertion of the pseudotemporalis profundus muscle; aps=aponeurosis of insertion of the pseudotemporalis superficialis muscle; Ca=caput absconditum of the pseudotemporalis superficialis muscle; Im=intramandibularis muscle, part of the pseudotemporalis superficialis muscle; Psp=pseudotemporalis profundus muscle; Pss=pseudotemporalis superficialis muscle; *=especially inclined part of the pseudotemporalis muscle. (A, after Iordansky, 1990; B, after Dzerzhinsky and Yudin, 1979.)

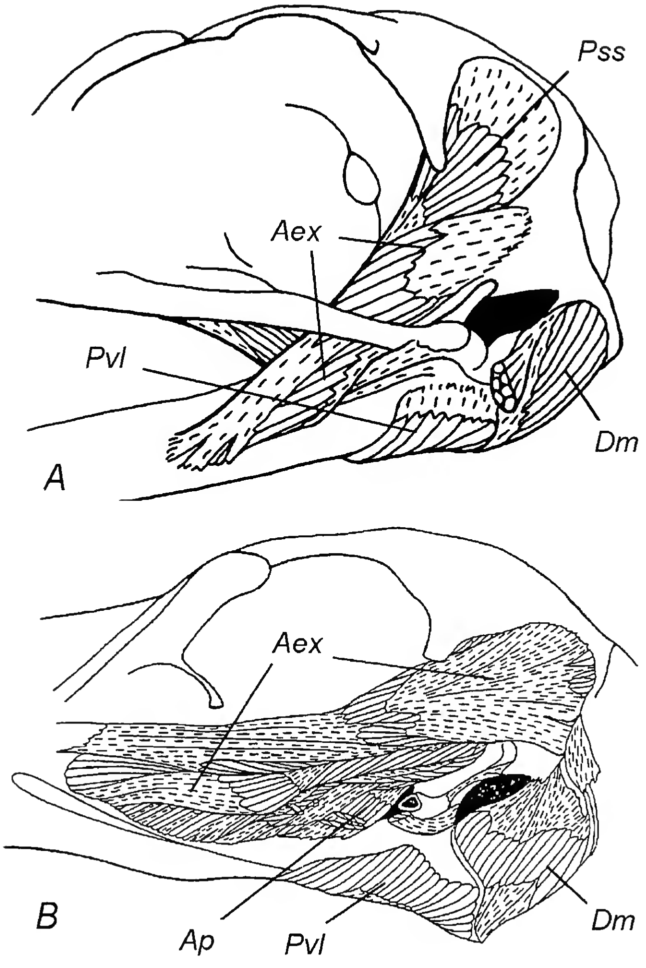

FIGURE 6.—Lateral surface of jaw adductors in lateral view: A, Rhea, *Rhea americana*; B, White-naped Crane, *Grus vipio*. Aex=M. adductor mandibulae externus; Ap=M. adductor mandibulae posterior; Dm=depressor mandibulae muscle; Pss=pseudotem-poralis superficialis muscle; Pvl=ventrolateral portion of the pterygoid muscle. (B, after Kuular and Dzerzhinsky, 1994.)

pression stresses run from the bill tip through the premaxillary and maxillary bones to the palatine and then almost directly to the apex of the basipterygoid process. In the roof of the mouth, the ostrich possesses a broad gap that is closed only by skin. This patch of skin gains a gliding support from the parasphenoidal rostrum via a long, thin, anterior extension of the vomer.

Source of the Medial Mandibular Process

The processus mandibulae medialis is highly specific for Aves. For example, in *Gobipteryx*, a fossil Mongolian bird, Elzanowski (1974) regarded this process as a distinctly avian character. The functional properties of the muscular portion (ventromedial portion of the pterygoid muscle) inserting on its tip are influenced significantly by the particular position of the tip. It is placed extremely high in the sagittal plane, so corresponding muscular forces pass almost through the pivot of the quadrato-mandibular joint (Figure 9A) and therefore apply a negligible adductory component to the mandible as compared to the retractory one. In the frontal plane, the tip of the process is extremely close to the midline, and therefore those muscular forces tend to rotate the caudal part of mandibular branch and so expand the lower jaw as a whole (Figure 9B; Yudin, 1961).

The functional conditions discussed above, however, do not seem to account for the first steps in the evolution of the medial mandibular process. There is a peculiarity in the paleognath jaw musculature that is more useful in this respect: the above-mentioned M. retractor palatini. I suggest that this muscle may have arisen by a joining of two muscular units—the ventromedial portion of the pterygoid muscle and the depressor mandibulae muscle. Thus, their primitive interconnection via the caudal portion of the mandible formed a two-link chain that foreshadowed the recent M. retractor palatini (Figure 10). The crucial event in their further evolution has been an optimization of their ability to exert a single force, which has been ensured by alignment of both muscular links, due to the displacement

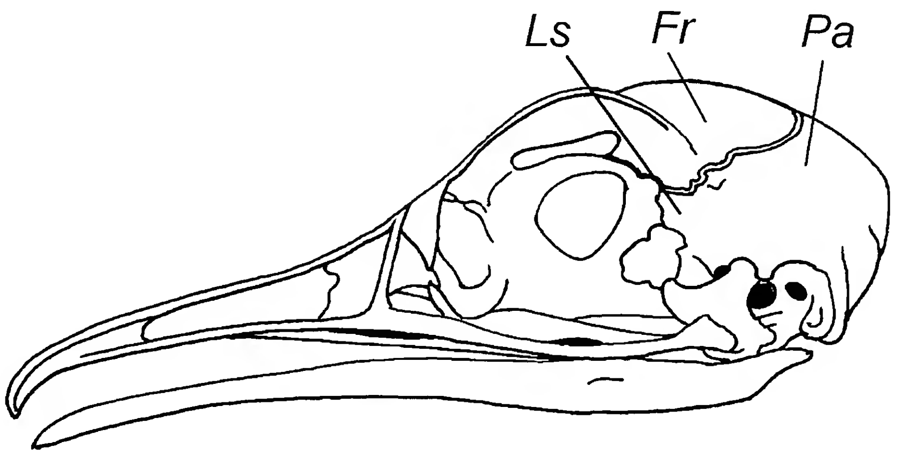

FIGURE 7.—Lateral view of tinamou skull (Tinamiformes), showing the loose articulation of the frontal with adjacent bones. Fr=frontal; Ls=laterosphenoid; Pa=parietal.

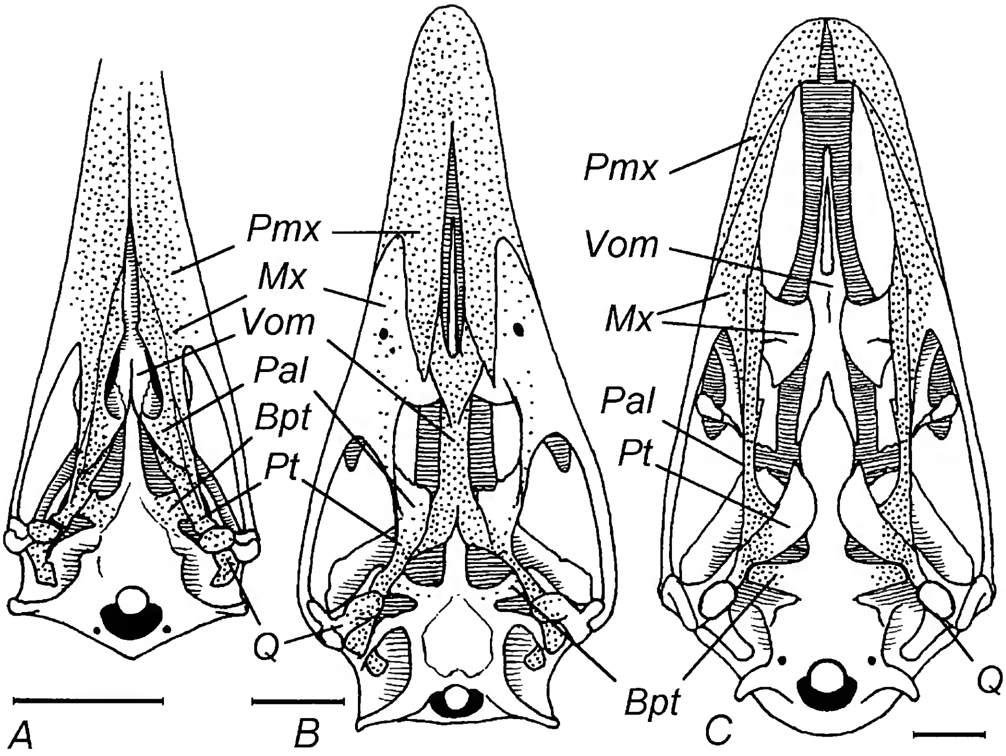

FIGURE 8.—Comparison of palate structures in ventral view: A, Kiwi, *Apteryx* sp.; B, Rhea, *Rhea americana*; C, Ostrich, *Struthio camelus*. Probable paths for transferring longitudinal compression forces stippled. Bpt=basipterygoid process; Mx=maxillary; Pal=palatine; Pmx=premaxillary; Pt=pterygoid; Q=quadrate; Vom=vomer. Scale=20 mm.

of their interconnecting point by means of the formation and gradual elongation of the medial mandibular process. After the alignment, this hypothetical digastric muscular complex must have separated from the mandible. Apparently, the recent occipito-mandibular ligament represents the reduced caudal belly of the digastric complex.

Conclusion

I would like to comment on the reinterpretation by McDowell (1978) of the homologies in the avian upper jaw and palate. It is, of course, tempting to use the kinetic mobility in the skull as a cause of fragmentation of a huge, ancient pterygoid bone into two; however, many traits in the general arrangement of the bones (primarily palatine position relative to the choana, premaxillary, etc.) seem to be consistent with the traditional interpretation that these two bones represent the reptilian palatine and pterygoid. The skull in ancient birds almost certainly had less internal mobility than it does in recent paleognaths, and such characters as the shape of the lateral rim of the palate or the pattern of epidermal papillae can hardly be valid. Finally, it is too difficult to accept McDowell's proposed loss of the maxillary bone in birds and his consequent thesis that the maxillopalatine of birds is equivalent to the reptilian palatine.

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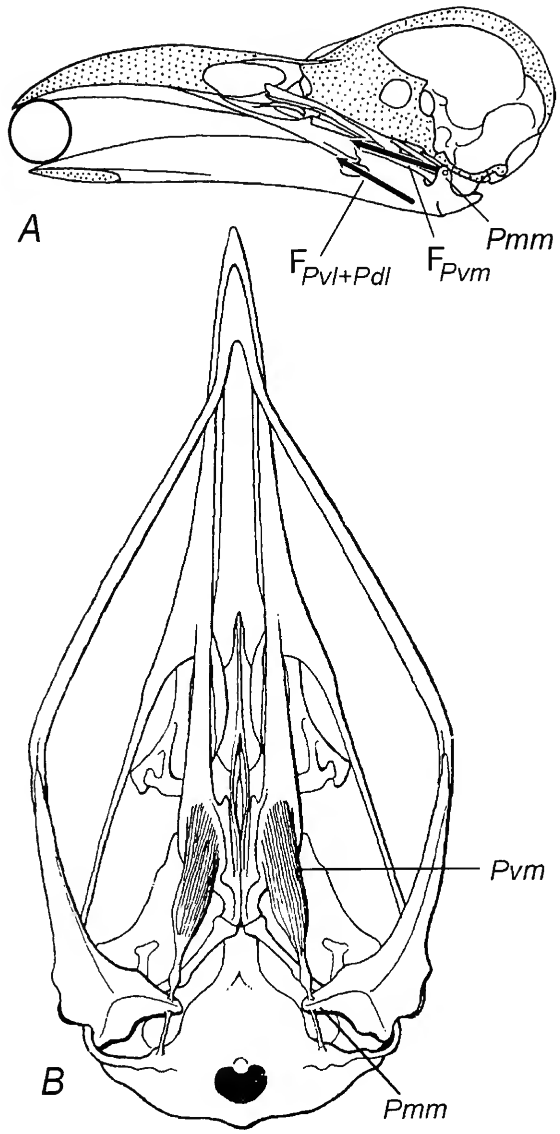

FIGURE 9.—Some functional effects of the medial mandibular process: A=skull of the Carrion Crow, *Corvus corone cornix* Linnaeus, in sagittal section, seen from left; B=skull of the Herring Gull, *Larus argentatus* Pontoppidan, with mandible broadened by contraction of the ventromedial portion of the pterygoid muscle, ventral view. F_{Pvm}=force of the ventromedial portion of the pterygoid muscle; $F_{Pvl+Pdl}$=force of its lateral portions; Pmm=processus mandibulae medialis; Pvm=ventromedial portion of the pterygoid muscle. (B, after Yudin, 1961).

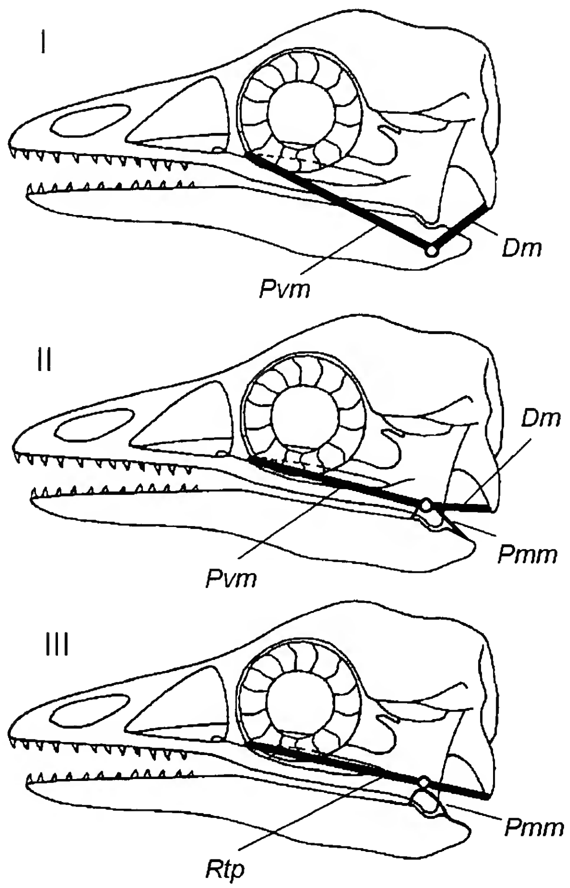

FIGURE 10.—Hypothetical stages in the formation of the proc. mandibulae medialis in birds, drawn on the model of the skull of *Archeopteryx* (Bühler, 1985). Dm=depressor mandibulae muscle; Pmm=processus mandibulae medialis; Pvm=ventromedial portion of the pterygoid muscle; Rtp=M. retractor palatini.

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The Relationships of the Early Cretaceous *Ambiortus* and *Otogornis* (Aves: Ambiortiformes)

Evgeny N. Kurochkin

ABSTRACT

Ambiortus from the Khurilt beds (Neocomian) of central Mongolia shows a combination of characters that confirms the assignment of this fossil to a separate order, Ambiortiformes. *Otogornis genghisi* Hou, 1994, of the Yijinhouluo Formation (earliest Cretaceous or latest Jurassic) of Ordos, China, was first described as *Aves* incertae sedis. *Ambiortus* and *Otogornis* share specialized characters, such as a thickened, three-edged acrocoracoid with an acute top; a flat, wide humeral articular facet of the scapula; ventral position of a small, oval humeral articular head; and a thin, long intermediate phalanx of the major wing digit. The generic status of *Otogornis* is supported by some other diagnostic characters. Several advanced characters demonstrate the assignment of *Ambiortus* and *Otogornis* to the Palaeognathae. These two forms show the occurrence of paleognathous birds in the Early Cretaceous of Central Asia.

Introduction

The Early Cretaceous *Ambiortus dementjevi* Kurochkin, 1982, was described as a member of the new family Ambiortidae and order Ambiortiformes, which was assigned to the infraclass Carinatae (Kurochkin, 1982). *Ambiortus* was based on an associated portion of the skeleton, including the vertebrae, the shoulder girdle, and some wing bones preserved on the main slab and counterslab, and also on the distal portion of the wing bones and feather imprints, which are preserved on an associated slab. Two papers containing more extensive description and comparison of this fossil were published later (Kurochkin, 1985a, 1985b). The surprising appearance of this Early Cretaceous true bird in the paleontological record made comparison with other birds very difficult. In these first papers I attempted to compare *Ambiortus* with members of the living Gruidae, Rallidae, Strigidae, Alcedinidae, Momotidae, and, superficially, with the Archaeopterygiformes, Ichthyornithiformes, Paleogene paleognaths (later described as Lithornithiformes Houde, 1988), and *Wyleyia* Harrison and Walker, 1973. However, further study and a possibility of a direct comparison with the Enantiornithes, *Archaeopteryx, Ichthyornis, Wyleyia, Paracathartes, Lithornis, Palaeotis,* and living Palaeognathae, and also additional preparation of the holotype of *Ambiortus,* showed the published anatomical descriptions and morphological comparison of this fossil to be incomplete and partly erroneous.

Evidence for the relationships of *Ambiortus* with the Palaeognathae was published beginning in 1985 (Kurochkin, 1985a, 1988, 1995a, 1995b). This mainly was based on comparison with the Paleogene Lithornithiformes studied by Houde and Olson (1981) and Houde (1988). Olson (1985) emphasized that *Ambiortus* shows some decided similarities with the Paleogene paleognathous birds and also may share some common characters of the humerus with *Ichthyornis.* Martin (1987, 1991) united *Ambiortus* with *Apatornis* and the Ichthyornithiformes. Cracraft (1986) concluded that *Ambiortus* can be assigned to the Carinatae, in which he included the Palaeognathae, Neognathae, and *Ichthyornis.* Sereno and Rao (1992) have placed *Ambiortus* outside the Ornithurae without character evidence. Chiappe (1995) considered *Ambiortus* to be the oldest probable ornithurine, yet one of unclear relationships. Elzanowski (1995) assigned *Ambiortus* to the Carinatae and primitive Neornithes, close to *Ichthyornis;* however, his cladistic analysis of the skeletal characters also placed the Enantiornithes, *Cathayornis,* and *Concornis* among the Carinatae. Obviously, *Ambiortus* has nothing in common with the Enantiornithes. In that paper, Elzanowski (1995) made mainly mistaken interpretations of skeletal characters in *Ambiortus* that are discussed below. Feduccia (1995, 1996) placed *Ambiortus* in the basal Ornithurae together with *Gansus,* the Hesperornithiformes, and Ichthyornithiformes.

Thus, controversial phylogenetic conclusions exist concerning *Ambiortus*, and it has remained isolated in the avian phylogenetic tree as the result of incomplete and questionable descriptions (Kurochkin, 1982, 1985a, 1985b), especially those

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concerning the amphicoelous structure of the vertebrae and the bones of the shoulder girdle. New preparation and observation of the specimen provide a complete and corrected anatomical description of this bird.

It was a great surprise to discover that *Ambiortus dementjevi* is similar to *Otogornis genghisi,* which was described by Hou (1994) from the Ordos Basin at the Chabu Sumu locality, Otog Qi, Yikezhao-meng, Inner Mongolia, China. The specimen was collected in the thin, grey green mudstones of the Yijinhuoluo Formation of the Zidan Group in the *Lycoptera*-bearing deposits and represents the earliest Cretaceous or even a Late Jurassic avian fossil from China (Hou, 1994). *Otogornis* is based on associated elements of the forelimb and shoulder girdle (VP-9607, holotype, Institute of Vertebrate Paleontology and Paleanthropology (IVPP), Beijing). The slab also displays some feather impressions. *Otogornis* was described as Aves incertae sedis and was compared with *Archaeopteryx, Chaoyangia,* and the enantiornithines *Sinornis* and *Cathayornis* (Hou, 1994). Earlier, the same specimen was assigned to the indeterminate Enantiornithes (Dong, 1993).

ACKNOWLEDGMENTS.—I thank very much L. Hou and Z. Zhou for permitting investigation of the holotype of *O. genghisi* in the IVPP collection. L. Martin prompted me to use for the investigation the mold from specimen 3790-272, which led to the discovery of a contact with the counterslab specimen 3790-271- (specimens in the Paleontological Institute, Russian Academy of Sciences (PIN)). Comparison with the lithornithids was made possible by the courtesy of R. Emry in the Department of Vertebrate Paleontology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. For comments on the manuscript and English corrections I am thankful to S. Lucas, R. Zusi, S. Olson, and two anonymous reviewers. The stereophotographs were made by S. Morton in the Faculty of Sciences of Monash University, Clayton, Australia. The x-radiograph of *Ambiortus dementjevi* was made by L. Martin and J. Chorn in the Museum of Natural History, University of Kansas. All drawings, including *Otogornis,* were made by the author. This study was supported by a travel grant and grant 96-04-50822 of the Russian Fund for Fundamental Research, as well as by funds from the IVPP, Academy of Sciences of China.

Age of the Khurilt Beds

The geological age of *Ambiortus* is problematical. It was found in Mesozoic rocks of the Gobian Altai in central Mongolia in the Khurilt-Ulan Bulak locality. This discovery caused some paleontologists to doubt the correct definition of the fossil and the age of the deposits. At present, no doubts exist about the advanced avian condition of this specimen. The geologic age of the Upper Cretaceous lacustrine shales and sandstones of the Khurilt locality, however, is discussed in contradictory terms by different experts in biostratigraphy, paleobotany, and paleoentomology, with the dates ranging from the latest Jurassic to the Aptian.

Numerous and various insects were collected in these beds (Zherikhin, 1978; Sinitsa, 1993). The insect fauna is very constant in a number of localities in central Mongolia (Khurilt, upper members of Kholbotoo, Bon Tsagan). This is known as the Bon Tsagan assemblage, the youngest among three Lower Cretaceous assemblages in central Mongolia (Ponomarenko, 1990). Dmitriev and Zherikhin (1988) supported an Aptian age of the deposits in these localities.

The plant associations of the Khurilt, neighboring deposits of the Kholbotoo, and of the middle levels of the Bon Tsagan localities include, following Krassilov (1982), four phytostratigraphic units in the Upper Cretaceous of Mongolia. The third unit is the *Baierella hastata* (Bennettitales; and its cones, *Karkenia mongolica*)/*Araucaria mongolica* zone, which includes localities of Shin Khooduk–Anda Khooduk level, and most of the paper shales of the Bon Tsagan, Kholbotoo Gol, Khurilt, Erdeni Ula, Shin Khooduk, and Modon Usoo localities. The sediments of the Khurilt and Kholbotoo localities were assigned by Krassilov (1982) to the Anda Khooduk Formation. The plant communities from these localities he correlated with the Aptian flora of the Russian Far East (Primorye). Thus, phytostratigraphic data suggest an Aptian age for the Khurilt beds (Krassilov, 1982).

Based on geological data, Martinson (1973) and Shuvalov (1975, 1982, 1993) referred the Khurilt and Kholbotoo beds to the Anda Khooduk Formation, which they correlated with the Hauterivian–Barremian.

Sinitsa (1993), based on the lithofacial data and ostracod assemblages, did not provide a definite age for the Khurilt beds and defined it as a task for future exploration. She specified that the Khurilt beds belong to the Khurilt Section of the Bon Tsagan Series. The Khurilt beds are underlaid by the Dund Argalant Series of the latest Jurassic, which includes the Anda Khooduk Formation (Tithonian), and are overlapped nearby by the sediments of the Kholbotoo Section (younger beds of the Bon Tsagan Series). In more western areas of Mongolia, the Bon Tsagan Series are overlapped by the Khoolsyn Gol Formation, which is correlated with the Aptian-Albian.

Perhaps the Mongolian and Chinese Lower Cretaceous shale sediments were deposited simultaneously. The problem of age determination of the lacustrine Lower Cretaceous beds in Mongolia is the same as for the Jehol Group in China (Matsukawa and Obata, 1994). The Khurilt outcrop and the upper members of the neighboring Kholbotoo outcrop are very similar to the grey green, thin-bedded sandy and oil shales and siltstones of the Jiufotang Formation in Liaoning Province of China. The Jiufotang Formation is a member of the Jehol Group, which is subdivided into four lithostratigraphic units: Yixian, Jiufotang, Shahai, and Fuxin formations (Smith et al., 1995). The Jiufotang Formation is correlated with the Berriasian–Valanginian (Li and Liu, 1994), or Tithonian–Valanginian (Lin, 1994), or even with the Tithonian (Chen and Chang, 1994). On the basis of fossil fishes, the Yixian and Jiufotang formations are correlated with the Late Jurassic and Neocomian, in agreement with the fish faunas of Japan, Kazakhstan, and western Europe (Fan, 1996).

Published radiometric ages for the base of the Yixian Formation include 137±7 Ma using K/Ar and 142.5 Ma using Rb/Sr (Wang, 1983; Wang and Diao, 1984), which corresponds with a Berriassian age, using the time scale of Harland et al. (1989). For the Fuxin Formation, K/Ar ages range from 100 Ma to 137 Ma (Mao et al., 1990), corresponding with an Aptian–Valanginian age. New age dates were reported for the Yixian Formation, however, that are based on a laser ^{40}Ar/^{39}Ar study of single mineral grains (Smith et al., 1995). This study estimated the age of the lower Yixian Formation as 121.2±0.3 Ma and 121.3±2.3 and 121.4±0.7 Ma for the upper Yixian Formation. Smith et al. (1995) also tested the absolute ages using ^{40}Ar/^{39}Ar in very fine crystallites of glaucony from the white lacustrine Ershilipu sediments that occupy a stratigraphic position between the upper and lower parts of the Yixian Formation. The resulting ages of 122.1±0.2 Ma and 122.5±0.3 Ma agree with the strict chronostratigraphic constraints imposed by the ^{40}Ar/^{39}Ar ages of the upper and lower Yixian Formation. Thus, Smith et al. (1995) provided an integrated age range of 121.1–122.9 Ma for the Yixian Formation, which corresponds to the Barremian using the time scale of Harland et al. (1989), and these dates are much younger than the K/Ar and Rb/Sr dates of other authors.

Thus, insects and plants suggest an Aptian age for the Khurilt deposits, but the geological data and ostracods indicate a Neocomian age. The probably contemporaneous Yixian and Jiufotang formations in northeastern China are assigned to the Neocomian on faunistic, plant, and radiometric data, although the laser ^{40}Ar/^{39}Ar study gives a Barremian age. I am inclined to accept a Neocomian age for the Khurilt deposits.

Comprehensive Description of *Ambiortus*

Ambiortus dementjevi is represented on three slabs. The main slab (PIN 3790-271+) bears the cervical and thoracic vertebrae, furcula, left scapula and coracoid, a portion of the sternum, some thoracic ribs, the proximal portion of the left humerus, distal portions of the radius and ulna, ulnare, the proximal portion of the left carpometacarpus, and phalanges of the major wing digit (Figures 1, 3–5). This slab also shows an isolated impression of a feather vane about 12 mm long and the probable impression of the soft body of the specimen, with small contour feathers that surround the body impression. The feathers and body impression are better represented on the counterslab (PIN 3790-271-). The counterslab bears small fragments of the vertebrae and a portion of the major metacarpal, and it has a good mold of the humerus, coracoid, clavicle, and carpometacarpus. A small associated slab (PIN 3790-272) shows just the mold of three phalanges of the major left wing digit, the mold of the ulna and major metacarpal, and a frag-

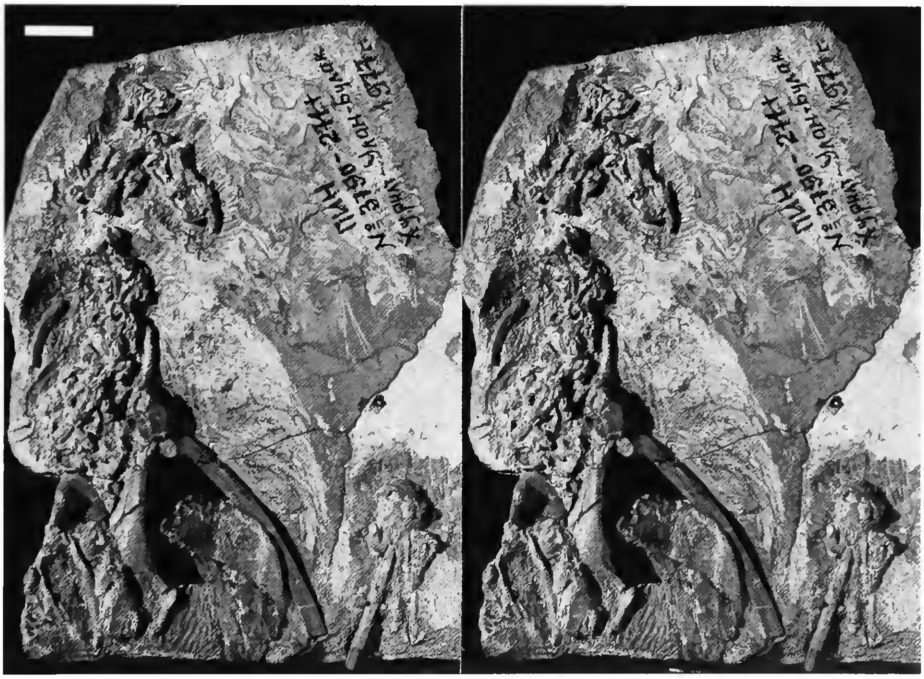

FIGURE 1.—Main slab with *Ambiortus dementjevi* Kurochkin, 1982, holotype PIN 3790-271+; Khurilt Ulan Bulak locality, central Mongolia, Neocomian. Stereopairs. (Scale bar=1 cm.)

ment of the radius that are continued from the main slab (Figures 2, 3). This slab also bears several impressions of the wing feathers. The counterslab and associated slab form a broken contact with each other (Figure 3).

VERTEBRAE.—The preserved 15 or 16 cervical and thoracic vertebrae (3–17(18)) are ventrally exposed on the main slab (Figures 1, 3, 5). The first (atlas) and second (axis) vertebrae are absent, although a probable fragment of the latter is preserved in front of the first preserved vertebra, which I consider to be the third cervical. The first two preserved vertebrae each have a short, wide, flat ventral body surface; thus, I consider them to be the third and fourth cervicals. Most of the portions of the probable fifth and sixth cervicals are disarticulated from the other vertebrae. The seventh and eighth vertebrae each show a long, flattened body ventrally. They have well-developed cranial zygapophyses with costal processes and caudal zygapophyses (Figures 1, 3, 5). The carotid processes form a shallow open carotid canal. The strong, paired, caudal, transverse processes are developed on the ventral side lateral to the caudal articular surface. Such processes are present in *Lithornis* and in *Rhea;* they are different from the postlateral processes in grebes (Zusi and Storer, 1969).

The ninth cervical was extracted in order to investigate the articular surfaces of the vertebral bodies because in earlier papers the vertebrae of *Ambiortus* were regarded as probably amphicoelous. Although this was widely used to establish the relationships of this bird, it appears to have been a misinterpretation. As a result of this new preparation of the vertebrae, it has become evident that the caudal articular surface of the eighth cervical and the cranial surface of the tenth cervical were certainly heterocoelous. The tenth and eleventh vertebrae have a longer centrum with a narrower ventral side than do those of the third and fourth vertebrae and those of the thirteenth through sixteenth vertebrae, but they have shorter centra than in the seventh and eighth vertebrae. The twelfth, thirteenth, and fourteenth cervical vertebrae show shortened bodies and enlarged costal processes represented only by the sturdy basal portions. The basal portions of two well-expressed ribs are preserved near the right side of the fifteenth vertebra. These ribs are small and represent the floating ribs. The sixteenth vertebra is very compressed. The seventeenth vertebra has a wide and nearly flat ventral body surface and a very narrow caudal articular surface. On the left side of this vertebra the dorsal portion of a large rib is present; it has two articular facets, although the dorsal one is not preserved in this sample. A probable portion of the eighteenth vertebra is preserved caudal to the seventeenth vertebra in the angle between the coracoid and sternum. The thirteenth through seventeenth vertebrae have shortened bodies. The ventral crests (hypapophyses) are not present in either the cranial cervical or the thoracic vertebrae. I think that this specimen preserves at least 15 cervical vertebrae, which mainly have wide and short centra. Thus, *Ambiortus* was a short-necked bird.

FIGURE 2.—Associated slab with *Ambiortus dementjevi,* PIN 3790-272; Khurilt Ulan Bulak locality, central Mongolia, Neocomian. (Scale bar=1 cm.)

SHOULDER GIRDLE.—The cranial portion and left costal margin of the sternum preserves the base of a thick pillar of the sternal keel and a damaged sternal costal margin (Figures 1, 3). The cranial surface of the pillar is directed down and somewhat caudally. The furcula is represented by the dorsal portions of both clavicles, which terminate at slightly thinned ends that are neither enlarged nor flattened. The small articular facet for the coracoid is directed caudomedially. The cross section of the clavicle in its middle portion is nearly circular. The medial side of the clavicle is slightly flattened. Originally, the holotype preserved the mold of the interclavicular symphysis, which was placed superficially on the level of the fifteenth vertebra. This was destroyed during preparation. The mold of the ventral furcula showed that the ventral portion of both clavicles have the same diameter as dorsal ones. In the interclavicular area, a thin, slightly projecting eminence around the symphysis was present, without any vestige of the hypocleideum.

In the left scapula, the caudal end of the scapular body is absent. The humeral articular facet is flat and wide and faces latero-cranially but is not nearly perpendicular to the scapular blade as noted by Elzanowski (1995). In its cranial area, the facet converges into a slightly convex, ellipsoidal coracoidal tubercle. A strongly projecting and sturdy acromion is very distinctive for this scapula (Figure 4). The acromion is dorsoventrally compressed, and its cranial ending is blunt and attenuated cranially. The dorsal surface of the acromion possesses a conspicuous dorsal tubercle (not crest) that is very similar to that in *Lithornis celetius* Houde, 1988. The acromion is not turned mediad, contrary to Elzanowski (1995). The scapular body is blade-like, strongly flattened lateromedially, and slightly

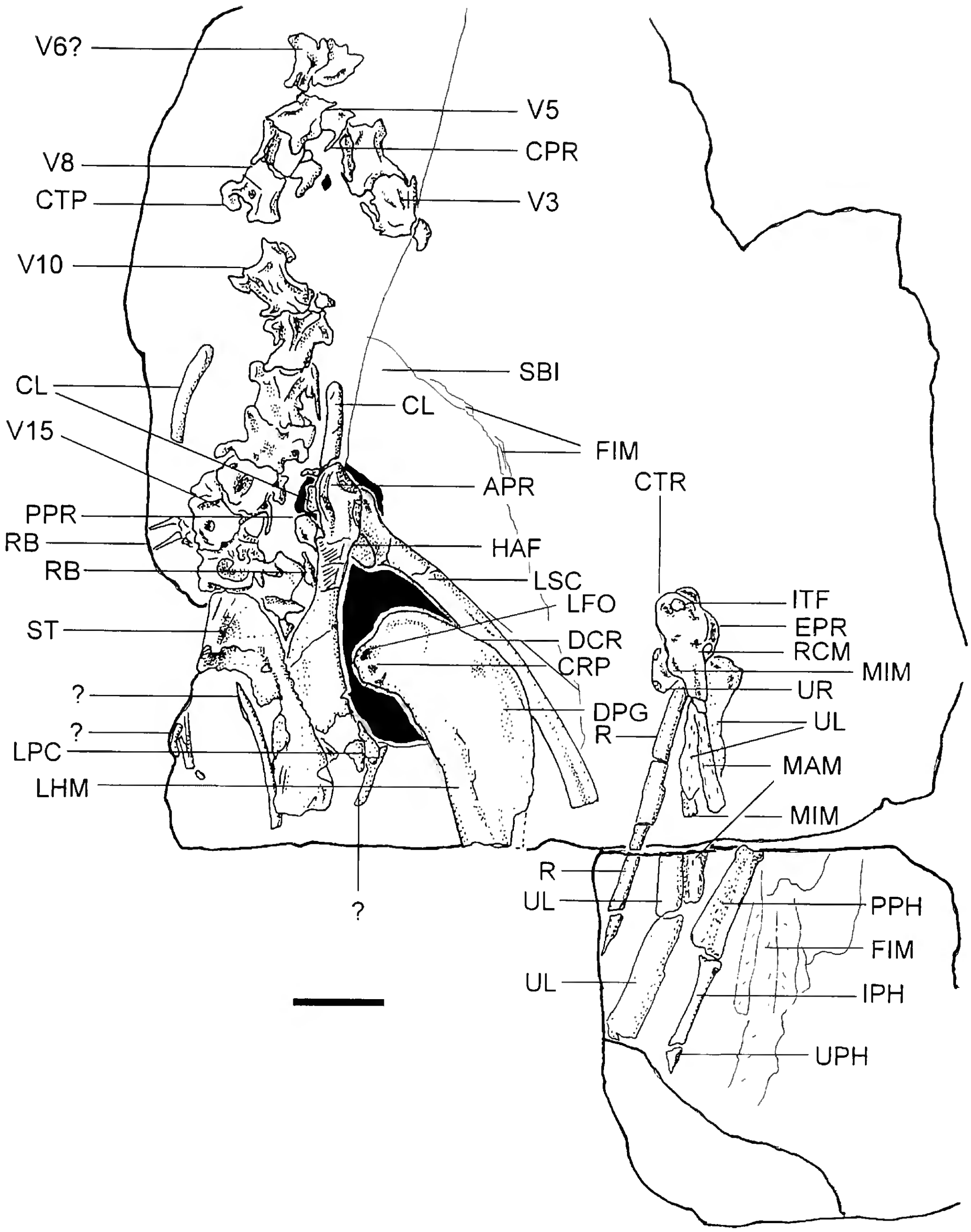

FIGURE 3.—Composition of the main slab (PIN 3790-271+) and of the mold of the associated slab (PIN 3790-272), with the holotypical partial skeleton of *Ambiortus dementjevi.* APR=acrocoracoid process, CL=clavicle, CPR=costal process, CRP=cranial pit, CTP=caudal transverse process, CTR=carpal trochlea, DCR=deltopectoral crest, DPG=deltopectoral groove, EPR=extensor process, FIM=feather imprints, HAF=humeral articular facet, IPH=inter-mediate phalanx of major wing digit, ITF=infratrochlear fossa, LFO=liga-mental fossa, LHM=left humerus, LPC=lateral process of coracoid, LSC=left scapula, MAM=major metacarpal, MIM=minor metacarpal, PPH=proximal phalanx of major wing digit, PPR=procoracoid process, R=radius, RB=rib, RCM=right carpometacarpus, SBI=soft-body imprint, ST=sternum, V3–V15=3rd–15th vertebra, UL=ulna, UPH=ungual phalanx of major wing digit, UR=ulnare. (Scale bar=1 cm.)

curved dorsally. The scapula has a moderately long body bearing an elongated tuberosity on the dorsolateral edge in its cranial half and has a well-expressed depression along the lateral surface of its caudal half.

The left coracoid is represented by the shoulder end and shaft. The sternal end is covered by matrix and sternal bone, but it is well seen in the x-radiograph (Figure 5). The sternal end is wide and flat, with a long-pointed medial angle and with a rectangular lateral process. Such a structure of the medial angle is very similar to that in *Lithornis plebius* Houde, 1988. The acrocoracoid is sturdy, relatively short, and its dorsal top is three-edged and bluntly acute. The craniomedial side of the acrocoracoid bears an elongate depression that probably represents an articulation for the clavicle. The lateral side of the acrocoracoid possesses a wide, slightly concave depression of the acrocoracohumeral tendon. Ventral to this depression, a relatively small humeral articular facet is located, the facet being exposed laterally. An ellipsoidal scapular cotyla is exposed caudolaterally and is located on an enlarged base of a wide, flat, long procoracoid process. The sternal portion of the coracoidal shaft is strongly broadened. None of the elements of the shoulder girdle are compressed, and they all preserve the true configurations of the bones.

WING BONES.—The proximal end of the left humerus was strongly compressed in its plane during preservation. The humeral articular head is small, bean-shaped, and located in the ventral position of the proximal end. The humerus has a well-developed deltopectoral crest beginning very close to the humeral articular head in the most proximal position of the proximal end; it is similar to that in *Lithornis plebius*. The deltopectoral crest is flat but is rather deflected dorsally, contrary to Elzanowski (1995), who described it as projecting laterally. Along the dorsal margin, a shallow groove appears in the proximal half on the cranial side. The bicipital crest and pneumotricipital fossa are absent; the latter is expressed only as a tricipital depression (Figure 4). The ventral edge of the proximal end of the humerus is remarkably projected ventrally. Its distal edge is like a boss. The cranial surface of this boss possesses a slightly pronounced cranial tubercle with a pit in the center. Cranially from this tubercle is a noticeable ligamental fossa (not a groove). *Lithornis plebius* also has a similar tubercle possessing a pit and has a ligamental fossa instead of a furrow. Such a ligamental fossa is probably the homolog of the transverse ligamental furrow. On the caudal surface of the proximal end, a small dorsal pit is developed in the usual place of the dorsal tubercle. A small ventral tubercle is represented on the caudal surface of a projecting ventral edge. The capital groove is not developed. A slightly elevated caudal margin runs along the middle of the shaft and is directed toward the middle of the humeral head.

The ulna is badly damaged. Only its distal end and a mold of a portion of the shaft are preserved on the main and associated

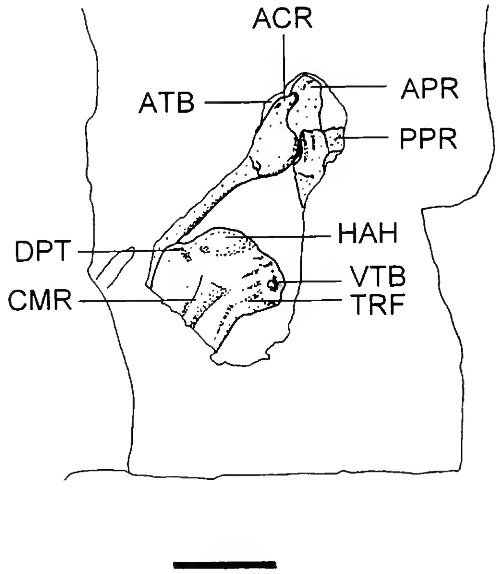

FIGURE 4.—Shoulder articulation in *Ambiortus dementjevi* on the opposite view of the main slab, PIN 3790-271+. ACR=acromion, APR=acrocoracoid process, ATB=acromial dorsal tubercle, CMR=caudal margin, DPT=dorsal pit, HAH=humeral artiular head, TRF=tricipital fossa, VTB=ventral tubercle. (Scale bar=1 cm.)

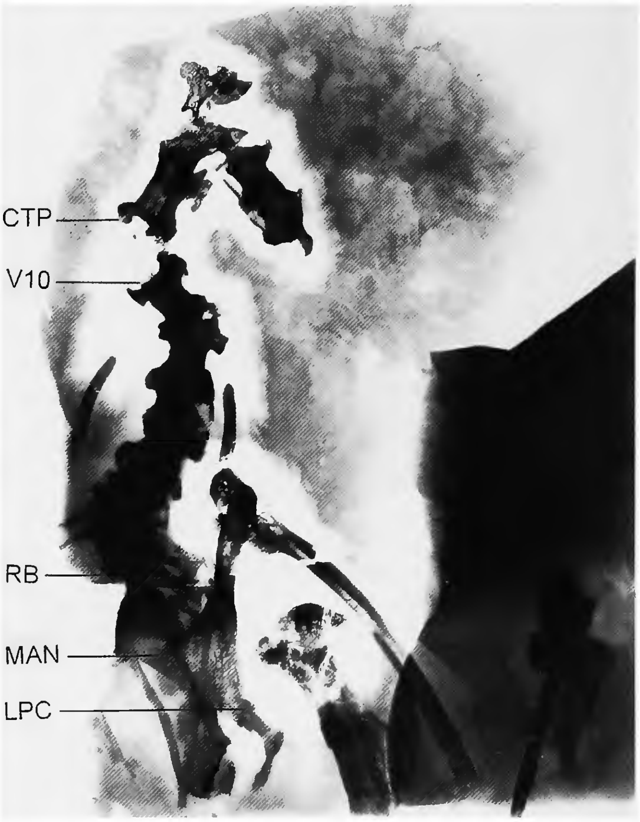

FIGURE 5.—X-radiograph of the main slab with *Ambiortus dementjevi*. The sternal end of the coracoid with the medial angle and structure of the vertebrae can be clearly seen. CTP=caudal transverse process, LPC=lateral process of coracoid, MAN=medial angle of sternal end of coracoid, RB=rib, V10=10th vertebra.

slabs, respectively. The radius also is represented by portions of the shaft on both these slabs (Figure 3). It shows a circular cross section in the midshaft. The ulnare lies near the proximal end of the carpometacarpus. This curved element exhibits just its oval-shaped proximal portion, in which a small fossa is developed in the place of attachment of the humerocarpal ligament. The left carpometacarpus displays its ventral side and the proximal articular surface (Figures 1, 3). It has a well-developed ulnocarpal trochlea and a deep infratrochlear fossa. The carpal trochlea appears to be small and narrow, and the extensor process is poorly developed, in accord with Elzanowski (1995). The pisiform process is either not preserved or is not developed. The major metacarpal is represented by bone fragments on the main slab and by a mold on the associated slab. The minor metacarpal is represented by the most proximal part of the base and by a mold of a small portion of the shaft on the main slab. The metacarpals are completely fused at their proximal ends. The proximal shafts of both metacarpals are similar in size. The molds of all three phalanges of the major wing digit are displayed on the associated slab, with the ventral sides exposed. The proximal phalanx has a typically avian morphology, with a flat cranial surface and a thin, flat caudal plate, with two divided depressions on the ventral side. The intermediate phalanx is long and thin, and it does not show a vestigial condition. The ungual phalanx is flat, short, and slightly bowed. The intermediate and ungual phalanges form a good articular joint with each other.

SOME FEATURES IN THE MORPHOLOGY OF *Ambiortus* AND *Otogornis*

One of the most characteristic properties of *Ambiortus dementjevi* was supposed to be the amphicoelous cervical vertebrae, as I had proposed in earlier publications on this fossil (Kurochkin, 1982, 1985a, 1985b). As emphasized above, however, the eighth and tenth cervical vertebrae are now known to have heterocoelous centra. New observations also revealed a contact between the broken edges of the counterslab and associated slab. Thus, the major metacarpal, radius, and ulna in the main slab show extension on the associated slab with specimen PIN 3790-272 that provides certain confirmation of belonging to the same specimen.

I have not attempted a detailed description of *Otogornis genghisi,* but I mention just some corrections to the original paper and the characters important for comparison with *Ambiortus dementjevi.*

Most characters of *Otogornis genghisi* that are used in this paper were published in the original description by Hou (1994). In contrast to Hou's observations, however, I discovered that the deltopectoral crest is present, the transverse ligamental furrow is only expressed as a distinctive fossa, the dorsal cotyla of the proximal end of the ulna is well preserved, and the metacarpals are fused at their proximal base, although this area is very crushed (Figures 6, 7).

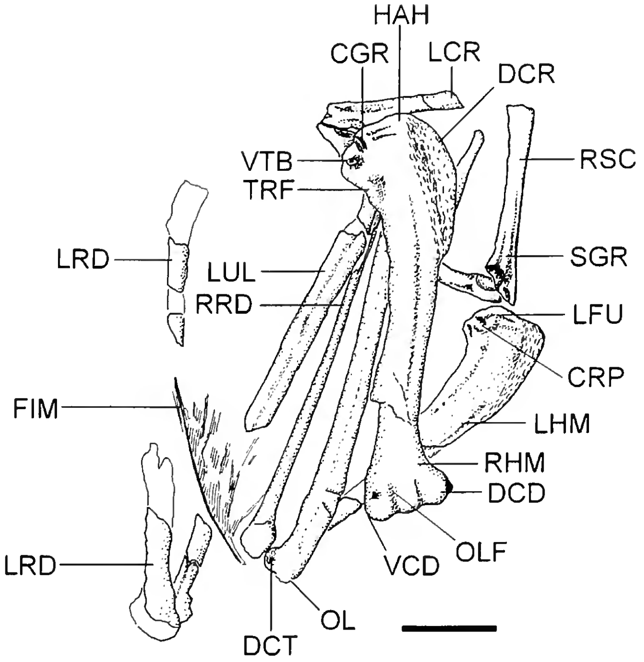

FIGURE 6.—*Otogornis genghisi* Hou, 1994, from the Chabu Sumu locality, Ordos Basin, China, Yijinhuoluo Formation. Cranial view; drawing made from a slide. CGR=capital groove, CRP=cranial pit, DCD=dorsal condyle, DCR=deltopectoral crest, DCT=dorsal cotyla, FIM=feather imprints, HAH=humeral articular head, LCR=left coracoid, LFU=ligamental furrow, LHM=left humerus, LRD=left radius, LUL=left ulna, OL=olecranon, OLF=olecranal fossa, RHM=right humerus, RRD=right radius, RSC=right scapula, SGR=scapular groove, TRF=tricipital fossa, VCD=ventral condyle. VTB=ventral tubercle. (Scale bar=1 cm.)

A wide, flat humeral articular facet in the scapula of *Otogornis* faces latero-cranially. The projecting ventral edge of the proximal end of the humerus in *Otogornis* possesses a small cranial tubercle with a pit in the center that is very similar to *Ambiortus.* Perhaps *Otogornis* is similar to *Ambiortus* and the Lithornithiformes in the specialized morphology of having a dorsoventrally compressed scapular acromion with a tubercle on its dorsal side. Despite being broken, the acromion of *Otogornis* shows some dorsoventral flattening with a prominence on the dorsal surface. The cranial portion of the lateral surface of the scapula bears a distinctive scapular groove.

The specimen of *Otogornis genghisi* exhibits the imprints of two wing feathers. Hou (1994) pointed out an important characteristic of these feathers, which is that they are not tightly arranged, i.e., there is no bonding of the barbs by barbules. *Ambiortus dementjevi* also preserves some feather imprints in the area of the wing feathers, although these show bonded feather vanes.

COMPARISON

The bones of the shoulder girdle and forelimb in *Otogornis genghisi* are somewhat longer than those in *Ambiortus de-*

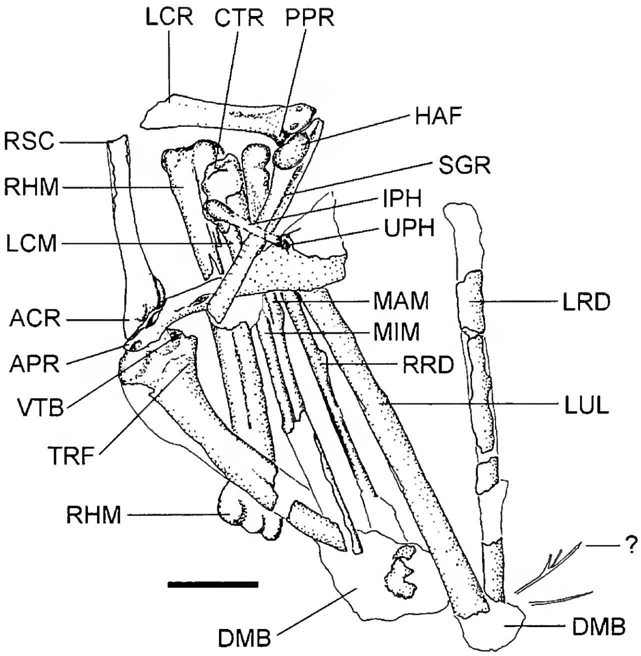

FIGURE 7.—*Otogornis genghisi* Hou, 1994. Caudal view. ACR=acromion, APR=acrocoracoid process, CTR=carpal trochlea, DMB=damaged bones, HAF=humeral articular facet, IPH=intermediate phalanx of major wing digit, LCM=left carpometacarpus, LCR=left coracoid, LRD=left radius, LUL=left ulna, MAM=major metacarpal, MIM=minor metacarpal, PPR=procoracoid process, RHM=right humerus, RRD=right radius, RSC=right scapula, SGR=scapular groove, TRF=tricipital fossa, UPH=ungual phalanx of major wing digit, VTB=ventral tubercle. (Scale bar=1cm.)

mentjevi, and they also look more robust. Comparison of the separate morphological characters, however, shows that these two Early Cretaceous birds have a close relationship. The characters and their conditions in *Ambiortus, Otogornis,* and some higher avian taxa are shown in Table 1. The Ichthyornithes and Neognathae are accepted as outgroups for determining polarity (advanced or primitive condition). The Enantiornithes are used only for general comparison because they have no close relationship with the Ornithurae.

Ambiortus and *Otogornis* share the combination of the following characters: a thickened, three-edged acrocoracoid with an acute top (character 8); a flat, wide humeral articular facet of the scapula; ventral position of a small, short, and oval humeral articular head (character 10); and a long, thin intermediate phalanx of the major wing digit (character 16). These characters provide evidence for a close relationship between *Ambiortus* and *Otogornis,* and for the assignment of *Otogornis* to the Ambiortiformes.

A convex coracoidal cotyla in the scapula (character 7) and concave scapular cotyla in the coracoid (character 9) unite *Ambiortus* and *Otogornis* with the Ornithurae. Two advanced characters support the assignment of *Ambiortus* to the Neornithes. These are the heterocoelous cervical vertebrae (character 1) and the U-shaped furcula (character 3). With the Palaeognathae, *Ambiortus* and *Otogornis* share the advanced condition of a projecting, dorsoventrally compressed scapular acromion (character 5) with a tubercle or prominence on its dorsal side (character 6); a projecting ventral edge of the humeral proximal end (character 13); and a remarkable cranial tubercle with a pit in the center of the cranial surface of this projecting edge (character 14). *Ambiortus* also shares with the Palaeognathae the strong, ventral, caudal transverse processes of the cervical vertebrae (character 2; unknown for *Otogornis*).

Ambiortus and *Otogornis* also have a number of generalized characters that are common to the Palaeognathae and/or Lithornithiformes and are primitive in respect to the Neognathae.

TABLE 1.—Distribution of some characters among *Ambiortus, Otogornis,* and other birds.

Character	*Ambiortus*	*Otogornis*	Ichthyornithes	Neognathae	Palaeognathae	Lithornithiformes	Enantiornithes
1. Cervical vertebrae	heterocelous	?	amphicelous	heterocelous	heterocelous	heterocelous	opisthocelous
2. Ventral caudal transverse process	present	?	absent	absent	present	present	absent
3. Furcula	U-shaped	?	U-shaped	U, V-shaped	U-shaped	U-shaped	V-shaped
4. Hypocleideum	absent	?	absent	absent or pesent	absent	absent	present
5. Acromion	projecting, blunt	projecting	attenuated	attenuated or short	projecting	projecting, acute	short
6. Acromial dorsal tubercle	present	present?	absent	absent	present	present	absent
7. Coracoidal cotyla	convex	convex	convex	convex	convex	convex	concave
8. Acrocoracoid	three-edged, acute	three-edged, acute	rounded	rounded or elongate	short, rounded	rounded	stick-like
9. Scapular cotyla	concave	concave	concave	concave or flat	concave	concave	boss
10. Humeral articular head	small	small	large	large	small	small	small
11. Bicipital crest	absent	absent	absent	present	absent	absent	absent
12. Pneumotricipital fossa	depression	depression	tricipital fossa	fossa or foramen	fossa or depression	fossa	fossa
13. Ventral edge, proximal end of humerus	strongly projecting	strongly projecting	projecting	rounded or projecting	strongly projecting	strongly projecting	rounded
14. Cranial tubercle	present	present	absent	absent	present?	present	absent
15. Transverse ligamental depression	fossa	fossa	absent	furrow	shallow furrow	fossa	present
16. Intermediate phalanx of major wing digit	long, thin	long, thin	short	long, flat	long, three-edged	?	long, flat

These are the absence of the bicipital crest and intumescence (character 11); the absence of the pneumatic foramen in the pneumotricipital fossa, being expressed only as an undivided tricipital depression (character 12); a small ventral tubercle on the proximal end of the humerus; the presence of a ligamental fossa instead of a transversal ligamental furrow (character 15); a rounded cross-section of the shaft of the radius; and the presence of an ungual phalanx on the major wing digit. These characters demonstrate that the Ambiortiformes have a common origin with other orders of paleognathous birds.

Otogornis differs from *Ambiortus* in having a smaller procoracoid process; a deep groove on the lateral side of the shoulder end of the scapula; a wide scapular blade (narrow in Ambiortus); a flat, elongated excavation along the cranial side of the deltopectoral crest; and the presence of a capital groove, which is divided into two furrows (Figures 6, 7). Differences in the detailed morphology of the scapula and humerus support their separate generic status, although it could be argued that they are only two species of a single genus.

Ambiortus dementjevi is smaller than *Otogornis genghisi.* The maximum width of the proximal end of the humerus of *A. dementjevi* is 13.0 mm, and the maximum width across the most projecting edge of the deltopectoral crest is 11.2 mm. The same measurements in *O. genghisi* are 15.8 mm and 12.2 mm, respectively.

Conclusions

Ambiortus from central Mongolia and *Otogornis* from the Ordos Basin, China, show a close relationship based on the shared, specialized characters 8, 10, and 16 in the structure of the forelimb and shoulder girdle (Table 1). At the same time, *Ambiortus* and *Otogornis* show some differences in the shoulder girdle and the forelimb that support their separate generic status.

The relationships of *Ambiortus* and *Otogornis* with other birds are determined by comparison with the Ichthyornithes, Neornithes, Palaeognathae, and Neognathae. *Ambiortus* and *Otogornis* share an advanced condition of characters 7 and 9, which are common to the Ornithurae. *Ambiortus* shares with the Neornithes an advanced condition of characters 1 and 3, which are unknown for *Otogornis.* At the same time, the Ambiortiformes share with the Palaeognathae (including Lithornithiformes) such specialized characters as 5, 6, 13, and 14, which suggests their assignment to the parvclass Palaeognathae, sensu Kurochkin (1995b). No common advanced characters were found for the Ambiortiformes, Ichthyornithes, and Enantiornithes. This study confirms that the Ambiortiformes are not closely related to the Ichthyornithes or the Neognathae and are totally unrelated to the Enantiornithes.

The Early Cretaceous Ambiortiformes were flying palaeognathous birds. Thereby, they document an early diversification of ornithurine birds into two main evolutionary branches: Palaeognathae and Neognathae.

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Enantiornithes: Earlier Birds than *Archaeopteryx?*

Zygmunt Bocheński

ABSTRACT

The oldest known remains of the Enantiornithes come from the Early Cretaceous of Spain and northeast China. They represent birds capable of flight, although it was not efficient enough to enable them to fly over the Turgai Strait, which at that time separated the eastern and western parts of the present-day Palaearctic. A comparison of the coastlines of the continents in consecutive epochs of the Jurassic and Cretaceous suggests that in order to spread by land over all of Eurasia, both Americas, and Australia, the Enantiornithes would have had to differentiate at the latest by the Middle Jurassic (Bajocian), or about 25 million years before the period from which *Archaeopteryx* is known (Tithonian).

Introduction

Remains of Cretaceous birds of the subclass Enantiornithes, as described by Walker (1981), are known from many localities in North and South America, Europe, Asia, and Australia (Bocheński, 1997) (Figure 1). The earliest remains may be the European representative, *Noguerornis gonzalezi* Lacasa from Spain, which has been referred to a period between the upper Berriasian and lower Valanginian (Lacasa, 1989). The remains of *Sinornis santensis* Sereno and Rao, *Cathayornis yandica* Zhou, Jin, and Zhang, and *Boluochia zhengi* Zhou from northeastern China come from the Valanginian (Sereno and Rao, 1992; Zhou, 1995a, 1995b). Three other Spanish species, *Iberomesornis romerali* Sanz and Bonaparte (1992), *Concornis lacustris* Sanz and Buscalioni (1992), and *Eoalulavis hoyasi* Sanz et al. (1996), are younger by several million years. The remaining Enantiornithes, from Asia (Mongolia and Uzbekistan), North and South America, and Australia have been obtained from deposits representing a period between the Albian and the Maastrichtian (Molnar, 1986; Chiappe, 1991, 1993; Dong, 1993; Lamb et al., 1993; Kurochkin, 1995b, 1996; Martin, 1995).

When describing particular forms included in this subclass, authors have paid attention to the characters indicative of active flying. Martin (1995) emphasized that, unlike the state observed in *Archaeopteryx,* the structure of the shoulder girdle and the possession of a keeled sternum indicate that these birds were able to rise from flat surfaces. On the other hand, the sternum and, especially, the carina sterni were proportionally very small, pointing to restricted flight efficiency that did not permit the birds to cover long distances. Poor powers of flight characterized all Sauriurae, in contrast to contemporary Ornithurae (Zhou, 1995c). The geographic situation of the earliest Early Cretaceous localities (Figure 2) as seen against a background of the paleocoastlines at that time (Smith et al., 1995) shows that Enantiornithes occurred on both sides of the Turgai Strait, which then was at least several hundred kilometers wide and constituted a substantial obstacle for terrestrial vertebrates, as pointed out earlier by Kurtén (1967–1970). Naturally, some cases of passive crossing of this barrier cannot be excluded, although they seem unlikely. The Turgai Strait existed uninterruptedly for many millions of years, from the Callovian to the Aptian (Smith et al., 1995).

Protoavis texensis Chatterjee is considered to be a bird by some authors (e.g., Chaterjee, 1991, 1994; Kurochkin, 1995b). Its detection in the Upper Triassic layers (Chatterjee, 1991, 1994) and the presence of true avian forms by the latest Jurassic (Hou, 1995) indicate that, despite the lack of direct evidence, the differentiation of birds occurred in the Jurassic. The differentiation of the European and East-Asiatic Early Cretaceous Enantiornithes on both sides of the Turgai Strait into rather high systematic units (i.e., orders and families according to Martin, 1995), or into various genera (Kurochkin, 1996), occurred independently under relatively stabilized biotopic conditions, and so they must have been the result of a long-lasting evolutionary process. Thus, it seems plausible that the Enantiornithes separated and spread in the Bajocian, 166–171 Ma BP (Haq and Van Eysinga, 1987), when it would still have been possible for them to spread over all the continents by land (Smith et al., 1995). European sea straits at that time were narrow and so could have been crossed much more easily than the

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FIGURE 1.—Distribution of localities, or groups of localities if situated close to each other, of enantiornithine birds (solid circles).

later Turgai Strait (Figure 3). Later on, there was no land connection between Laurasia and Gondwana until the Tithonian, when the present Gibraltar Strait was already very narrow. It seems, however, that the present-day Iberian Peninsula was colonized from other parts of Europe in the Valanginian-Berriasian because previously it had been an island surrounded by more or less wide seas. After the Tithonian, the part of the Tethys dividing Laurasia and Gondwana was wide again until the Tertiary. Probably the enantiornithine birds inhabiting these parts of the earth evolved independently during that time.

The colonization of Gondwana took place in the Bajocian via the eastern part of North America and Africa (although we do not have any evidence for the occurrence of the Enantiornithes in Africa), in view of its land connection with South America

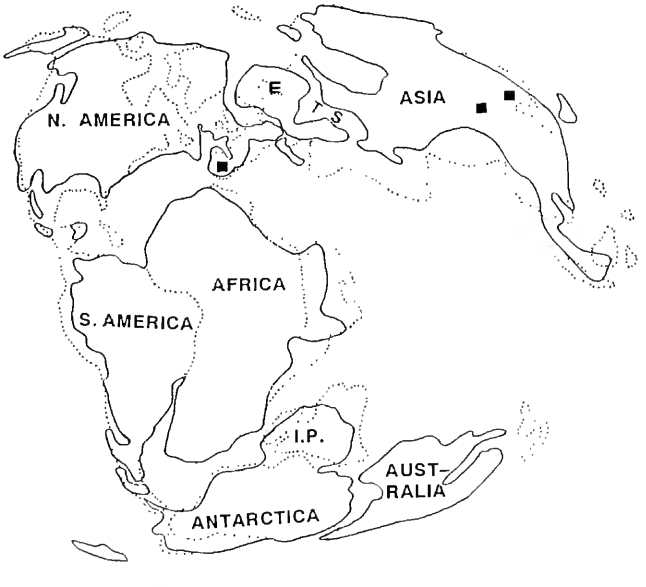

FIGURE 2.—Coastlines in the Valanginian–Berriasian, 138 Ma BP (modified from Smith et al., 1995, reprinted with the permission of Cambridge University Press). Squares indicate Early Cretaceous enantiornithine localities in Spain and northeastern China, which at that time were situated on continents divided by the Turgai Strait. (E=Europe, IP=Indian Peninsula, TS=Turgai Strait.)

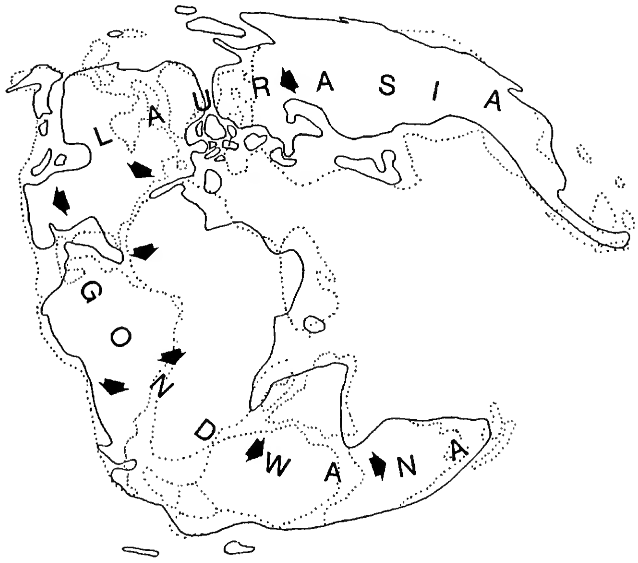

FIGURE 3.—Coastlines in the Bajocian, 170 Ma BP (modified from Smith et al., 1995, reprinted with the permission of Cambridge University Press). Arrows indicate hypothetical directions of dispersal of Enantiornithes.

and Australia by way of the Antarctic (Figure 4). A second wave of colonization of North America was possible later, independent of the colonization of Gondwana, in the Early Cretaceous (Valanginian).

In Chiappe's (1991) opinion, the Enantiornithes evolved in Gondwana, whereas Zhou (1995a) claims that Laurasia was their cradle. In Chiappe's (1991) conception, the whole process of colonization of the earth ran in the opposite direction, which, from the viewpoint of the history of continents, also is possible. If the Enantiornithes separated in the Bajocian, they theoretically could have originated anywhere on the earth. *Vorona berivotrensis* Forster et al. (1996), discovered in Madagascar and considered to be a sister group of the Enantiornithes, speaks in favor of Chiappe's conception. On the other hand, the age of the remains and the differentiation of the forms from Laurasia seem to support Zhou's (1995a) opinion, and this is the reason for adopting my present course of reasoning. No matter which of these two theories is right, the history of continents indicates that the subclass Enantiornithes evolved in the Middle Jurassic, more than 25 million years before *Archaeopteryx*.

The genera *Nanantius* and *Enantiornis* were first described from Gondwana in the Albian of Australia (Molnar, 1986) and the Maastrichtian of South America (Walker, 1981), respectively. The acceptance of land dispersal for the Enantiornithes against a background of the history of continents raises doubts that the Late Cretaceous remains mentioned from Uzbekistan and the Gobi Desert (Nesov and Panteleev, 1993; Kurochkin, 1995a, 1996) could actually belong to these genera. Even if their flight abilities were considerably greater than in the Early Cretaceous Enantiornithes, at that time the oceans between all the places mentioned above were too wide to permit crossing (see Figure 4 and Rich, 1976). It also is doubtful that the genus *Nanantius* would have survived for 25 million years (i.e., from the Albian to the Campanian) or even longer.

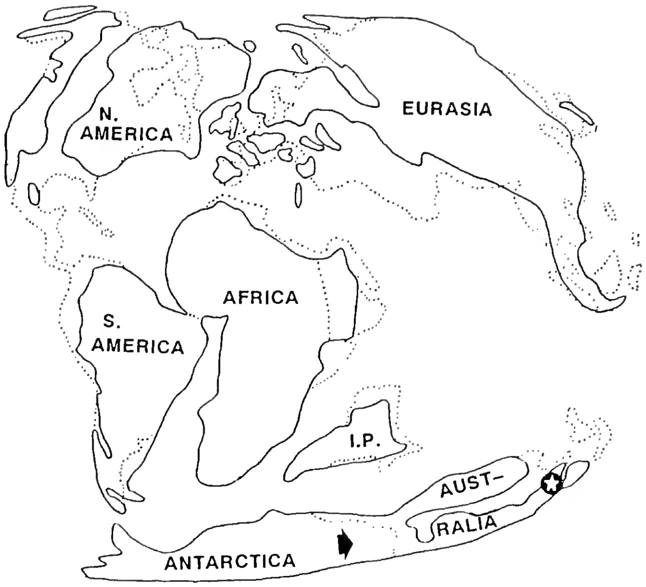

FIGURE 4.—Coastlines in the Albian, 105 Ma BP (modified from Smith et al., 1995, reprinted with the permission of Cambridge University Press). The star indicates the Albian locality of *Nanantius* in Queensland. Arrow indicates the latest possibility of colonization of Australia, assuming that the Antarctic was colonized earlier (not later than in the Tithonian). (IP=Indian Peninsula.)

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Feathered Dinosaur or Bird? A New Look at the Hand of *Archaeopteryx*

Zhonghe Zhou and Larry D. Martin

ABSTRACT

A detailed examination of wrist and manus skeletons in *Archaeopteryx,* and their comparison with those of modern birds, demonstrates an overwhelmingly avian appearance, much more so than has been previously recognized. Many workers have considered feathers to be the only indisputable evidence for the avian identity of this early bird. Although only a few skeletal characters have been used to support its avian identity, we believe that this is due to a lack of detail in previous analyses. We offer a list of eight uniquely derived avian characters or character complexes in the wrist and manus of *Archaeopteryx.* This further indicates that *Archaeopteryx* is a bird, with wings used for flying rather than for predation, and provides some fundamental skeletal differences between the oldest birds and their immediate ancestors. We extend our comparisons to the only other bird with *Archaeopteryx*-like morphology in the manus, *Confuciusornis,* and show how the wrist and manus may provide useful clues for discerning potentially older and unknown birds in the future. In addition, the large number of uniquely avian characters in the wrist and manus contrasts with a more primitive anatomy in other parts, providing another example of mosaic evolution, as the structure of the wing modernized at a more rapid rate than other anatomical units.

Introduction

Since the discovery of *Archaeopteryx* in 1861, extensive studies have been conducted on this genus, and the past two decades marked a new era of study for Jurassic birds. One result has been the resurrection, mainly by Ostrom in the 1970s, of the theory of the dinosaur origin of birds. This hypothesis derives most of its support from comparison between *Archaeopteryx* and a few theropod dinosaurs, primarily *Deinonychus.* Although strongly challenged by ornithologists and many paleornithologists, this theory has been broadly acclaimed among vertebrate paleontologists. Ostrom even went farther, stating that, were it not for the remarkable feather imprints, both of the early *Archaeopteryx* specimens (London and Berlin) would have been identified unquestionably as coelurosaurian theropods (Ostrom, 1976). This argument has been echoed in an extensive literature. Less attention has been paid to the significant similarity between *Archaeopteryx* and modern birds apart from the feathers and claws (Feduccia and Tordoff, 1979; Feduccia, 1993).

The wrist and manus bones in *Archaeopteryx,* when submitted to detailed analysis and comparison with modern birds, illustrate many avian skeletal characters that are important to the flight of birds and that were subject to complex morphological change in early avian evolution.

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Character Analyses

A total of eight uniquely derived avian characters or character complexes from the wrist and manus skeletons of *Archaeopteryx* are recognized. We have been able to examine the originals or good casts of all seven known specimens of *Archaeopteryx,* especially the Berlin and Eichstätt specimens. Ostrom listed several theropod dinosaurs as having the closest wrist and manus structure to *Archaeopteryx.* Among the genera most frequently used in comparisons are *Deinonychus, Velociraptor, Ornitholestes,* and *Chirostenotes;* therefore, our comparisons will focus on the similarities between *Archaeopteryx* and modern birds on one hand, and the difference between *Archaeopteryx* and these dinosaurs on the other. The homologies of the digits of birds and dinosaurs is still controversial among paleontologists and embryologists (Hinchliffe, 1985; Martin,

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1991). In this paper we use a "1, 2, 3" numbering of the digits in birds, but we have no objection to the "2, 3, 4" identification of embryologists. If the latter scheme is accepted, almost all comparison with dinosaurs disappears. These characters are as follows.

1. The semilunate carpal (Figure 1) is centered on the second metacarpal (see Martin, 1991). In modern birds, this is known to be a single distal carpal (II or III). A similar bone, supposedly homologous to the semilunate carpal in *Archaeopteryx,* is found in *Deinonychus, Sinornithoides,* and *Velociraptor* (Ostrom, 1995). In *Archaeopteryx* (Wellnhofer, 1974), the semilunate carpal is in contact with the first and second metacarpals, but the articulating surface of the second metacarpal is about 2.5 times as long as that of the first one. In contrast, in *Deinonychus, Sinornithoides,* and *Velociraptor* the semilunate carpal is articulated almost equally with each of the first two metacarpals. From embryological evidence (Holmgren, 1955), it is known that the semilunate carpal is centered on the second metacarpal in modern birds and that this is clearly an advanced avian character.

2. The third metacarpal slants ventrally toward the distal end as in modern birds (Figure 2), as clearly revealed in the Eichstätt and Berlin specimens of *Archaeopteryx.* The phalanges of the outer digit also are lower and flatter than those of the middle digit. As a result of this, the Eichstätt, Berlin, and Solnhofen specimens show the third digit (as preserved) crossed by the second digit. This relationship exists in part because the shafts of the feathers ride over the outer phalanges and insert in a fold of skin that forms the edge of the fleshy portion of the wing. The manus of birds is bound together in the postpatagial skin that bears the flight feathers. An impression of the postpatagium appears to be present on the Berlin specimen and is indicated in Heilmann's restoration of the wing (Heilmann, 1926, fig. 21). It is not clear whether his restoration of the patagium was based on the specimen or was inferred from modern birds. The fact that the feathers extend onto the digit and are enclosed

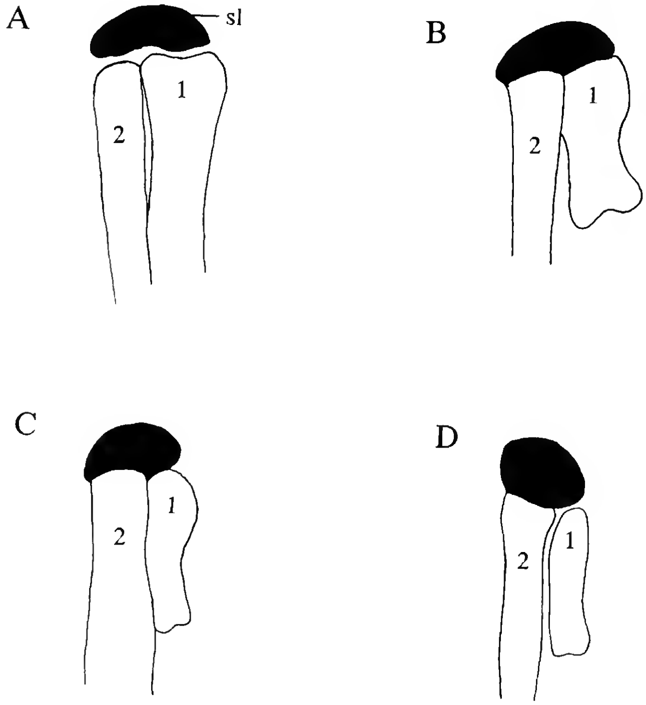

FIGURE 1.—Comparisons of the articulation between the semilunate carpal (black) and the metacarpals: A, *Velociraptor mongoliensis* Osborn (modified from Ostrom, 1976); B, *Deinonychus antirrhopus* Ostrom (modified from Ostrom, 1976); C, *Archaeopteryx* (modified from Wellnhofer, 1974); D, a 19-day-old *Struthio camelus* Linnaeus (modified from Holmgren, 1955). Drawings not to scale. (sl=semilunate carpal, 1=metacarpal I, 2=metacarpal II.

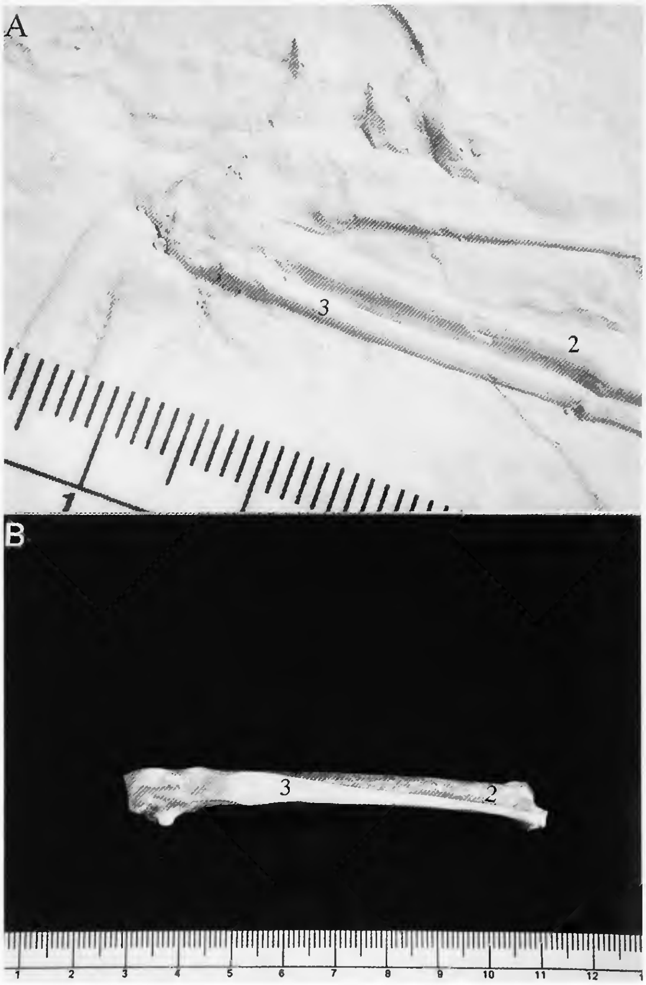

FIGURE 2.—Comparisons of the carpometacarpus: A, *Archaeopteryx* (cast of Berlin specimen in the Natural History Museum of the University of Kansas) in dorsal and slightly posterior view; B, a modern bird, *Bubo virginianus* (Gmelin), in posterior view to show the similarly ventrally slanting profile of metacarpal III toward the distal end. (2=metacarpal II, 3=metacarpal III.)

in the skin of the patagium makes it impossible for the manus to actually grip objects or act as a prey-capture mechanism.

The proximal portion of the third metacarpal is markedly anteroposteriorly compressed and is tightly attached to the posterior side of the second metacarpal. This character is obviously present in modern birds but is absent in *Deinonychus.*

3. Four carpals are present in an avian arrangement (Martin, 1991). In the Berlin specimen (de Beer, 1954), there are four preserved carpals, and they are even better displayed in the Eichstätt specimen (Wellnhofer, 1974). Two of them are the ulnare and radiale, which serve to connect the manus with the forearm (Fisher, 1957), and the third (and largest) is the semilunate carpal. The fourth carpal is relatively small and fuses to metacarpal III (IV?) in later birds (Figure 3). No dinosaurs have been described with these four carpals in an avian arrangement. The semilunate has a proximal articulating facet for the ulna on the ulnare. The Eichstätt ulnare is better preserved and exposed than in the other specimens. Its tight articulation with a semicircular external condyle on the ulna facilitates the stabilization of the distal portion of the wing. In addition, the third metacarpal does not extend as far proximally as the other two. In *Archaeopteryx,* proximal to the third metacarpal, there is a small carpal ("x-bone" of Hinchliffe (1985)) that in modern birds fuses with the semilunate carpal to form the proximal end of the carpometacarpus (Figure 3).

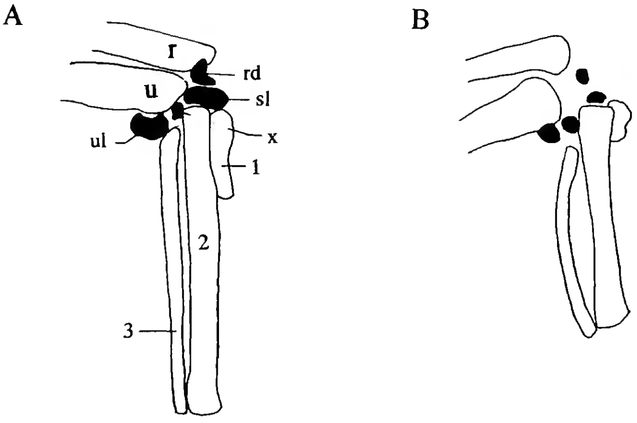

FIGURE 3.—Comparisons of the wrist pattern: A, *Archaeopteryx* (a reconstruction based on Wellnhofer, 1974); B, a modern bird, *Gallus gallus* (Linnaeus) (modified from Hogg, 1980). Drawings not to scale. (r=radius, rd=radiale, sl= semilunate carpal, u=ulna, ul=ulnare, x="x-bone" of Hinchliffe (1985), 1= metacarpal I, 2=metacarpal II, 3=metacarpal III.)

4. The distal metacarpals are simplified. The articulations between the metacarpals and the phalanges are as in modern birds and are different from dinosaurs. The distal end of the first metacarpal is markedly narrower than the proximal end, and the contact between the first and second metacarpals is straight and tightly appressed along its length. Modern birds all have a fused carpometacarpus, and this fusion is clearly a derived character for birds. The first and second metacarpals diverge distally in *Deinonychus* (Ostrom, 1976).

5. The second metacarpal is more robust than the other two. This character in *Archaeopteryx* is related to the support of the feathers provided by this element. In *Deinonychus, Sinornithoides,* and *Velociraptor* the first metacarpal is, on the contrary, more robust than the second one, indicating a totally different adaptation for the hand. The second digit in *Archaeopteryx* also is more robust than the other two (Wellnhofer, 1988). In *Deinonychus* and *Oviraptor* the first digit is more robust than the second one. The first digit of *Archaeopteryx* is proportionally the same length as that of the juvenile Hoatzin (*Opisthocomus*) and is well suited to climbing (Heilmann, 1926). In modern birds the first digit is reduced and is never robust, whereas in *Deinonychus* and *Velociraptor* the first digit is relatively massive.

6. The proximal end of the first metacarpal is simple and round. This appears to be another avian character unknown in dinosaurs.

7. The first and second phalanges of the second digit form a high, sharp ridge on their dorsal surfaces. This ridge assists in the attachment of the primary feathers and is not known in *Deinonychus* or *Velociraptor.*

8. The distal end of the first phalanx of the second digit anteroposteriorly is as wide as, or slightly wider than, the proximal end. In theropod dinosaurs such as *Deinonychus, Oviraptor,* and *Ornitholestes,* the first phalanx of the second digit is wider proximally than distally. In *Archaeopteryx* the posterior margin of the distal portion of this phalanx is slightly convex in shape compared with the concave posterior margin in dinosaurs. Both of these characters become progressively more advanced in *Confuciusornis, Cathayornis* (Zhou et al., 1992), and modern birds (Figure 4). In modern birds, the distal portion of the first phalanx, together with the proximal portion of the second phalanx, forms a prominently expanded convex posterior margin of the main digit, which provides a combined, solid, bow-shaped support for the primary feathers.

We should note that the above-mentioned characters are not functionally independent from each other. They are mostly a result of the morphological requirements of feathered flight.

Confuciusornis is the only other bird known with an *Archaeopteryx*-like morphology in the manus. It also is probably the oldest bird known except *Archaeopteryx.* All of the above characters that can be ascertained are present in *Confuciusornis,* the most notable being characters 1, 4, 6, and 8. Character 3 also appears to be recognizable in the holotype of *Confuciusornis,* although the wrist area is somewhat crushed.

Conclusions

Ostrom (1976) argued that the chief difference between the hands of *Archaeopteryx* and those of theropods is one of size, all of the theropods being larger. Also, the fingers are relatively

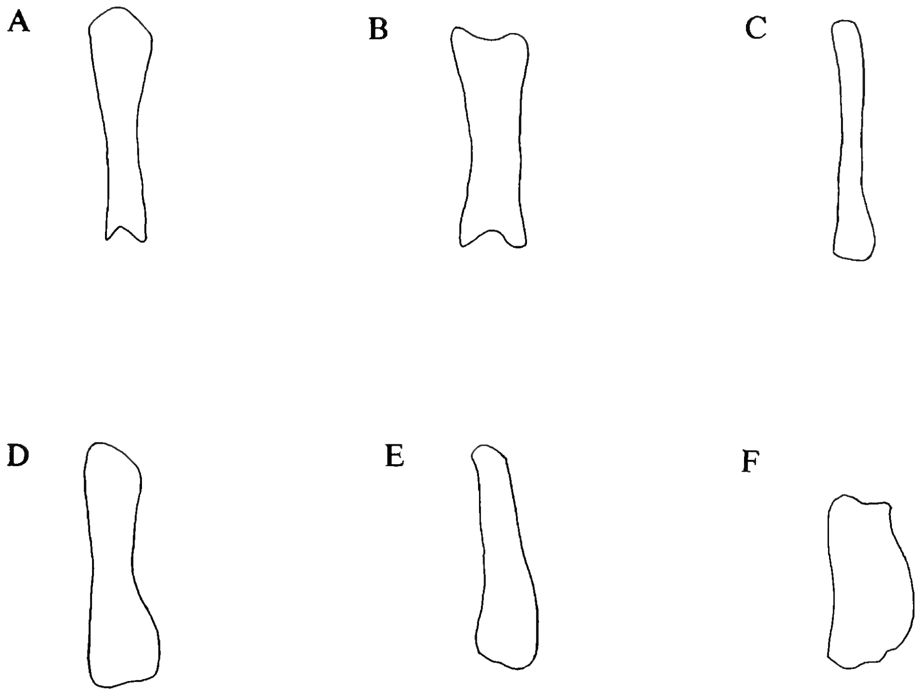

FIGURE 4.—Comparisons of the first phalanx of the second manual digit in dorsal view: A, *Ornitholestes hermanni* Osborn (modified from Osborn, 1917); B, *Deinonychus antirrhopus* (modified from Ostrom, 1976); C, *Archaeopteryx bavarica* Wellnhofer (modified from Wellnhofer, 1993); D, *Confuciusornis sanctus* Hou et al. (from a cast of the holotype of *Confuciusornis*); E, *Cathayornis yandica* Zhou et al. (modified from Zhou et al., 1992); F, *Meleagris gallapavo* Linnaeus. Drawings not to scale.

shorter in the theropods. In addition to the differences mentioned by Ostrom, *Archaeopteryx* has many advanced avian attributes of the wrist and hand, with the complex and peculiar pattern of the avian carpometacarpus already formed at this early stage of avian evolution. Without these specializations, the attachment of the primary feathers to the hand would be hardly imaginable, let alone flight.

Vazquez (1992) discussed the functional morphology of the avian wrist and stated that *Archaeopteryx* lacks many of the features of modern birds and was probably incapable of executing all the kinematics of modern avian powered flight. Although we might agree that modern birds have a wrist better designed for powered flight, *Archaeopteryx* is not so deficit in those features as Vazquez (1992) supposed. As shown by Martin (1991), *Archaeopteryx* has a basically avian wrist, with all of the bones found in modern birds, including an L- or V-shaped cuneiform (ulnare) to glide on the articular ridge of the carpometacarpus. This fact has been missed by most workers, including Martin (1983), because the preservation in *Archaeopteryx* usually shows only the dorsal or ventral side. Fortunately, the Eichstätt specimen (Wellnhofer, 1974, figs. 8, 9) presents palmar and anconal (ventral and dorsal) views of the same specimen. In palmar view the ulnare is large and elongate; in anconal view it is small and round. It could therefore be either pyramid-shaped, which would make it unlike the shape of any known relative, including other birds or dinosaurs, or L-shaped as in modern birds but not in dinosaurs. We accept the L-shaped interpretation.

The perching capability of *Archaeopteryx* has recently been argued with strong evidence (Feduccia, 1993). The wing claws in *Archaeopteryx* are long and curved. The first digit diverges from the others (Zhou, 1995). The manual digits are relatively slender. All these characters, in combination, seem to show an overwhelmingly avian pattern and show that the wings could not have been used for predation (Ostrom, 1974). It seems more reasonable to suggest that the oldest bird, although limited in flying power, lived an arboreal life just as do most modern birds, with its wings used for both flight and climbing.

The appearance of feathers was the critical point in avian evolution, and the modern appearance of the feathers in *Archaeopteryx* has often been noted (Feduccia and Tordoff, 1979; Norberg, 1995). The close match of the bones of the wrist and manus with modern birds suggests that flight played a vital role in the early evolution of birds. Furthermore, there was coevolution of the skeleton and feathers as two inseparable parts of the flight mechanism.

The recognition of many avian characters in *Archaeopteryx* is important not only for identifying more fragmentary fossils but also for recognizing potential protobirds from even older strata. Because more and more people believe that *Archaeop-*

teryx is a side branch in avian evolution (Martin, 1983; Feduccia, 1995), the oldest ancestor of birds might have existed in the Early or Middle Jurassic or even Late Triassic. The recent Chinese finding of a Late Jurassic-Early Cretaceous beaked bird (Hou et al., 1995) seems to lend further credibility to this proposal. Many of the characters discussed above may appear to be subtle, but their importance and evolutionary implication are probably no less than many superficially significant morphological changes. Although many shared features have been suggested between theropod dinosaurs and *Archaeopteryx,* they often lack the detailed similarity we should expect in homologous characters.

Ostrom (1985) recognized only two uniquely avian characters in *Archaeopteryx:* an ossified furcula and feathers. The disclosure of eight uniquely avian characters in the wrist and manus of *Archaeopteryx* provides further evidence for mosaic evolution in the vertebrate history, and encourages us to examine the anatomy of these unique fossils more closely.

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Implantation and Replacement of Bird Teeth

Larry D. Martin and J.D. Stewart

ABSTRACT

Study of the teeth of the Mesozoic birds *Hesperornis, Parahesperornis, Ichthyornis, Cathayornis,* and *Archaeopteryx* provides new evidence for avian tooth implantation and replacement. Birds share with crocodilians and, to a lesser extent, mammals, a complex mode of tooth implantation, with deep sockets walled lingually by the dentary, maxilla, or premaxilla. These walls crowd the replacing teeth so that early in ontogeny the teeth migrate labially and continue their development under the crown of their predecessor. They thus form a vertical tooth family, as opposed to the horizontal tooth family found in dinosaurs and most other tetrapods. Birds, crocodilians, and mammals have root cementum on their teeth and presumably attach teeth to the socket with periodontal ligaments. The sockets in mammals and presumably in birds are formed by the outside of the periodontal sac, whereas cementum is deposited by the inside of the sac. Bird teeth are initially formed in a groove, and ontogenetically the sockets (in socket-forming species) form first at the front of the jaw. Socket formation then proceeds posteriorly, as in crocodilians. Young dinosaurs have the lingual side of the jaw around the teeth open, so that the roots are exposed. The sockets form around dinosaur teeth as bone of attachment, which is probably the same periodontal bone that forms sockets in mammals, crocodilians, and birds. The sites of new tooth formation extend lingually within the so-called "special foramina" that separate the interdental plates. The interdental plates represent the surrounding attachment bone and are similar to the attachment bone in pleurodont lizards. In fact, dinosaurs might be characterized as having a superpleurodonty that results in sockets.

Introduction

In our previous paper on avian teeth (Martin et al., 1980), we called attention to numerous features shared by crocodilians and birds but not found in theropod dinosaurs. At that time, we were unaware of how fundamentally different the whole dental system is in crocodilians and dinosaurs and how similar the dentition is in crocodilians and birds.

The characteristic tooth morphology of crocodilians and birds includes a flattened, unserrated crown that becomes constricted as it approaches the crown/root juncture. The tooth is narrow at this point and then expands into a cement-covered root at least as broad as the crown and usually broader. Resorption begins as circular to oval pits in the lingual side of the root, and the replacement tooth has most of its formative history beneath the tooth that it will replace (below or above depending on lower or upper dentition). This morphology is found in all of the Triassic and Early Jurassic crocodilians that we have been able to examine. For instance, this tooth form is very clearly shown in acid-prepared specimens from the Liassic (Early Jurassic) marine crocodilian Pelagosaurus in The Natural History Museum, London, collections.

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Discussion

Aside from the nature of the teeth themselves, their mode of implantation in vertebrates also has proven to be useful in working out relationships. The earliest reptiles had acrodont teeth, as are found in the labyrinthodont amphibians and the captorhinomorph reptiles (Figure 1A). In the earliest diapsid reptile known (Petrolacosaurus), this condition has been modified (Reisz, 1981) by the upward (in the lower dentition) exten-

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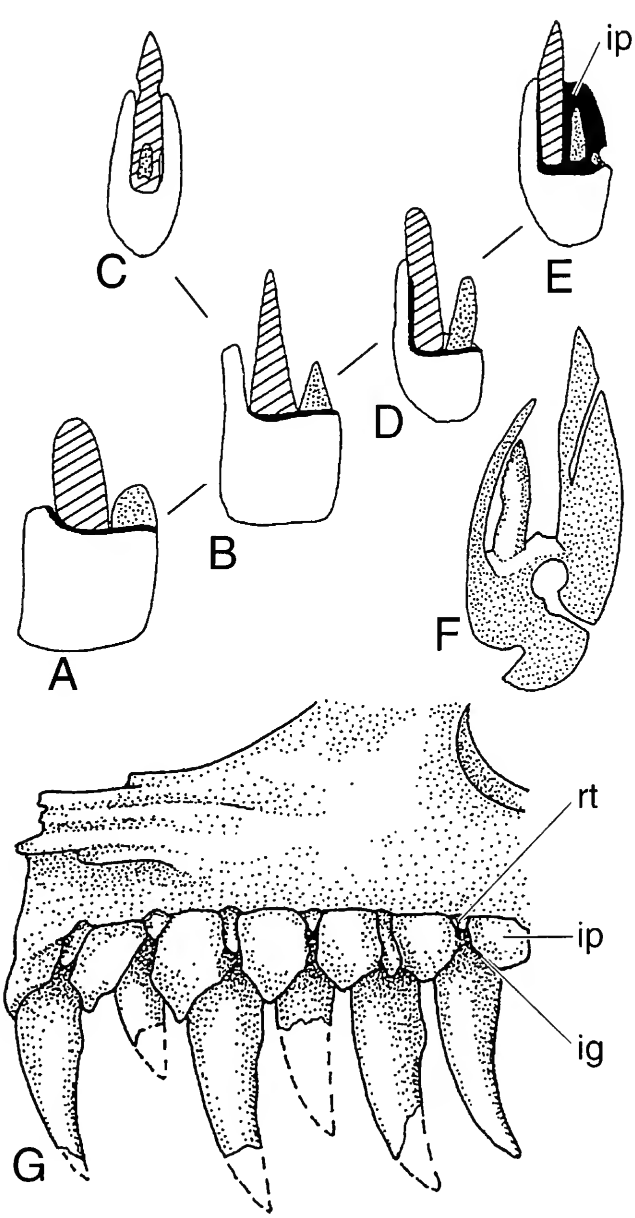

FIGURE 1.—A–E, Cross-sectional diagrams showing relationships of the tooth-bearing bone (unshaded), attachment bone (black), adult tooth (diagonal hatching), and replacement teeth (stippled): A, stem-reptiles (acrodont); B, earliest diapsid reptile (*Petrolacosaurus*); C, crocodilians and birds (thecodont with a groove); D, lizards (pleurodont); and E, "thecodonts" and dinosaurs (thecodont through superpleurodonty). F, cross section of a dentary of *Troodon* showing the replacement tooth standing lingual to its predecessor (modified from Currie, 1987, fig. 1d). G, medial view of the maxilla of the theropod dinosaur *Megalosaurus* (modified from Charig, 1979:15), showing replacement teeth (rt), interdental groove (ig), and interdental plate (ip).

sion of the labial margin of the tooth-bearing bones so that the teeth rest on a shelf (Figure 1B). Replacement teeth form lingually to the teeth they replace, and this probably inhibits the formation of an inner bony wall. The teeth are attached to the bony shelf by a highly cancellous bone called "bone of attachment" (Tomes, 1923). Attachment bone also surrounds the developing teeth, which are able to migrate labially through it. Edmund (1969:126) briefly discussed attachment bone, saying that it "appears to be embryologically and histologically identical with the alveolar bone of mammals and thecodont reptiles. It develops from the dentigenous bone near the base of the new tooth, fuses with it, and is, in turn, resorbed in the process of shedding of the old tooth." It also attaches the roots of the teeth of lizards to the labial side of the jaw, thus forming the pleurodont condition (Carlson, 1990). In mammals the periodontal sac encloses the developing tooth and deposits bone (cementum) around the root using the mesenchymal tissues on its inner surface. Imbedded in the cementum are collagenous fibers from the periodontal sac, called periodontal ligaments, that also become imbedded in the bone laid down by the external surface of the sac (Carlson, 1990), which corresponds to bone of attachment. Mammalian teeth have a very limited replacement sequence and have dense, well-formed alveolar bone. Attachment bone of animals with continuous replacement is constantly being remodeled. It has the distinct porous (fibrous) morphology of bone that is subject to rapid resorption and regrowth.

The tooth when embedded in the jaw is within the dental sac and thus can be surrounded by attachment bone. The dental lamellae form tooth papillae on the lingual side in an ordered sequence. This is generally true for all vertebrates, and primitively much of the formation of a replacement tooth occurs lingual to the tooth it will replace. The tooth migrates through the easily reconfigured attachment bone and is always internal to the dense bone of the jaw.

Because the tooth family is lingual, it is not obstructed by a labial wall supporting the root. An outer wall helps the teeth to resist outward strain, but stabilizing the teeth to inward pressure is attained either by fusing the teeth (Figure 1D) to the labial wall (pleurodonty) or by building an inner wall lingual to the tooth row (thecodonty). In the latter case, space for the tooth family must still be provided.

Archosaurs evolved two solutions to the problem of building an inner wall. One method was to bring up the inner edge of each tooth-bearing bone to form a groove (Figure 1C). In its most primitive stages this groove may not have contained complete septa, although it seems likely that the groove would have had some constrictions around the teeth. This is essentially the situation that we see in young crocodilians and in young birds. In these archosaurs, the required anteroposterior stabilization of the dentition is provided in part by expanding the roots of the teeth so that they nearly contact one another, and this also gives more surface for periodontal ligaments. The more advanced condition is seen in adult crocodilians. Here, lingual and labial projections meet to form septa, and teeth of adult crocodilians tend to have less bulbous roots than do the teeth in juveniles (Martin et al., 1980). An alternate solution is expansion of the attachment bone until it forms the lingual wall, which is found in several archosaur groups, including dinosaurs (Figure 1E–G). This is not surprising when we consider that it is merely an elaboration of bone that was already involved with fixing the teeth to the jaw. In carnosaurs, this expansion forms structures that have been variously termed "interdental rugosae" (Osborn, 1912), "interdental plates" (Madsen, 1976), or "infradental plates" (Gardiner, 1982). In the mandible, these "plates" lie on top of the dentary and are slightly labially inset to the lingual wall. In the upper jaw, they lie beneath the maxilla and premaxilla, slightly labial to the lingual walls (Figure 1F,G). They are generally bounded anteriorly and posteriorly by vertical grooves leading into foramina at the base of the plates. The foramina also are connected by a horizontal groove on the ledge at the base of the interdental plates. Each foramen is paired to one tooth site and commonly contains a developing tooth (Figure 1G). The grooves and foramina may mark the sites for the dental lamellae, an interpretation that is consistent with their termination at the location of newly deposited tooth crowns. Because the grooves are at the tooth sites of the jaw, the flat attachment bone between them is "interdental." Interdental plates of this sort occur in most saurischians and in many thecodonts (Martin et al., 1980). The only significant variation we have seen in the morphology of interdental plates is the occasional obliteration of the vertical grooves in presumably older individuals. That the interdental plates are continuous with the interdental septae and distinct from the tooth-bearing bones themselves was observed by Osborn (1912) and Walker (1964).

Each method of lingual wall formation is accompanied by a characteristic mode of tooth replacement. In fact, in the crocodilian mode of replacement, the new tooth has most of its formation in the pulp cavity of its predecessor. This mode of replacement also is facilitated by the expanded root and was described by Edmund (1960:114–115) thus: "The crown of a replacement tooth develops within the body of the old tooth, mainly below the neck separating the wider base from the narrower crown. In this way the diameter of the replacement crown can become greater than that of the crown of the tooth within which it lies." The signature feature of this type of replacement is a pit that completely surrounds the developing replacement tooth (Figure 2E,F), a feature that is absent in all of the many thousands of known dinosaur teeth. Edmund (1969:186) pointed out that saurischian dinosaurs differ from crocodilians in that the replacement tooth did not enter its predecessor's pulp cavity at an early stage, but seems to have been associated with progressive lingual resorption, with the resulting appearance of having dissolved its way into the lingual wall. The new tooth does not become central in the alveolus until it is about half grown, and much of its predecessor has been resorbed. Frequently a replacement tooth can be seen in the alveolus lingual to its predecessor, the latter being still perfectly functional. From the discussions of Edmund (1960, 1969), and from examination of many saurischian specimens, it is clear that the replacement teeth of saurischians form and continue in an upright position to their maturity. In carnosaurs the replacement teeth form rows on the lingual side of the mature tooth, and we have seen as many as three generations of teeth ranked side by side. In crocodilians, however, the replacement tooth prepares to enter the pulp chamber of its predecessor by first tilting toward it (Figure 2G). The developing crown then passes in and upward through a circular resorption window in its predecessor (Figure 2F). The teeth of crocodilians are attached by periodontal ligaments running from the jaw bones to the root cementum on the expanded roots (Miller, 1968). This mode of attachment has not been recognized in other diapsid reptiles, which also may lack the necessary root cementum.

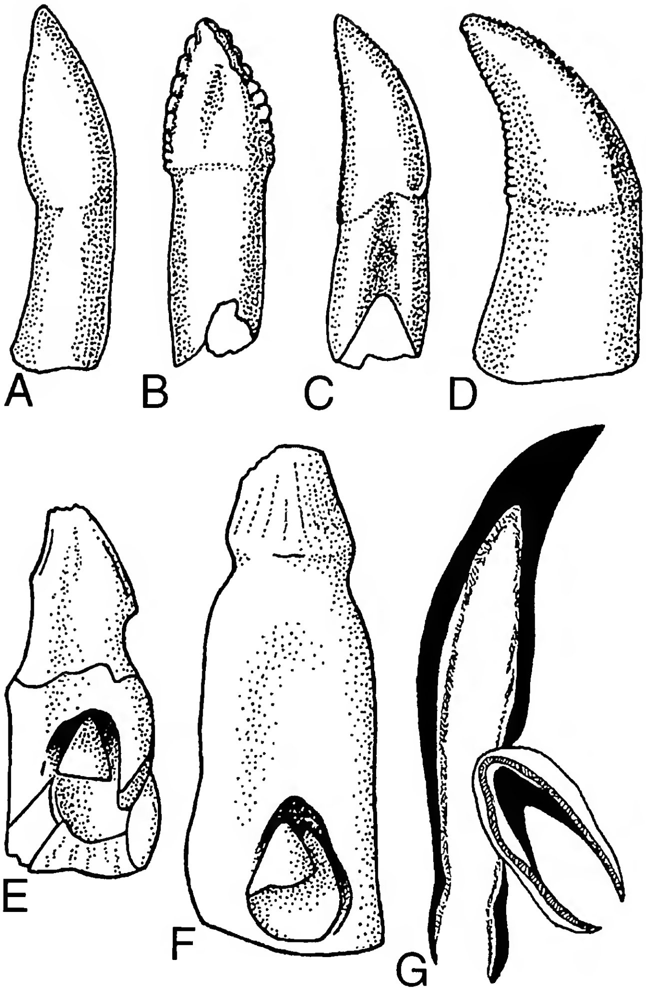

FIGURE 2.—A–D, Teeth of theropod dinosaurs thought by various authors to be especially close to birds: A, *Mononykus* (modified from Perle et al., 1993); B, *Troodon;* C, *Saurornitholestes;* D, *Dromaeosaurus* (C–D modified from Currie et al., 1990). Teeth showing constricted crown, replacement tooth tip, and expanded base: E, bird, *Parahesperornis alexi* Martin; F,G, crocodilian, *Alligator;* G, lateral cross section showing the tilted replacement tooth resorbing the root of its predecessor (modified from Edmund, 1962).

Bird teeth do contain circular or oval replacement pits that are closed on the bottom, and the developing crown also must tilt as it enters the root of its predecessor (Figures 2E, 3A–D). They also have root cementum (Schmidt and Keil, 1958), and therefore their teeth are attached with periodontal ligaments.

Peyer (1968) reported the presence of tooth cementum in crocodiles among modern reptiles and among ichthyosaurs in fossil reptiles, but in ichthyosaurs it is developed only in the geologically younger forms (Peyer, 1968:146). Ichthyosaurs also developed expanded roots, and Peyer (1968:146) suggested that this was "to offer the connective tissue fibers an adequate surface for attachment." It seems likely that in crocodilians, birds, and ichthyosaurs, the expanded roots are related to a combination of problems resulting from teeth set in a groove. We have not clearly identified the crocodilian pattern of thecodonty in any other diapsid reptile, but we would expect that the peculiar mode of tooth replacement would accompany it, if it does occur elsewhere.

Currie (1987) made an effort to identify bird-like characteristics in the jaws and teeth of troodontid theropods but figured a cross section (reproduced herein as Figure 1F) showing a typical dinosaurian lingual replacement pattern and interdental plates (Currie, 1987, figs. 1, 3). The crowns of the teeth are wider than the roots and are widest at the point that they join the roots (not waisted). The teeth are heavily serrated (Figure 2B). In other words, they do not show a single feature thought to characterize bird teeth (Martin et al., 1980). Currie and Zhao (1993) published a drawing of an undetermined dinosaur tooth (?dromaeosaurid) thought to show an oval replacement pit; however, this tooth was an isolated find, was poorly figured, and cannot be relocated. No other dinosaurian taxa with bird-like teeth have been identified in the 20 years since the unique features of bird teeth were first described (Martin et al., 1980). Currie and Zhao (1993:2245) also suggested that because bird teeth tend to drift out of the jaws after death, they could not have been attached by cementum. This must be based on a misunderstanding because the decay of the periodental ligaments would release the teeth of birds and young crocodilians, which would be found as relatively intact teeth with roots attached, as noted by Currie and Zhao (1993). This happens much more rarely with dinosaurs, where the teeth are fixed by attachment bone. It also should be pointed out that theropod dinosaurs have relatively much more room for the lingual tooth family than is found in either birds or crocodilians (contrary to Currie and Zhao, 1993:2245). The ornithomimid dinosaur *Mononykus*, considered to be a bird by some (Perle et al., 1993), has teeth (Figure 2A) resembling those of the ornithomimid *Pelecanimimus*, not those of birds.

Elzanowski and Wellnhofer (1996) took the opposite tack by attempting to show that the jaws and teeth of *Archaeopteryx* are like dinosaurs rather than like other toothed birds. This

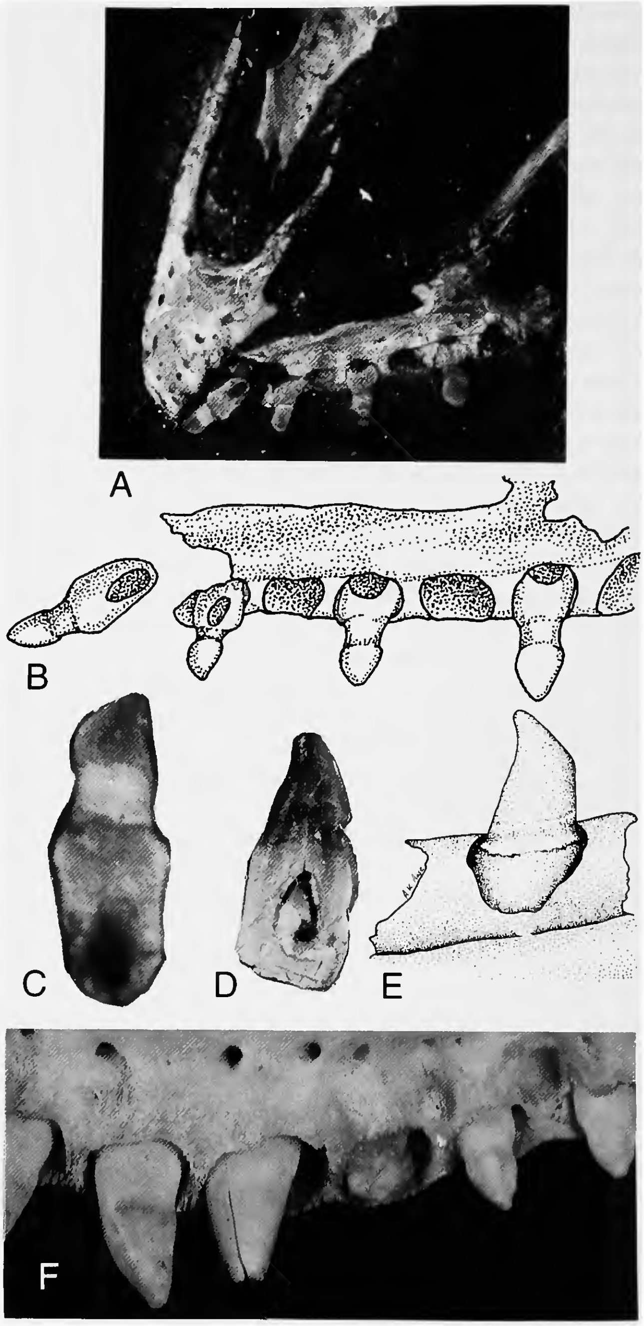

FIGURE 3.—A–C, Lingual views of the premaxillary and maxillary teeth of *Archaeopteryx lithographica* von Meyer, London specimen (BMNH 37001): A, left premaxilla and right maxilla; B, maxilla and isolated tooth; C, isolated tooth (from right premaxilla?); D, *Parahesperornis alexi*, left lower tooth (from the holotype); E, drawing taken from photograph of a tooth of the seventh specimen of *Archaeopteryx* (in Wellnhofer, 1993, pl. 6: fig. 3), showing similarity to sockets in the London maxillary; F, right, lingual view of an alligator maxilla showing similarity of tooth and socket formation to A and B.

would seem unlikely at the outset because the enantiornithine birds of China have *Hesperornis*-like teeth, almost certainly establishing this structure as primitive for birds. Examination of the London specimen of *Archaeopteryx* shows typical avian structure, with a waisted crown, expanded root, and oval replacement pits (Figure 3A–C). Elzanowski and Wellnhofer (1995:42) deny the presence of expanded roots in *Archaeopteryx* in spite of the fact that such roots are clearly shown in Wellnhofer (1988, pl. 8: figs. 2, 4; 1993, pl. 6: figs. 1, 3, 5). It also is ironic that the first mention of expanded roots in bird teeth dates back to the first description of teeth in *Archaeopteryx* by Evans (1865), and this was later confirmed by Edmund (1960). There is an excellent oblique photograph (Wellnhofer, 1993, pl. 5: fig. 9) of the seventh specimen of *Archaeopteryx* showing the waisted crown and expanded root typical of other birds and the so-called interdental plates crossing as tooth septa. Although the features of bird teeth may be most easily seen in large isolated specimens from *Hesperornis* and *Parahesperornis,* it is clear that all known bird teeth are closely similar to each other and that the teeth of *Archaeopteryx* are not atypical or especially primitive. The claim for interdental plates (Elzanowski and Wellnhofer, 1996) in the seventh skeletal specimen is based on the labial margin of the jaw being higher than the lingual margin and exposing distinct alveolar septa (interdental plates?) between the tooth sites. In fact, this condition is better displayed in the London maxillary (Howgate, 1984), where it has been interpreted as a tooth socket (Martin, 1991). Because the alveolar bone of the sockets and the attachment bone of the interdental plates are ultimately derived from the same source, we must carefully describe what is meant by interdental plates versus sockets. When interdental plates are present, they generally expose the replacement teeth, and most of the length of the root is surrounded on the lingual side by the interdental plates. The jaws of the seventh specimen of *Archaeopteryx* are spread and compressed so that we get a slightly oblique view of the jaws on the slab (see Wellnhofer, 1993, pl. 4: fig. 1). We are indebted to Wellnhofer (1993) for excellent photographs that clearly show the crown-root juncture on the teeth of the seventh example and show that the constriction at the base of the crown is almost at the lingual edge of the mandible (Figure 3E), so that the replacement teeth are mostly hidden by the side of the dentary as in other birds.

When we look at typical interdental plates (Figure 1G), we see that not only the socket but also part of lingual side of the jaw is produced by the interdental plates, and that there is a distinct groove separating the individual plates, terminating in the "special foramina" and the replacing teeth. The replacing teeth lie to the lingual side of the adult tooth as shown by the replacing tooth in *Troodon* (Figure 1F). These are not the relationships shown in the London *Archaeopteryx* (Figure 3A–C) or in the seventh specimen (Figure 3E). The intersepta of the tooth sockets of the London maxilla closely resemble a similar view of an alligator maxilla (Figure 3F), as well as the sockets of *Archaeopteryx* (Figure 3E) so well photographed by Wellnhofer (1993). A close examination of Wellnhofer's photographs also shows the intersepta widening again as they come to the labial edge, as expected in a dorsal view of the socket. If the view were entirely medial, we would not expect to see this widening, even if these were interdental plates (see Figure 1G).

The condition in coelurosaurs is not as clear as it is in carnosaurs. *Compsognathus* is reported by Ostrom (1978) to have small interdental plates. Dromaeosaurs were not thought to have interdental plates (Colbert and Russell, 1969). According to Currie (1995), dromaeosaurs have fairly typical interdental plates forming much of the lingual side of the jaw below the sockets except that the grooves fuse across, forming a solid wall. This should indicate a modified tooth replacement, and indeed it appears that the tooth family may be thrown into diagonal lines so that replacing teeth are both lingual and posterior, as, for example, in the overlapping replacement tooth in the ramus of *Deinonychus* illustrated by Ostrom (1969). This is not bird-like, nor is the covering of the interdental plates by special bones (supradentary) in *Allosaurus* and *Tyrannosaurus* (intercoronoid of Brown and Schlaikjer, 1940). It is clear that coelurosaur teeth are very similar to the teeth of carnosaurs and do not show the specialized type of tooth replacement found in birds (Figure 2A–D).

Conclusion

The argument that birds are related to dinosaurs is now most often restated that birds are dinosaurs. If this is the case, we would expect their anatomical structures to maintain similarity under a very rigorous analysis. We see that this is not true for almost any aspect of tooth form, implantation, or replacement. The tooth structures identified as interdental plates in *Archaeopteryx* by Wellnhofer (1993) do not agree in detail with those structures in dinosaurs and can be closely duplicated by crocodilians. We now know from the abundant Chinese enantiornithine material that the tooth form of birds is similar in all known groups of birds and must have been established at least by the Jurassic. Crocodilians and birds form the inside walls of their tooth-bearing bones differently from dinosaurs and have a different mode of tooth replacement. Their common ancestor with dinosaurs may not have been "thecodont" in the descriptive sense of that word. Crocodilians have derived features that prevent them from being ancestral to birds, but a sister-group relationship is still possible.

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Humeral Rotation and Wrist Supination: Important Functional Complex for the Evolution of Powered Flight in Birds?

John H. Ostrom, Samuel O. Poore, and G.E. Goslow, Jr.

ABSTRACT

To achieve a better understanding of the function of the M. supracoracoideus in extant birds, we measured the mechanical properties and actions of the supracoracoideus in the European Starling (*Sturnus vulgaris* Linnaeus) and a pigeon (*Columba livia* Gmelin). We performed three sets of acute in situ experiments by direct nerve stimulation. We measured length-active and length-passive tension, forces of humeral elevation and rotation (torque), and humeral excursion (elevation and rotation). The supracoracoideus is capable of generating a tetanic force 7–10 times the bird's body weight, imparts a torque about the longitudinal axis that is greater than its force of humeral elevation, and, when tetanically stimulated, elevates the humerus a limited 50°–60° above the horizontal but rotates it through 80°. We conclude that the primary role of the supracoracoideus is high-velocity rotation of the humerus, a movement critical to achieving the upstroke portion of the wingbeat cycle. In addition, we propose that high-velocity humeral rotation may also serve to augment supination of the wrist during upstroke.

A morphologically derived supracoracoideus to produce rapid humeral rotation and the skeletal features associated with it, an acrocoracoid, triosseal canal, and tuberculum dorsale, are not evident in *Archaeopteryx* or *Sinornis.* These features also appear undeveloped in *Iberomesornis* and *Concornis,* are unknown in *Cathayornis*, and apparently are not preserved in the most recent find, *Confuciusornis.*

Introduction

In order for a flapping wing stroke to be effective, the wing surface must be converted from an aerofoil to a "nonaerofoil" surface as the wing changes from the powered downstroke to the recovery upstroke, either powered or unpowered. The wing of birds is pronated and extended during the downstroke to provide maximum surface area for both lift and thrust, but it is supinated during the recovery upstroke so as to minimize the surface area and thereby reduce drag. The focus of this contribution centers around the M. supracoracoideus and its role in modern birds for augmenting supination at the wrist. These data provide a new perspective on the fossil record of birds.

The statement written twenty years ago that "any consideration of the evolution of flight must start with *Archaeopteryx*" (Ostrom, 1976a:3) is more important today than when it was written. This is because more is now known about the anatomical details of *Archaeopteryx,* especially after publication of the last three finds (Wellnhofer, 1974, 1988, 1992, 1993), and because of advances in our understanding of bird flight mechanics (Gauthier and Padian, 1985; Ostrom, 1986, 1994, 1995; Jenkins et al., 1988; Rayner, 1988a; Dial et al., 1991; Vazquez, 1992; Pennycuick, 1993). This fact is brought home in a most compelling manner when the now seven nearly complete, articulated specimens of *Archaeopteryx* are compared with the often incomplete, solitary Mesozoic bird specimens (*Iberomesornis, Sinornis, Cathayornis, Concornis, Otogornis, Confuciusornis,* and others) that have been reported since the Eichstätt specimen was recognized. Recognition in the Eichstätt specimen of the maniraptoran-like semilunate carpal (Ostrom, 1976a, 1976b) resulted in a careful reevaluation of the hypothesis of the theropod origin of birds (Hecht et al., 1985; Schultze and Trueb, 1991) and the origins of flight in birds (Padian, 1986; Gauthier and Padian, 1989; Bock and Bühler, 1995). These arguments aside, however, from a functional standpoint this same semilunate carpal was central to the maintenance of pronation during downstroke and to the execution of supination during upstroke.

After meticulous investigations of the morphology of the avian carpal-metacarpal complex and functional morphology of the pigeon carpometacarpus, Vazquez (1992, 1995) demonstrated that the articular surface of the trochlea carpalis in modern birds acts to automatically supinate the hand upon wrist

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flexion. Ostrom's analysis also can be extended to address the presence of the semilunate carpal, the precursor of the trochlea carpalis, in *Archaeopteryx;* it too may have served for automatic supination of the hand and metacarpus (Vazquez, 1992). Such supination undoubtedly served to streamline the distal portion of the wing during the upstroke, an action necessary to reduce profile drag (Rayner, 1988b). Our experimental evidence concerning the action of the supracoracoideus in powered flight reveals this muscle's potential for increasing the rate, and perhaps extent, of supination during upstroke. These findings underscore the functional importance of a morphologically derived supracoracoideus with a dorsally directed tendon in modern birds. The implications of these findings have been reported (Poore et al., 1997).

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Wrist Anatomy

THE MANIRAPTORAN WRIST

Important to this discussion of supination of the hand in modern birds is a review of the evolution of the wrist in maniraptoran theropods and *Archaeopteryx.* Unknown before 1964, the semilunate carpal of theropods was first reported in 1969 (Ostrom, 1969a), and a detailed, functional interpretation followed a few months later (Ostrom, 1969b). That analysis has apparently been accepted. It was shown therein that the semilunate carpal element of *Deinonychus* (and later of *Velociraptor* and other maniraptoran taxa) articulated in a tight, rigid union with the first and second metacarpals distally. The opposite proximal surface was a well-finished trochoidal articular surface that permitted a high degree of flexion-extension with the ulna (Figure 1). Because of its highly canted or pronounced asymmetrical shape on the proximal surface, the semilunate carpal also forced the metacarpus to supinate (circumduct) up to 45° as the wrist was flexed. At the carpal joint, supination must have been just as important as flexion because the articular facet was well formed and highly finished in all of the specimens in which it was found. That particular kind of wrist motion was believed at the time (1969) to have been an important part of the predator action of *Deinonychus,* the first taxon in which it had been found. Subsequently, when recognized in other maniraptoran specimens (*Velociraptor, Stenonychosaurus,* and *Sinornithoides*), it apparently was presumed to have served a similar raptorial role related to the function of the manus.

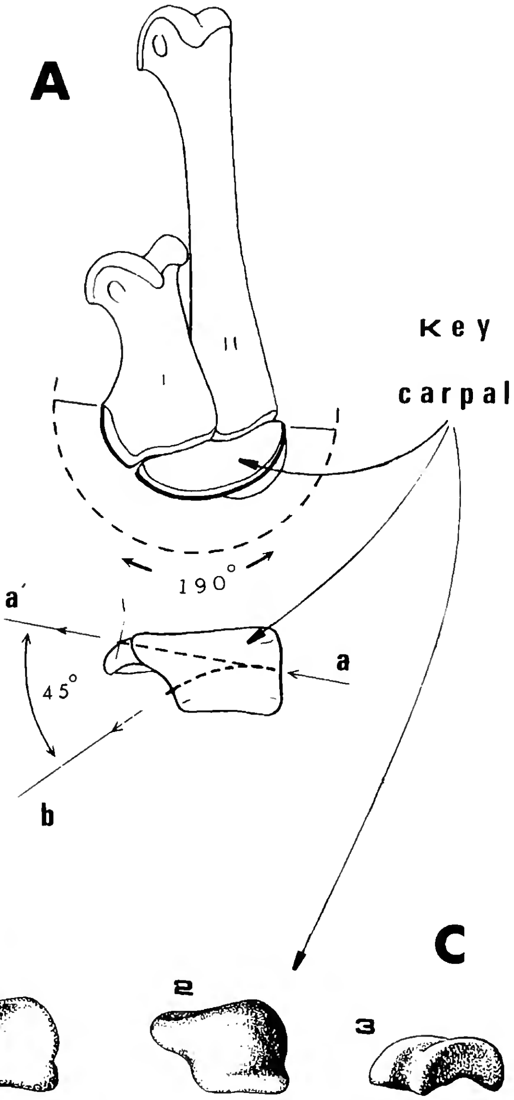

FIGURE 1.—Key components of a maniraptoran theropod (*Deinonychus antirrhopus* Ostrom) forearm to illustrate hypothesized action imposed by the semilunate carpal (key carpal) during flexion-extension: A, metacarpals I and II and their relationship to the key carpal; B, the asymmetrical proximal ginglymus of the key carpal causes supination (circumduction) of the closely adjoined metacarpus through approximately 45°; C, surface aspects of the key carpal: 1=distal articular surface, 2=proximal articular surface, 3=lateral surface. (Modified from Ostrom, 1969b.)

Although the biomechanical actions that were produced by this particular wrist appear quite obvious, exactly what biological role these movements played in maniraptoran life is not so apparent. It is now clear that this semilunate carpal is characteristic of the clade, but the adaptive meaning of these clade-common unique wrist movements that seem to have been typical of maniraptoran theropods remains unknown.

THE WRIST OF *Archaeopteryx*

Revelation of the remarkable details of the anatomy preserved in the Eichstätt specimen (the fifth) of *Archaeopteryx* (Wellnhofer, 1974) caused renewed interest in the question of the origin of birds, culminating in the 1984 International *Archaeopteryx* Conference (Dodson, 1985) in Eichstätt, Germany (Hecht et al., 1985). Although not unanimous, that conference reached a consensus that the ancestral stock from which birds arose was probably a primitive archosaurian, but the details of this origin soon dissolved into three distinctly different hypotheses that persist to this day: the primitive thecodontian theory (Hecht and Tarsitano being the principal advocates), the crocodylomorph theory (championed effectively by Walker, Martin, and Whetstone), and the theropod ancestral theory (argued by Ostrom, Padian, and Wellnhofer, sometimes by Gauthier, and occasionally by others).

The most important evidence provided by the Eichstätt specimen is the well-preserved semilunate carpal almost exactly as it is preserved in *Velociraptor* and *Sinornithoides* from Mongolia and China, respectively (Figure 2). The semilunate carpal appears to have functioned in the same way in these forms, just as originally visualized in *Deinonychus* (Ostrom, 1969b); flexion at the wrist forced a pronounced supination (circumduction) of the metacarpus-manus. If this interpretation also is correct for *Archaeopteryx,* as we believe, that carpal manipulation has profound implications regarding the flight capability of the Urvögel and has even stronger implications concerning the early stages of flapping flight in birds.

Because of this apparent wrist action in *Archaeopteryx,* supination was initially equated with the modern avian wrist (Ostrom, 1976a), where the shape of the modern carpometacarpus is so similar to that formed by the semilunate carpus-metacarpus complex of the Eichstätt specimen. In fact, the trochlea carpalis of the modern carpometacarpus forms the key articulation essential for modern flapping bird flight (Vazquez, 1992). It was proposed that the maniraptoran-like semilunate carpal, through time, fused with metacarpals I and II to form the modern carpometacarpus with its distinctive trochlea carpalis and its unique action so characteristic of all flying birds (Ostrom, 1976a).

As Vazquez (1992) described, flexion of the wrist of the modern avian wing forces the more distal wing segments to supinate, streamlining those wing components for the ensuing upstroke. Flexion at the wrist displaces the cuneiform distally, causing it to slide along the trochlea carpalis, which results in supination, although there are no muscles that directly supinate the hand (Vazquez, 1995, and references therein). Thus, supination is dependent on the trochlea carpalis-cuneiform complex and air resistance on the dorsal surface of the wing during upstroke. In addition to the wrist's osteology, we propose herein that a derived supracoracoideus contributes to supination by rapidly rotating the humerus on its longitudinal axis. Below we report the experimental evidence to support this position.

The Role of the M. Supracoracoideus in Flapping Flight

Numerous derived features characterize the pectoral girdle and associated musculature of the Neornithes. The most striking of these, and the one that represents an extreme departure from a primitive tetrapod organization, is that of the M. supracoracoideus. The supracoracoideus in all birds possessing powered flapping flight lies deep to the pectoralis, arises from the carina, sternum, and coracoclavicular membrane, and possesses a bipinnate architectural organization of its fascicles. The most distinctive feature of the supracoracoideus, however, is the course of its tendon of insertion (Figure 3). The tendon passes dorsally through the triosseal canal (formed by the coracoid, scapula, and furcula) and attaches on the dorsal aspect of the humerus above the glenohumeral joint. The seemingly obvious function of this dorsally inserting tendon is that the supracoracoideus is for wing elevation. The presence or absence of this anatomical arrangement has been a central question in debates concerning the evolution of flapping flight and has been given considerable attention in interpreting the flight capabilities of the Late Jurassic bird *Archaeopteryx* (Ostrom, 1976a, 1976b; Olson and Feduccia, 1979).

We studied the in situ contractile properties of the supracoracoideus to clarify its role during flapping flight in two species of extant birds, the European Starling (*Sturnus vulgaris* Linnaeus) and a pigeon (*Columba livia* Gmelin). Starlings and pigeons contrast in their wing loading (wing area/body weight) and flight styles. In both species, we measured the absolute force generated by the supracoracoideus, the humeral excursion (elevation and rotation), and the forces of humeral elevation and humeral axial rotation.

Electrical activity of the supracoracoideus of a starling flying in a wind tunnel (Dial et al., 1991) and pigeons in free flight (Dial et al., 1988) begins in late downstroke and ends prior to the upstroke-downstroke transition. The electrically active period is not coincident in time with force. The electromechanical delay reported in the pectoralis during flight in starlings (Biewener et al., 1992) and pigeons (Dial and Biewener, 1993) suggests electrical activity anticipates force at burst onset by several milliseconds (ms). After electrical activity ceases, however, force continues for 20–25 ms, leading us to conclude the force produced by the supracoracoideus in both species is sustained through most of the upstroke. We used as a reference for our physiological measurements the wing kinematics for European Starlings reported in the cineradiographic study by Dial et al. (1991). Kinematic data of comparable precision are not available for the pigeon; we made estimates from Brown (1951) and Simpson (1983). The downstroke-upstroke transi-

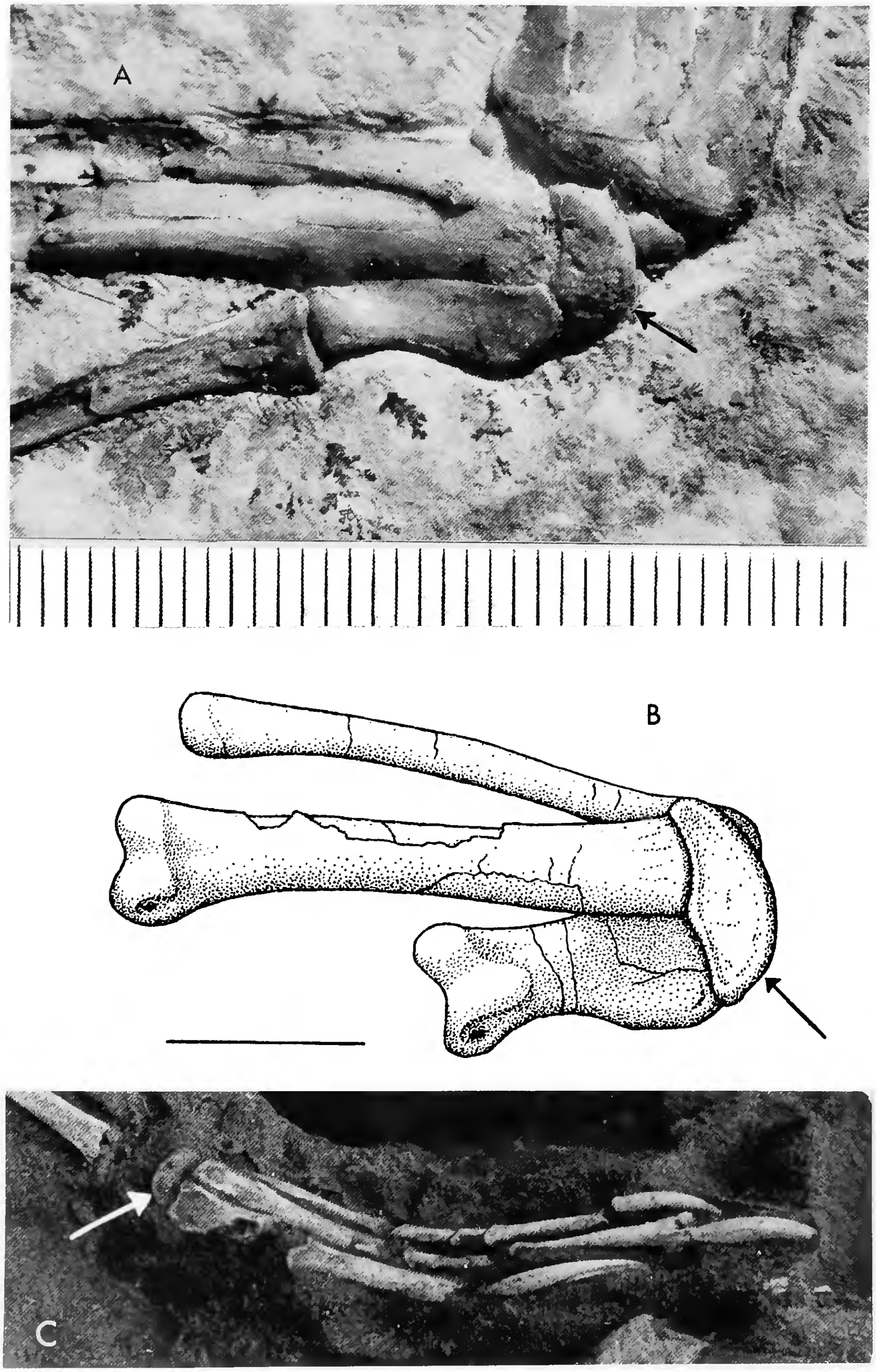

FIGURE 2.—Articular joints of the wrist: A, *Archaeopteryx lithographica* von Meyer (Eichstätt specimen), scale units=0.5 mm; B, *Deinonychus antirrhopus*, scale bar=30 mm; C, *Velociraptor mongoliensis* Osborn, image ~half size. Arrows indicate the semilunate carpal in each. (After Ostrom, 1995.)

tion in both species begins with the humerus below the horizontal and is characterized by a rapid sequence of events, including retraction of the humerus, elevation, and rapid flexion at the wrist and elbow.

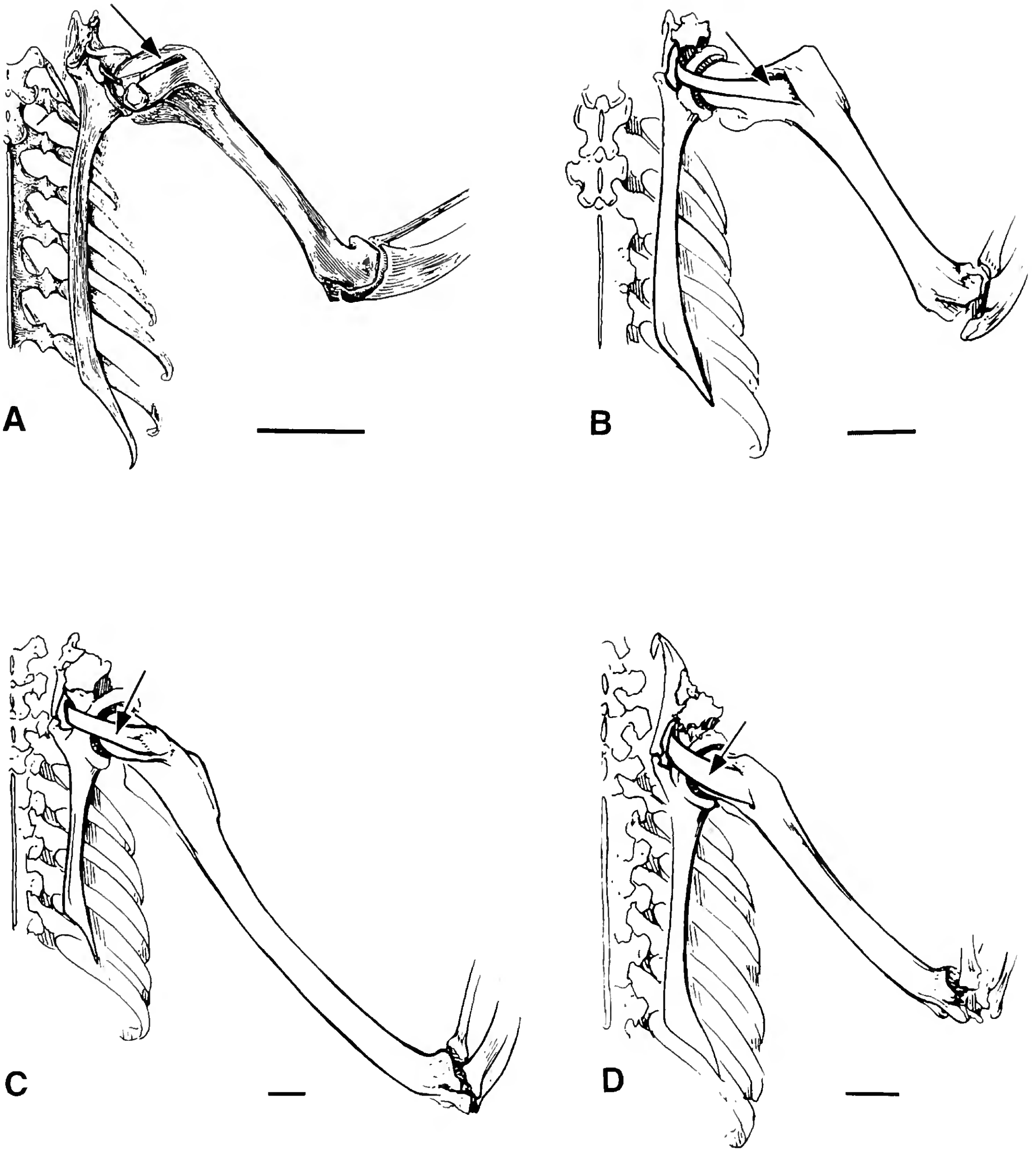

FIGURE 3.—Dorsal view of the right shoulder to illustrate the emergence of the supracoracoideus tendon (arrow) through the triosseal canal to the tuberculum dorsale (external tuberosity) and its favorable angle for humeral rotation in four birds with different flight characteristics. A, European Starling (*Sturnus vulgaris*), a representative passeriform. During upstroke, the angle of retraction becomes more acute, increasing the ability of the tendon of insertion to rotate the humerus on its longitudinal axis. A sesamoid bone, the Os humeroscapularis, serves to deflect the tendon to maintain optimality for humeral rotation. B, pigeon (*Columba livia*), a representative columbiform specialized for vertical ascent and descent. The ability of this species to take off from a flat surface is dependent on the supracoracoideus. C, Great Black-backed Gull (*Larus marinus* Linnaeus), a charadriiform that soars and uses relatively low amplitude wingbeats during flapping flight. Note the relatively large tuberculum dorsale. A decreased angle of retraction coupled with a large tuberculum dorsale results in relatively high torque. D, Atlantic Puffin (*Fratercula arctica* (Linnaeus)), a charadiiform specialized for wing-propelled diving. The supracoracoideus in this and other wing-propelled divers is relatively large to rotate the wing under water. Each scale bar=1 cm.

All experiments in this study were performed in accordance with National Institutes of Health guidelines for animal research and were approved by the Institutional Animal Care and Use Committee of Brown University. We measured the mechanical properties and actions of the supracoracoideus in eight acute in situ experiments for each species by direct nerve stimulation. All experiments were performed following anesthesia with ketamine (60 mg/kg) and xylazine (6 mg/kg); supplemental ketamine was given as needed. We bisected the lattisimus dorsi and rhomboideus muscles to expose the brachial plexus and isolate the nerve to the supracoracoideus. We intubated the birds unidirectionally via the trachea (80% oxygen, 20% nitrogen) after opening the posterior air-sacs. We severed all components of the brachial plexus except the nerve to the supracoracoideus to prevent stimulation of adjacent muscles. Following surgical preparation we clamped the sternum and coracoid to a rigid frame and maintained body temperature at 40° C with warmed avian ringers and a heat lamp. We mounted the supracoracoideus nerve on silver bipolar electrodes and established a stimulation voltage (2× threshold) to elicit a twitch or a tetanus. For four birds of each species, we measured maximal tetanic tension by connecting the tendon of the supracoracoideus directly to a force transducer.

ROTATION AND ELEVATION.—We made independent measurements of the rotational force (torque) about the longitudinal axis of the humerus and of the force of elevation on the humerus during isometric contraction of the supracoracoideus for two birds of each species. To measure torque, we threaded a short piece of silver wire (0.38 mm diameter) through a small hole drilled in the deltopectoral crest, attached the wire to the force transducer, and measured isometric force at that point. We placed a 23-gauge pin in the shaft of the humerus to prevent elevation while still permitting "free" rotation about the bone's longitudinal axis. To measure elevational force, we secured the humerus to the transducer with surgical silk. We stimulated the supracoracoideus nerve tetanically with the humerus positioned at joint angles of elevation/depression and protraction/retraction coincident with the downstroke-upstroke transition and midupstroke of flight.

EXCURSION OF THE HUMERUS.—We measured the total in situ elevation excursions of the humerus during tetanus of the supracoracoideus for two birds of each species. During these measurements, the humerus was not restricted in any way but was allowed to move during stimulation. We stimulated the nerve tetanically (60 hertz; 500 ms train duration) and measured elevation of the humerus with a protractor. We made all elevational measurements relative to the dorsal border of the scapula in lateral view. Subsequent to the elevation measurements, we measured rotation by placing a 23-gauge pin guided by a rack and pinion through a small hole drilled in the distal end of the humerus. We threaded the needle into the long axis of the humeral shaft, which served as a pivot for rotation while restricting the elevational component of movement. We placed a 26-gauge pin perpendicular to the long axis of the humerus, which served as a dial with which to measure the degree of rotation. We made measurements at the two wing positions noted earlier; the downstroke-upstroke transition and midupstroke.

Discussion

The downstroke-upstroke transition in both species begins with the humerus depressed below the horizontal (10° for starling, estimated 10° for pigeon). The angle formed by the long axis of the humerus and the vertebral column in dorsal view at the downstroke-upstroke transition is about 55°–60° in both species. Upstroke commences by retraction, rotation, and elevation of the humerus, flexion of the elbow, and flexion/supination of the wrist. During upstroke, the right humerus rotates counterclockwise about its longitudinal axis and elevates about 40° above the horizontal (Figure 4). During muscle shortening the potential for active force production decreases as the humerus is rotated and the wing is elevated. Nevertheless, at humeral angles corresponding to the downstroke-upstroke transition, we measured tetanic forces of 6.5 ± 1.2 newtons (N) in the starling ($n=3$) and 39.4 ± 6.2 N in the pigeon ($n=6$); forces 8 times or more the body weight of each species. The supracoracoideus imparted an average isometric force for rotation measured at the deltopectoral crest for the starling of 4.9 N (downstroke-upstroke transition) and for the pigeon of 32.1 N. The forces at the midupstroke positions were about half of these values. Although we measured in situ humeral rotations of up to 80°, maximum elevations of the humerus were only about 55° above the horizontal. From these data we conclude the primary action of the supracoracoideus to be high-velocity rotation of the humerus about its longitudinal axis during wing upstroke; active wing elevation may be of secondary importance.

Further support for this conclusion comes from an analysis of the glenoid and the anatomical arrangement of the avian supracoracoideus. The avian shoulder joint is structurally derived and functionally complex. The glenoid, best described as a hemisellar (half-saddle) joint, faces dorsolaterally and articulates with a bulbous humeral head. Jenkins (1993) reviewed the structural/functional evolution of this joint and provided an interpretation of its function based on a cineradiographic analysis of the wingbeat cycle. His study illustrated the articulation of the humeral head on a dorsally facing surface of the glenoid, the labrum cavitatis glenoidalis, which allows for full abduction of the wing into the parasagittal plane at the upstroke-downstroke transition. We believe full abduction is not so much by elevation of the humerus but by rotation about its longitudinal axis. It bears emphasis that during the wingbeat cycle of European Starlings flying in a wind tunnel, where we have precise cineradiographic data, the angle formed by the long axis of the humerus and the vertebral column is never greater than 55° (Jenkins et al., 1988, fig. 1; Dial et al., 1991, fig. 4). We have made in situ measurements of humeral protraction/retraction in anaesthetized, intact starlings and pigeons. The humerus cannot be drawn forward to intersect the body axis at an angle greater than 60°–65° unless forced; its forward angle beyond these angles is constrained by the ligaments and muscles surrounding the shoulder.

The mechanics of the musculoskeletal organization of the supracoracoideus also supports our conclusion. The supracoracoideus in both pigeons and starlings, as well as in all other species

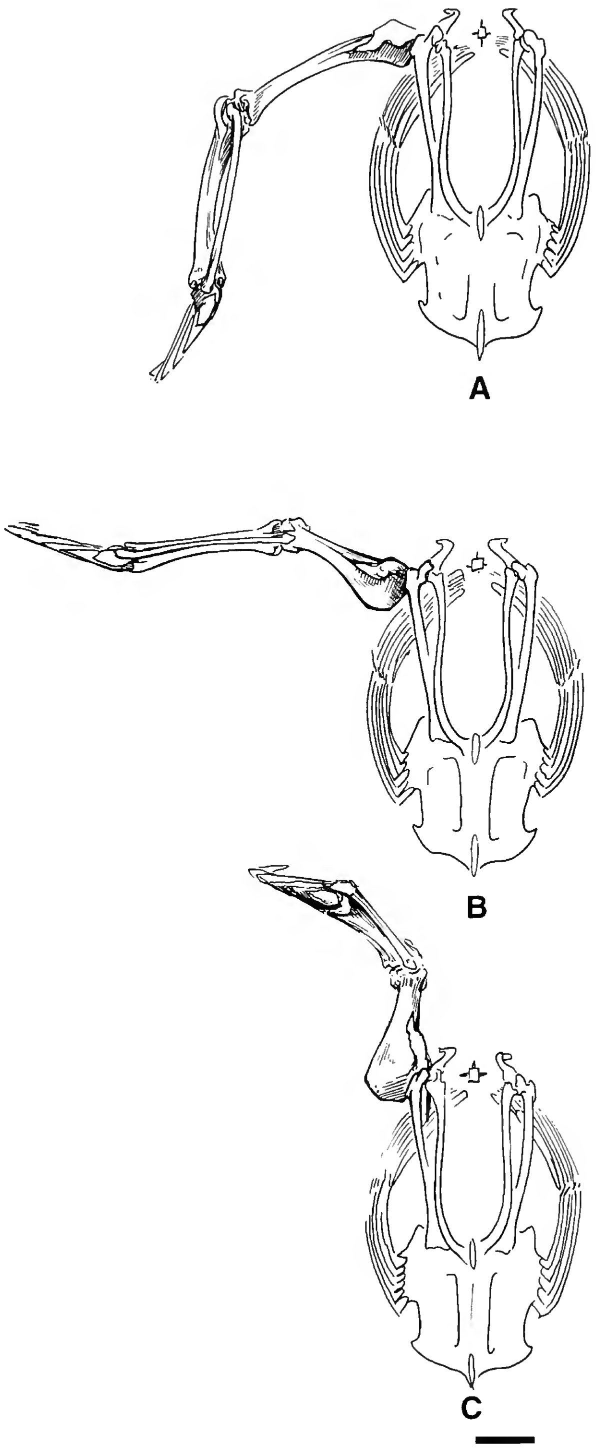

FIGURE 4.—Wing of the European Starling (*Sturnus vulgaris* Linnaeus) during upstroke in frontal view (after Dial et al., 1991) at the downstroke-upstroke transition (A), midupstroke (B), and upstroke position (C) at maximum humeral rotation and elevation. At the downstroke-upstroke position, the humerus is depressed 10° below the horizontal and the hand is pronated. During upstroke, the humerus rotates 80° on its longitudinal axis and elevates 55° above the horizontal, and the hand is fully supinated. Scale bar=1 cm.

we examined (see Figure 3), is a bipinnate muscle with relatively short but numerous fascicles. This architecture is favorable for high forces and limited excursion. Additionally, the tendon of insertion inserts circumferentialy on the long axis of the humerus, further contributing to the role of the supracoracoideus as a humeral rotator. The moment arm of the tendon of insertion in both species is short; we estimate its maximum to be 2 mm in the starling and 4 mm in the pigeon. Although the mechanical advantage of the supracoracoideus is low, its high input force, particularly at the downstroke-upstroke transition, is favorable for the production of high-velocity movements at the distal portion of the wing. We predict that during the upstroke, the distal portion of the wing experiences extremely high rotation velocity. Although still to be determined, these rotary forces may act to augment supination at the wrist in addition to supination provided by the trochlea carpalis-cuneiform complex.

THE FOSSIL EVIDENCE

In view of the evidence for the role of the supracoracoideus during the wingbeat cycle in modern birds, the obvious question before us is, when did the supination/humeral rotation action of the supracoracoideus come into play? Rotation of the humerus by the supracoracoideus is enhanced by the leverage provided by the tuberculum dorsale (external tuberosity), the derived site of insertion of the supracoracoideus (Figure 3). Reorientation of the supracoracoideus to this insertion on the humerus is accomplished by the passage of the tendon through the triosseal canal and around the acrocoracoid. At what point in the fossil record can we recognize any of these features?

None of these features have been noted in any of the specimens of *Archaeopteryx* (Figure 5). As reported by Sereno and

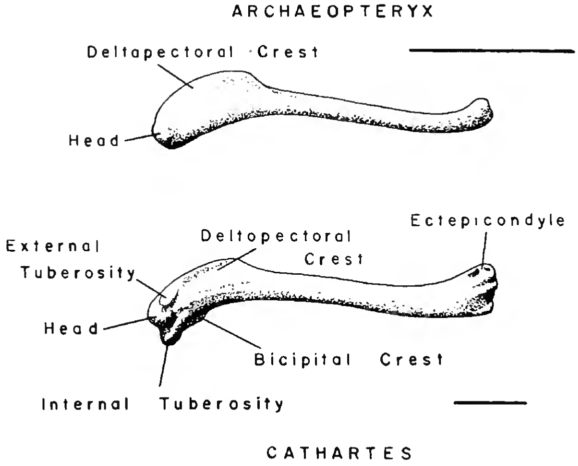

FIGURE 5.—Comparison of the humeri of *Archaeopteryx* and a modern flying bird, the Turkey Vulture (*Cathartes aura* (Linnaeus)), in dorsal aspect. Humeri are drawn to unit length for easy comparison; each scale bar equals 3 cm (external tuberosity=tuberculum dorsale). The humerus of *Archaeopteryx* is devoid of most of the tubercles and crests that are well developed in most modern birds. Most of these features are the attachment sites of muscles that retract and rotate the humerus. (After Ostrom, 1976a.)

Rao (1992), the critical region of *Sinornis* is not preserved, so we have no evidence. Zhou and Zhang (1992) did not note either feature in any of the material of *Cathayornis,* and the specimens of *Iberomesornis* (Sanz et al., 1988; Sanz and Bonaparte, 1992) and *Concornis* (Sanz et al., 1988; Sanz et al., 1995) do not show them either (confirmed by JHO). The precise stratigraphic source of the newly reported *Confuciusornis* is in doubt, but Hou (1995; see also Hou et al., 1995) made no mention of either feature.

EARLY STAGES OF FLIGHT

Sy (1936) described humeral axial rotation as a mechanism for the execution of wing upstroke and downstroke in pigeons and generalized its importance for other relatively small birds possessing powered flight. His observations that pigeons with bilateral tenotomy of the supracoracoideus are capable of flight, but cannot take off from the ground, are often cited in discussions of the evolution of powered flight (Olson and Feduccia, 1979; Ostrom, 1976b; Ruben, 1991). Perhaps less appreciated was Sy's (1936) identical procedure on at least one adult crow, for which he reported not only normal takeoff but normal flight. Sokoloff et al. (1994), in a cinematographic/electromyographic analysis of adult starlings, bilaterally denervated ($n=4$) or tenotomized ($n=2$) the supracoracoideus and reported that all birds but one could take off, but not without difficulty. Of particular importance are their observations that takeoff and flight in these deprived birds is not normal. In our estimation, the extent of impairment incurred by loss of the supracoracoideus for different species is a function of wing loading (body weight/wing area), the mechanical organization of the supracoracoideus, or some combination thereof. We believe the impaired takeoff capability of birds deprived of a functional supracoracoideus relates to their inability to rapidly rotate the humerus on its axis.

The earliest unequivocal evidence pertaining to bird flight is that of *Archaeopteryx.* There is no debate concerning its stratigraphic age. There is no question about its avian affinities. The famed feather impressions on most of the seven specimens establish that if *Archaeopteryx* flew, a feathered airfoil was available. The apparent presence of an ossified sternum in the most recently found specimen suggests that a skeletal origin for the pectoralis (and supracoracoideus?) existed in at least some of the specimens, as is also suggested by the pronounced deltoid crest on the humerus for insertion of the pectoralis. The supracoracoideus of *Archaeopteryx* was not diverted to a dorsal insertion, however, and thus could neither rapidly rotate the humerus nor augment supination of the distal wing.

Conclusions

In summary, *Archaeopteryx* was apparently incapable of the high-velocity rotation of the humerus about its longitudinal axis that would have been generated by a derived supracoracoideus with a dorsally inserting tendon. The subsequent evolution in later forms of an acrocoracoid, dorsally inserting tendon, and tuberculum dorsale resulted in (1) rotation of the humerus on its longitudinal axis to position the forearm and hand so their extension orients the fully outstretched wing in the parasagittal plane (i.e., the wing's ventral surface faces laterally, the position appropriate for the beginning of the subsequent downstroke), (2) increased speed of the upstroke, and (3) augmented supination of the hand to reduce drag. By relocating the site of insertion of the supracoracoideus to an elevated position on the dorsal surface of the humerus (the novel external tuberosity), wing supination was accelerated, and the range of movement perhaps increased. Such augmentation of supination and an increase in the velocity of upstroke must have provided high selective value, particularly for rapid takeoff and landing.

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A Comparison of the Jaw Skeleton in Theropods and Birds, with a Description of the Palate in the Oviraptoridae

Andrzej Elzanowski

ABSTRACT

Similarities to birds in the structure of the jaws and palate suggest that oviraptorosaurs (oviraptorids and caenagnathids), therizinosauroids, and ornithomimosaurs are the closest theropodan relatives of birds, which is in conflict with recent phylogenetic reconstructions based on postcranial evidence. No specific avian similarities could be found in the jaws and palate of dromaeosaurids. The ectopterygoid of the oviraptorids connects the lacrimal to the palatine, as does the avian uncinate (lacrimopalatine). This and other cranial similarities between the oviraptorosaurs and ornithurine birds raise the possibility that oviraptorosaurs are the earliest known flightless birds. With *Archaeopteryx* and the theropods providing evidence of plesiomorphic conditions, similarities in the mandibles, teeth, and tooth implantation in the Ichthyornithidae and Hesperornithidae may be interpreted as synapomorphies supporting monophyly of the Odontognathae.

Introduction

Until recently, evidence for the theropod relationships of birds was derived almost exclusively from the postcranial skeleton (Ostrom, 1976; Gauthier, 1986; Holtz, 1994, 1996). Cranial comparisons have been used primarily by the proponents of alternative hypotheses (Tarsitano, 1991), with the notable exceptions of Currie's (1985; see also Currie and Zhao, 1993) studies of *Troodon* and Raath's (1985) studies of *Syntarsus*. Unequivocal cranial evidence for the theropod relationships of birds has only recently been provided by the exceptionally well-preserved skull of the seventh skeleton of *Archaeopteryx* (Elzanowski and Wellnhofer, 1995, 1996).

The skull of *Archaeopteryx*, however, turned out to be very different from that of any known theropod, and the relationships of birds within the theropods remain unsettled, as do the relationships between the theropod taxa (Russell and Dong, 1993; Holtz, 1996). The major cladistic analyses based primarily on postcranial characters (Gauthier, 1986; Holtz, 1994, 1996) singled out the dromaeosaurids as the closest relatives of birds and, thus, echoed Ostrom's (1976) comparisons of *Archaeopteryx* to *Deinonychus*. This is inconsistent with cranial evidence, at least from the palate and jaws, which does not support a dromaeosaurid relationship for birds.

The present paper provides a detailed description of the oviraptorid palate and examines avian similarities in the bony jaws and palate of oviraptorosaurs, therizinosauroids, and ornithomimosaurs. The oviraptorosaurs include the families Oviraptoridae and Caenagnathidae (=Elmisauridae), and the latter includes *Chirostenotes* (=*Caenagnathus*) (Sues, 1997).

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The Oviraptorid Palate

The holotype of *Oviraptor philoceratops* Osborn, which was for half a century the only known oviraptorid specimen, has a badly crushed skull that provides virtually no information about the cranial interior (Osborn, 1924; Smith, 1992). Well-preserved oviraptorid specimens had been collected over

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20 years ago by the Polish- and Soviet-Mongolian expeditions, but the first review of their osteology was published only recently (Barsbold et al., 1990), and most of the long-known Mongolian cranial specimens still need to be thoroughly studied. New finds of oviraptorids, including an embryonic skeleton, have been reported from Mongolia (Norell et al., 1994; Dashzeveg et al., 1995).

The following description is based on the skull of *Oviraptor* sp. (ZPAL MgD-I/95) in the collection of the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland. This specimen has been illustrated and interpreted in the context of broad, primarily functional, comparisons (Osmólska, 1976) but was never described in detail. Osmólska's (1976) reconstruction of the oviraptorid palate proved correct except for details of the median pterygoid contact. Barsbold (1983a, fig. 12) published an illustration of the similar palate of *Oviraptor philoceratops,* which is not accompanied by a description and contains a misinterpretation of the vomer as the rostral part of the pterygoid.

Both the premaxilla and maxilla bear sharp tomial edges that suggest a cutting function of the jaws (Figure 1). The palatal shelves of the premaxillae and maxillae form an entirely closed "secondary" palate. The two shelves of each bone remain separated by a median suture. Dorsal to the shelves, the body of the premaxilla encloses a spacious sinus. The ventral (palatal) surface of the premaxillary shelves is overlapped by the maxillary shelves.

Each maxillary shelf is made of two longitudinal bulges separated by a shallow groove. The shelf is separated from the tomial edge by a deep, probably neurovascular, groove that empties into an opening at the suture with the premaxilla. The tomial edge is continuous with the lateral wall of the bone, which overlaps the premaxilla rostrally. The medial wall is seen in part as a perpendicular strut, visible in the antorbital fenestra (Figure 2A), that rises in the midlength of the bone and leaves a large maxillary foramen in front. The medial and lateral walls are both fenestrated and enclose a spacious maxillary sinus (a part of the antorbital fossa) that extends all the way to the caudal (jugal) end of the bone (Figure 2A). The maxilla of *Oviraptor philoceratops* has a similar structure (Barsbold et al., 1990, fig. 10.1A).

The maxilla is forked caudally (Figure 1). Each palatal shelf has a prominent knob- or tooth-like caudomedial process. The two caudomedial processes brace the vomer. Caudolaterally, the maxilla continues as a palato-jugal wing that articulates with the palatine, jugal, ectopterygoid, and lacrimal.

The vomer is tightly held between the maxilla and the pterygoid. The rostral end of the vomer is strongly expanded and composed of a median knob and lateral wings. The knob is braced and the wings are overlapped by the caudomedial processes of the maxilla. The convoluted suture to the pterygoid suggests a deep interdigitation.

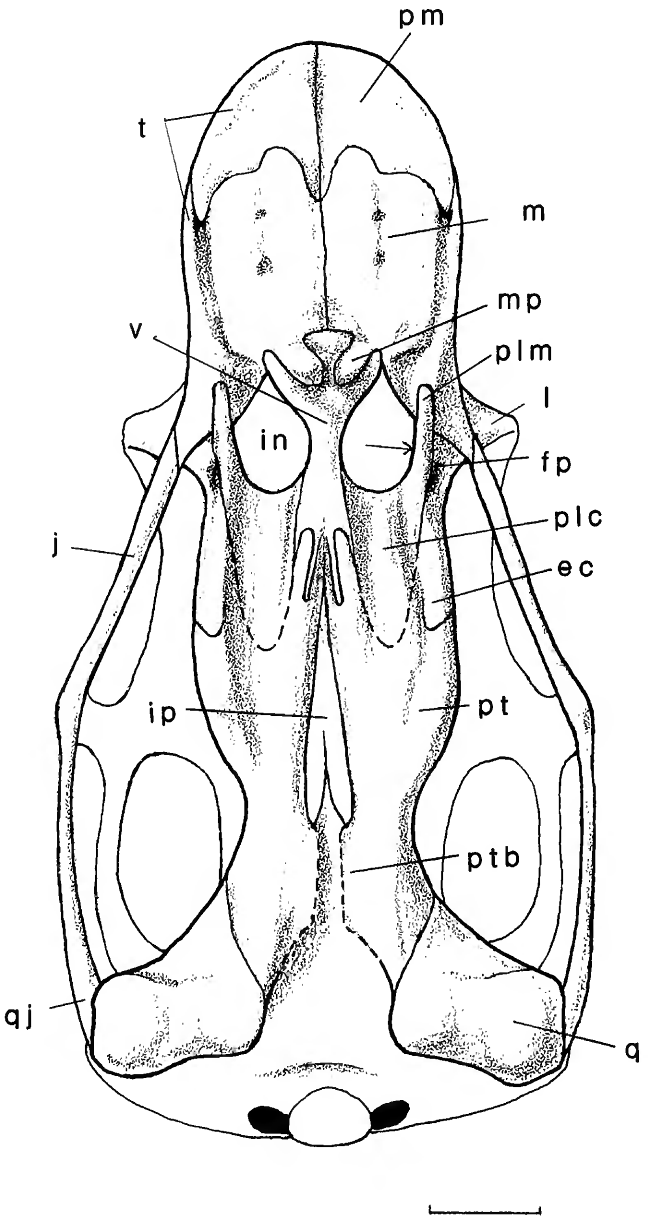

FIGURE 1.—Reconstruction of the oviraptorid bony palate based on the specimen ZPAL MgD-I/95. Arrow points to the palatine's ascending wing (invisible in this view, see Figure 2). Scale bar=10 mm. (ec=ectopterygoid, fp=postpalatine fenestra, in=internal naris, ip=interpterygoid vacuity, j=jugal, l=lacrimal, m=maxilla, mp=tooth-like caudomedial process of maxilla, plc=choanal conch (pterygoid wing) of palatine, plm=maxillary process of palatine, pm=premaxilla, pt=pterygoid, ptb=basal wing of pterygoid, q=quadrate, qj=quadratojugal, t=tomial edges of premaxilla and maxilla, v=vomer.)

The palatine is composed of the maxillary process, which is its only prominent rostral process, and the pterygoid (caudal) wing, which encloses the choana caudally. The maxillary process has a triangular ascending wing that forms the lateral wall of the choana and articulates with the lacrimal dorsally and the maxilla rostrally (Figure 2B). The pterygoid wing, which is paper-thin and poorly preserved, is strongly convex-concave dor-

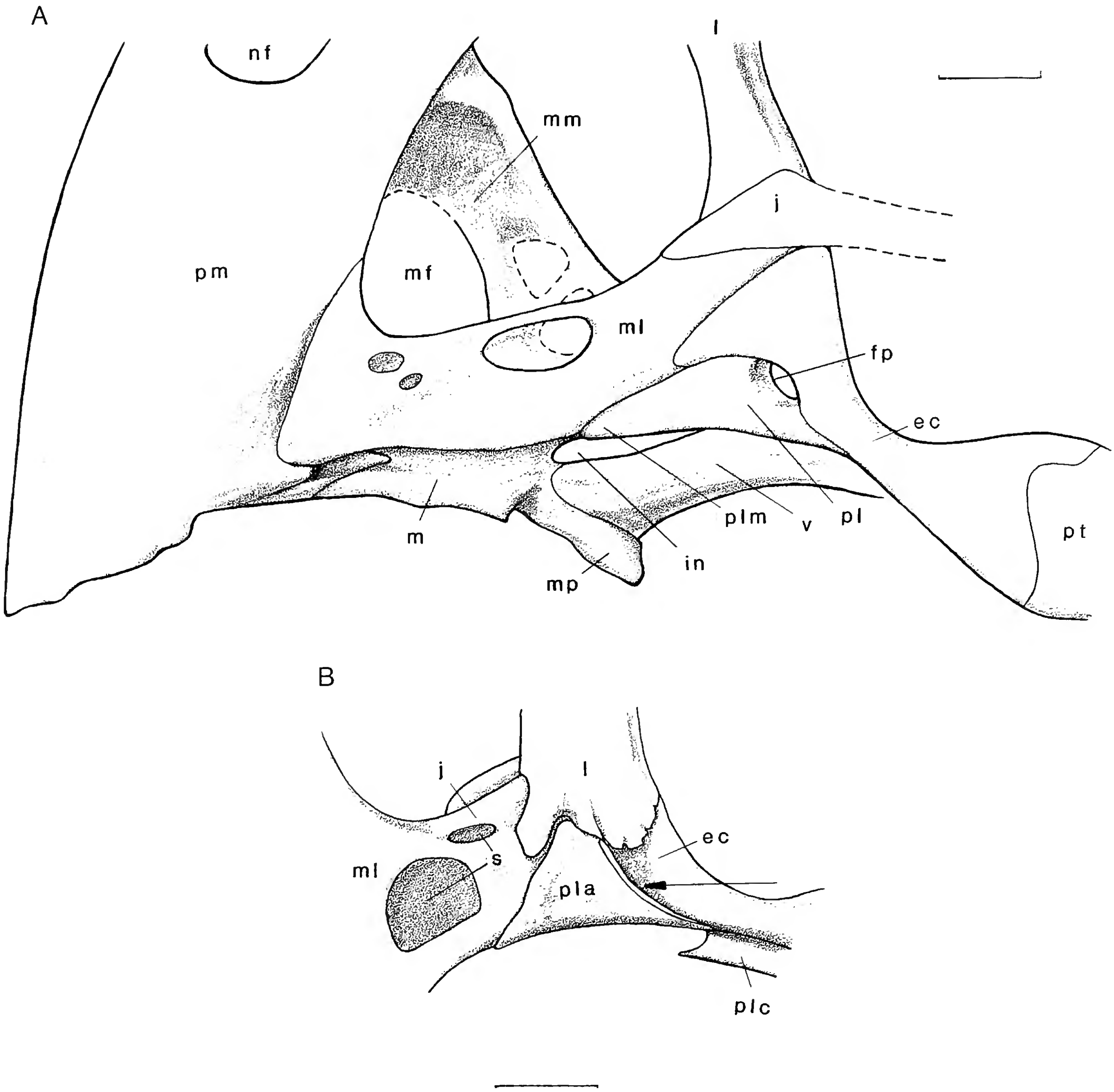

FIGURE 2.—Oviraptorid specimen ZPAL MgD-I/95: A, upper jaw in lateral view; B, lateral wall of the choana in medial view, with a schematic reconstruction of the pterygoid wing of the palatine (plc). Arrow points to a narrow pocket that opens laterally by the postpalatine fenestra. Each scale bar=5 mm. (ec=ectopterygoid, fp=postpalatine fenestra, in=internal naris, j=jugal, l= lacrimal, m=maxilla, mf=maxillary foramen, ml=lateral wall of caudal maxillary sinus, mm=medial wall of caudal maxillary sinus, mp=tooth-like caudomedial process of maxilla, nf=nasal foramen, pl=palatine, pla=ascending wing of palatine, plc=choanal conch (pterygoid wing) of palatine, plm=maxillary process of palatine, pm=premaxilla, pt=pterygoid, s= openings to caudal maxillary sinus, v=vomer.)

soventrally: its dorsal vault fits in the ventral trough of the pterygoid and appears to be partly fused with that bone. The rostromedial corner of the wing probably formed a diminutive counterpart of the vomeral process of other theropods (Elzanowski and Wellnhofer, 1993, fig. 4), as in *Oviraptor philoceratops* (Barsbold et al., 1990, fig.10.1D). Laterally, the palatine is separated from the ectopterygoid by a vestigial postpalatine ("palatine") fenestra (Figure 2A). The fenestra leads to a flat bony pocket, which opens medially by a long fissure between the ascending wing of the palatine and the ectopterygoid (Figure 2B). Although the palatine/pterygoid contact is not preserved, there is no indication of the presence of a pterygopalatine ("subsidiary palatine") fenestra between the pterygoid wing of the palatine and the pterygoid.

The details of pterygoid structure remain unclear due to its tight contact with or fusion to the adjacent bones. The rostral end of the pterygoid cannot be precisely distinguished from the palatine and ectopterygoid but seems to be forked rostrally. The rostral part of the bone is strongly concave ventrally and receives the pterygoid wing of the palatine. The caudal part of the pterygoid has a short wing for the basipterygoid articulation and a quadrate wing that closely adheres to what has been identified as the pterygoid ramus of the quadrate (Barsbold et al., 1990, fig. 10.1A). The pterygoquadrate articulation, at angles to the long axis of the pterygoid, is very tight and does not suggest any mobility.

The ectopterygoid provides a smooth rostral continuation of the thick lateral margin of the pterygoid. (A large bone in the type specimen of *Oviraptor philoceratops* that is attached to the caudal end of the pterygoid was identified as an ectopterygoid (Smith, 1992), which is clearly a mistake, the bone probably being the left quadrate.) The ectopterygoid is oriented vertically, almost in a parasagittal plane, and its rostral end lies much more dorsally than does the caudal end (Figure 2A). The rostral end articulates primarily with the lacrimal and maxilla and marginally contacts the jugal and the ascending wing of the palatine (Figure 2). The ectopterygoid is well delimited from the pterygoid across the ridge, but the suture wanes more medially (in the trough). The medial margin of the bone is overlapped by the palatine. Rostrally, the two bones are separated by a small postpalatine fenestra, which is well exposed in lateral view (Figure 2A) but is barely exposed in ventral view (Figure 1).

The lacrimal is oriented transversely, and its cross section gradually expands from a flattened lateral ridge to a broad medial base (Figure 2A). Its ventral extremity is irregularly crenate (Figure 2B).

Comparisons

Characters of the Oviraptoridae (Figures 1, 2; Barsbold et al., 1990), Caenagnathidae (Figure 5; Sternberg, 1940; Currie et al., 1993; Sues, 1997), Therizinosauroidea as represented by *Erlikosaurus* (Clark et al., 1994), and Ornithomimosauria (Osmólska et al., 1972; Barsbold and Osmólska, 1990) that are specifically shared with *Archaeopteryx* (Elzanowski and Wellnhofer, 1995, 1996), *Confuciusornis* (Hou et al., 1995), *Gobipteryx* (Elzanowski, 1977, 1995), the Odontognathae (Marsh, 1880; Elzanowski, 1991), and other ornithurine birds (Jollie, 1957; Elzanowski, 1995) are analyzed below, and their distribution is summarized in Table 1. All these characters show the opposite states in the Dromaeosauridae (Colbert and Russell, 1969; Ostrom, 1969; Sues, 1977; Currie, 1995) and usually in *Allosaurus* (Madsen, 1976) and other tetanuran theropods. The subdivision of birds and, especially, the definition of Ornithurae, follow Elzanowski (1995).

Unfortunately, very little is known about the jaws of troodontids, which show some avian similarities in their braincase (Currie, 1985; Currie and Zhao, 1993). Similar to the troodontids are jaw fragments of *Archaeornithoides* (Elzanowski and Wellnhofer, 1992, 1993), which may in fact represent a juvenile troodontid. One of the main reasons for describing it as a separate genus in a family of its own was its tooth structure,

TABLE 1.—Potential cranial synapomorphies of the Ornithomimosauria (Omim), Therizinosauroidea (Ther), Oviraptoridae (Ovir), Caenagnathidae (Caen), and birds as represented by *Archaeopteryx* (Arch), *Gobipteryx* (Gobi), and *Hesperornis* (Hesp). The opposite character states (0) are present in the Dromaeosauridae and the majority of known theropods. Parentheses indicate that the homology of noted similarities may be open to interpretation. A=ambiguous character state. See text for complete definitions and discussion of the characters.

Character	Omim	Ther	Ovir	Caen	Arch	Gobi	Hesp
1. Palatine with long maxillary process	1	1	1	1	1	1	1
2. Coronoid absent	1	1	1	1	1	1	1
3. Intraramal articulation absent	1	1	1	1	1	1	0
4. Maxilla with broad palatal shelf	1	1	1	1	?	1	1
5. Quadrate head bent backwards	1	1	1	?	1	1	0
6. Palatine with broad pterygoid wing	0	1	1	1	1	1	1
7. Pterygoid with basal process	(1)	0	1	?	A	?	1
8. Ectopterygoid in rostral position	A	1	1	?	0	(1)	(1)
9. Articular and surangular co-ossified	0	1	0	1	0	1	1
10. Articular with lateral process	0	1	1	1	0	1	1
11. Articular with medial process	0	0	1	1	0	1	1
12. Mandibular symphysis fused	0	0	1	1	0	1	(1)
13. Jugal bar rod-shaped	0	0	1	?	0	1	1
14. Ectopterygoid contacts lacrimal	?	0	1	?	0	?	(1)

which is unlike that in any theropod. Theropod teeth were once strongly believed not to vary with age (Currie et al., 1990), but this belief has been refuted by the discovery of subconical, unserrated teeth in dromaeosaurid hatchlings (Norell et al., 1994). Similar teeth are present in *Archaeornithoides* and may have been present in the early juveniles of troodontids.

MAXILLA.—The maxilla has broad palatal shelves that meet at, or at least approach, the midline in the Therizinosauroidea, Oviraptoridae, Caenagnathidae, Ornithomimosauria, *Archaeornithoides, Hesperornis,* and the paleognaths except *Struthio.* A fairly broad palatal shelf of the maxilla was probably present in *Gobipteryx.* Unfortunately, contrary to previous interpretations, the palatal aspect of the maxilla (as well as premaxilla) remains entirely unknown in *Archaeopteryx.*

In *Hesperornis* each palatal shelf of the maxilla ends with two processes, the lateral and the medial palatine process. The medial process, known as the maxillopalatine, is the only portion of the palatal shelf that remains in *Struthio* and the neognaths. The peg-like process of the oviraptorids and caenagnathids corresponds in position to the maxillopalatine of neornithine birds in being a caudomedial extension of the palatal shelf that contacts the vomer.

At least in the oviraptorosaurs, *Archaeornithoides,* and birds, the maxillary shelf provides a floor for the caudal maxillary sinus. Other theropods are believed to have only the rostral sinus (Witmer, 1990). Among Mesozoic birds, the caudal maxillary sinus is well documented in *Hesperornis* (Witmer, 1990) and may have been present in *Archaeopteryx,* although the evidence of its presence in the fifth skeleton provided by Witmer (1990:360, fig. 14) is probably incorrect (Elzanowski and Wellnhofer, 1995). The upper jaw of the fifth skeleton, however, contains a vertical, median or paramedian element (Elzanowski and Wellnhofer, 1995, fig. 7X) that is similar in shape and location to the medial wall of the caudal sinus in the oviraptorids.

PALATINE.—The palatine of the ornithomimosaurs, therizinosauroids, oviraptorids, caenagnathids (Sues, 1997, fig. 2), and birds has a maxillary process that is much longer than the rostromedial vomeral process and overlaps the maxillary palatal shelf ventrally. In the neornithines, including *Hesperornis,* the maxillary process is known as the premaxillary process because it extends even further rostrally and reaches the premaxilla. The palatine has a broad pterygoid (caudal) wing that overlaps the pterygoid ventrally in the therizinosauroids, oviraptorids, birds, and probably in caenagnathids.

In the ornithomimosaurs, the palatine has a dorsal, transversely oriented process situated close to the lacrimal (Osmólska et al., 1972:116, 136). A prominent transverse crest is present in *Archaeopteryx* in a comparable location (Elzanowski and Wellnhofer, 1996:89, fig. 9A), and three transverse crests are present in *Chirostenotes* (Sues, 1997, fig. 2). In contrast, the dorsal process of the palatine that ascends to the lacrimal in the oviraptorids is oriented in the parasagittal plane (Figure 2B).

PTERYGOPALATINE FENESTRA.—Gauthier (1986) used the pterygopalatine (subsidiary palatine) fenestra as one of two diagnostic cranial characters of the newly defined Coelurosauria, although it is known to be present in only two of the originally included families, the ornithomimosaurs and dromaeosaurids. The pterygopalatine fenestra has been subsequently identified in *Archaeornithoides,* the therizinosauroids, and tentatively in *Chirostenotes* and *Gobipteryx.* This fenestra is lacking in the oviraptorids (Figure 1). In *Hesperornis* and other neornithines there is no separate fenestra, although the situation in *Gobipteryx* suggests that it may have merged with the choana. The lack of an appropriate embayment in either the palatine or pterygoid of *Archaeopteryx* suggests either the absence of this fenestra or a configuration similar to that in the neornithines. The uncertain status of the pterygopalatine fenestra in birds makes it of little use in the search for avian relatives.

ECTOPTERYGOID AND POSTPALATINE FENESTRA.—The ectopterygoid is situated rostrally and, as a result, the postpalatine (palatine) fenestra is reduced in the oviraptorids (Figures 1, 2) and therizinosauroids (although it is unclear whether the fenestra is present in the latter). The fenestra is much smaller in *Gallimimus* (Osmólska et al., 1972:108) than it is in the dromaeosaurids and may be even smaller, if present at all, in *Ornithomimus edmontonicus* Sternberg (ROM 851), where the ectopterygoid is preserved in contact with the lacrimal (pers. obs.) in a position very different from that reconstructed in *Gallimimus.* In the oviraptorids and *Erlikosaurus,* the ectopterygoid is lateral to the palatine, which is due to its rostral position and the presence of the pterygoid wing of the palatine. This also may be true of the Caenagnathidae (Sues, 1997:701). Although the ectopterygoid is positioned caudally in the fifth specimen of *Archaeopteryx,* it may have overlapped, at least in part, the long pterygoid wing of the palatine.

The oviraptorid ectopterygoid differs from that of *Archaeopteryx* and from other theropods, including the therizinosauroids, in the lack of the jugal hook, its distal articulation primarily with the lacrimal and maxilla rather than the jugal, and its strongly slanting position between the lacrimal and the palatine (Figure 2). In all these differences, the oviraptorid ectopterygoid agrees with the avian uncinate (uncinatum=lacrimopalatinum), which in the neornithine birds articulates with the caudoventral margin of the lacrimal and descends caudoventrally to the palate (Figure 3). Although in modern birds the uncinate tapers toward the ventral tip and either articulates with the palatine or ends free above it, in oviraptorids the bone flares out ventrally and articulates with both the palatine and the pterygoid. This difference may be accounted for by the reduction of the rostral part of the pterygoid (which became separated and reduced as the hemipterygoid) in the neornithine birds. In *Hesperornis* the uncinate probably approached or marginally contacted the large hemipterygoid (Elzanowski, 1991, fig. 3). The uncinate of extant birds is clearly a vestigial structure that is extremely variable in shape.

The uncinate is widespread among the neornithines. It has been found in the Struthionidae and Rheidae among the paleog-

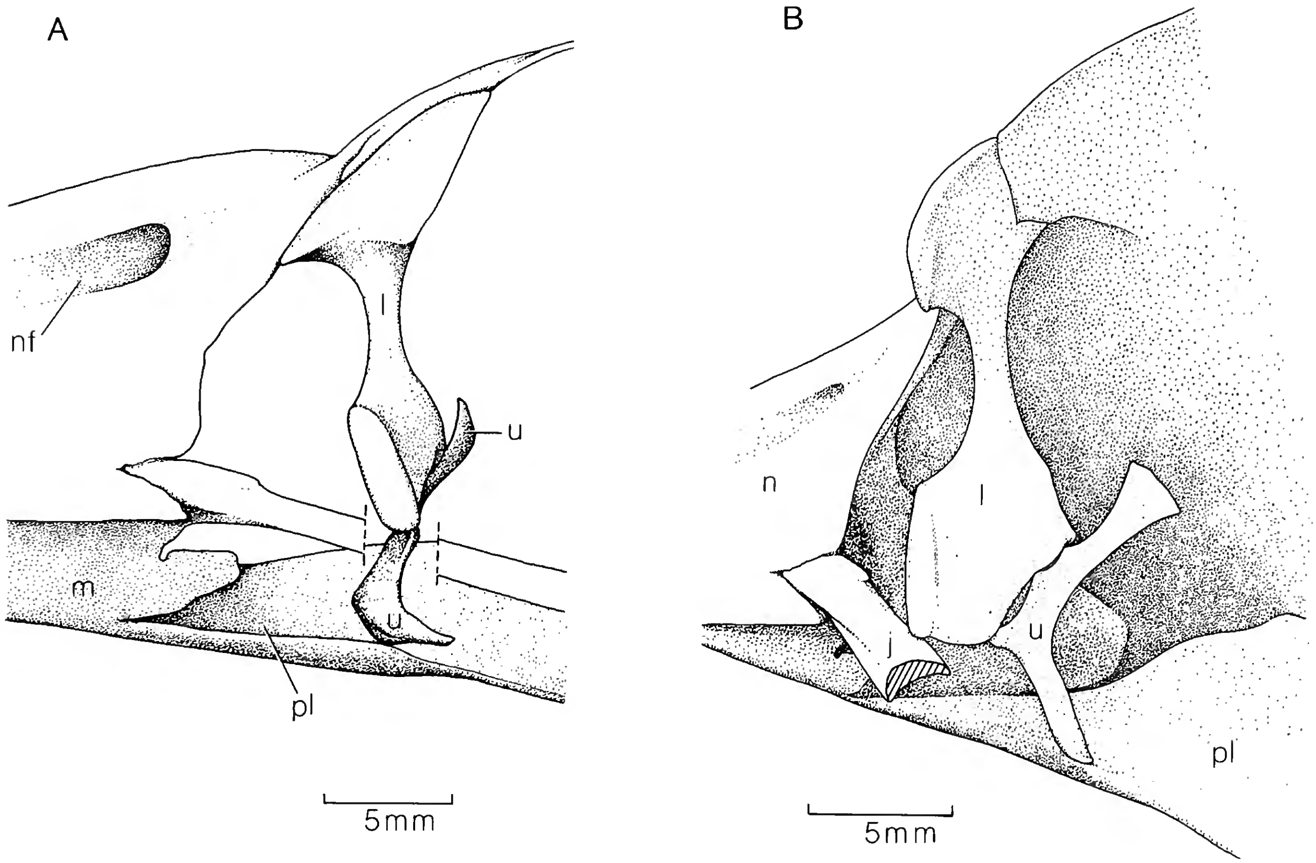

FIGURE 3.—*Fregata magnificens* Mathews (Neognathae). The antorbital area of the skull in A, lateral, and B, dorsolaterocaudal views. Each scale bar=5 mm. (j=jugal, l=lacrimal, m=maxilla, n=nasal, nf=nasal foramen, pl=palatine, u=uncinate (lacrimopalatine).)

naths and in nine families representing six neognathous orders, including Fregatidae (Pelecaniformes), Procellariidae and Diomedeidae (Procellariiformes), Laridae and Alcidae (Charadriiformes), Cariamidae (Gruiformes), Accipitridae (Falconiformes), and Cuculidae and Musophagidae (Cuculiformes) (Burton, 1970; pers. obs.). Monophyly of this set of taxa is out of the question, and four of the included orders (Pelecaniformes, Procellariiformes, Charadriiformes, and Gruiformes) have been repeatedly considered to be among the earliest neognathous branches. In addition, strong evidence of the presence of the uncinate has been found in *Hesperornis* (Elzanowski, 1991). This suggests that the presence of the uncinate is plesiomorphic at least for the neornithines and that an ancestral bone was present in the primitive, pre-neornithine birds.

The origin of the uncinate has remained obscure. Frank (1954:232) suggested that it is an avian neomorph. Burton (1970) raised the possibility of its derivation from a ligament (which is more widespread than the bone) but admitted that this begs the question of the origin of the ligament. McDowell (1978) mapped the uncinate to the archosaurian ectopterygoid because this bone appeared to be the only possible avian homologue for a reptilian element that lies lateral to the pterygoid and caudal to the maxilla. Thus far, no intermediate condition has been found. The oviraptorid ectopterygoid provides at least a structural intermediate between the reptilian ectopterygoid and the avian uncinate. Whether it is an evolutionary intermediate remains to be decided in a broader phylogenetic analysis. The similarities to the avian uncinate cannot be homologous unless the oviraptorids are more closely related to the ornithurine birds than is *Archaeopteryx* because the latter possesses a typical theropodan, hooked ectopterygoid, which is preserved in a caudal position in the fifth (Eichstätt) skeleton.

BASIPTERYGOID ARTICULATION.—The pterygoid has a basal process for the articulation with the cranial base in oviraptorids (Figure 1), *Hesperornis,* and the majority of those neognaths that have a basipterygoid articulation (sensu stricto) as distinguished from the rostropterygoid articulation of the galliforms and anatids (Weber, 1993). The basal process is well developed in many Charadriiformes and some Caprimulgiformes (Steatornithidae, Caprimulgidae, Nyctibiidae) and in all the Turnicidae, Anhimidae, Columbidae, Sagittariidae, Strigiformes, and Trogonidae (Figure 4). The pterygoid of the Procellariidae and Pelecanoididae has a rostral wing that extends to the rostral end of the bone and articulates only caudally with the basipterygoid process. The basal articular surface is least set off from the shaft of the pterygoid in the Cathartidae.

The basal process of the pterygoid is poorly developed in *Archaeopteryx,* and the structure of the basipterygoid articulation remains unknown in *Gobipteryx,* which makes the phylogenetic significance of this character somewhat ambiguous. Because the basal process of the oviraptorids (and probably in the caenagnathids, the basipterygoid articulation of which is very similar to that of oviraptorids) is distinctly better developed than it is in *Archaeopteryx,* it is interpreted herein as another possible synapomorphy linking the oviraptorosaurs to the ornithurines.

The quadrate ramus of the pterygoid is closely appressed on the braincase in the oviraptorids, ornithomimosaurs, and therizinosauroids. The basipterygoid process is virtually absent in the oviraptorosaurs, which have the articular surface of the pterygoid developed directly on the cranial base (Sues, 1997, fig. 3), and the same seems to be true of the therizinosauroids (Clark et al., 1994:20). The identification of the basipterygoid processes in the ornithomimosaurs remains uncertain. Their quadrate wing of the pterygoid has a prominent medial process that seems to abut the cranial base at the level of mandibular articulation (i.e., behind the sphenoid capsule). This is clearly visible in an undescribed skull (ROM 851) of *Ornithomimus edmontonicus* (pers. obs.). The apparent basal process of the pterygoid was left uninterpreted in *Gallimimus bullatus* Osmólska et al. (Osmólska et al., 1972, fig. 2; Barsbold and Osmólska, 1990, fig. 8.1), and the basipterygoid articulation was identified farther rostrally on the sphenoid capsule, a contact that is unlike a theropodan basipterygoid articulation and may have arisen as a result of the transverse expansion of the capsule.

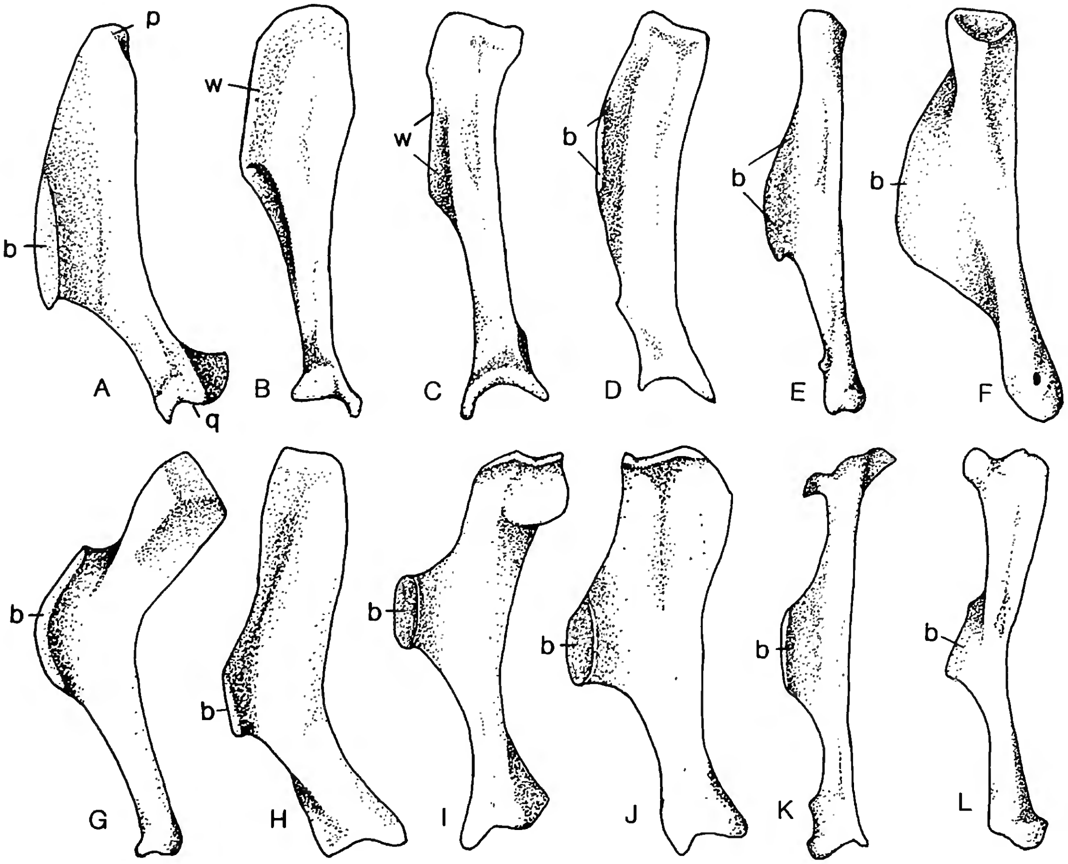

FIGURE 4.—The pterygoid in various neognathous birds, medioventral view: A, *Turnix varia* (Latham); B, *Pelecanoides urinatrix* (Gmelin); C, *Procellaria aequinoctalis* Linnaeus; D, *Coragyps atratus* (Bechstein); E, *Sagittarius serpentarius* (Miller); F, *Anhima cornuta* (Linnaeus); G, *Chauna torquata* (Oken); H, *Columba fasciata* Say; I, *Philomachus pugnax* (Linnaeus); J, *Vanellus vanellus* (Linnaeus); K, *Trogon rufus* Gmelin; L, *Strix aluco* Linnaeus. In B–E, the length of the basal articular surface on the pterygoid (indicated by "b" in D,E) is much greater than the rostrocaudal width of the basipterygoid process. (b=basal process, p=palatine articular surface, q=quadrate articular surface, w=rostrobasal wing.)

In the troodontids (Currie, 1985; Currie and Zhao, 1993) the basipterygoid processes are strong but are directed caudolaterally rather than rostrolaterally as in other theropods. This precludes a typical theropod basipterygoid articulation, and their facets are strongly concave, which suggests a basal process on the pterygoid (the caudal part of which is unknown in the troodontids). In the dromaeosaurids and most of the remaining theropods, the pterygoids have sockets that receive prominent basipterygoid processes of the sphenoid.

QUADRATE.—In the dromaeosaurids and most of the remaining theropods, the caudal profile of the quadrate is straight, and the quadrate socket in the squamosal opens more or less ventrally. In contrast, the quadrate head is bent backward in the oviraptorids (Maryańska and Osmólska, 1997), *Erlikosaurus*, ornithomimosaurs, troodontids, *Gobipteryx*, and the majority of other ornithurines except for Hesperornithidae, *Ichthyornis*, and some modern birds. In *Archaeopteryx* the caudal bend of the quadrate head may be partly obscured by the position in which the quadrate is preserved; it is exposed in caudal aspect in the seventh skeleton and in rostral aspect in the fifth skeleton. The oviraptoid quadrate alone agrees with that of the ornithurines in having an otic capitulum for the articulation with the braincase, the pterygoid articular surface approaching the medial mandibular condyle, and a distinct (but shallow) quadratojugal cotyla (Maryańska and Osmólska, 1997).

CORONOID.—The coronoid bone is absent in the oviraptorosaurs (Figure 5), ornithomimosaurs, *Erlikosaurus*, and all adult birds, including *Archaeopteryx* and *Gobipteryx*. It may have been incorporated into the prearticular (Nemeschkal, 1983a), and a tiny splint of bone just rostral to the tip of the prearticular in the hatchling Golden Eagle (*Aquila chrysaetos* (Linnaeus)) probably is a vestige of the coronoid (Jollie, 1957).

ARTICULAR AND PREARTICULAR.—The articular of ornithurine birds (including *Gobipteryx*), but not *Archaeopteryx*, co-ossifies with the prearticular, surangular, and angular at various, mostly posthatching, stages of development. The articular and surangular are co-ossified in the caenagnathids, *Erlikosaurus*, and all other adult ornithurines. The articular is co-ossified with the angular and surangular in *Avimimus*, in which the prearticular is not preserved (Kurzanov, 1987). The articular is separated by sutures from the adjacent bones in the ornithomimosaurs, oviraptorids, and other theropods, including dromaeosaurids and *Allosaurus*.

The articular surface for the quadrate is expanded both medially and laterally beyond the ramus in ornithurine birds. The lateral expansion is coextensive with the small lateral process that bears it. By contrast, the medial expansion covers only the basal part of the prominent medial process, which provides an area of attachment for the pterygoideus muscle. In *Gobipteryx*, however, there is no connection between the medial expansion of the articular surface and the medial process, which may or may not be due to damage. There is no evidence of any distinctive projections of the articular surface in *Archaeopteryx* or in the ornithomimosauria. The articular surface is strongly expanded laterally but not medially in *Erlikosaurus* and is expanded both medially and laterally in the oviraptorids and caenagnathids. The two projections in the oviraptorosaurs are similar to those in *Gobipteryx* (Elzanowski, 1974, fig. XXXIII/2).

Aside from being reduced in a few neognaths (such as the phasianids), the prearticular shows two fairly distinctive morphologies. It turns dorsally and expands into an ascending blade in *Erlikosaurus*, the majority of theropods (including the dromaeosaurids), *Archaeopteryx*, *Hesperornis* (pers. obs.), and some neognaths (e.g., Spheniscidae, Laridae). The prearticular continues far rostrally as a straight bony rod in the caenagna-

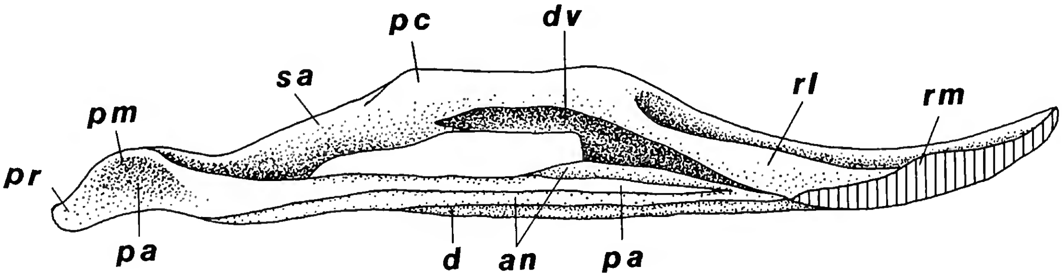

FIGURE 5.—Mandible of *Chirostenotes pergracilis* (=*Caenagnathus collinsi* R.M. Sternberg), CMN 8776 in medial view. The medial aspect of this mandible has been hitherto described only by Sternberg (1940, fig. 2). Sternberg's illustration showed a well-defined caudal outline of the dorsomedial process of the dentary, whereas in reality this process seems to be fused to the surangular. Absent from the mandible is the splenial, which may have fallen off, as frequently happens in birds, but it also is possible that it was reduced because the mandible is unusual in having a rostral extension of the angular that reaches the symphysis. The prearticular extends to the tip of the retroarticular process and covers the articular, which is fused to the surangular but not to the prearticular. (an=angular, d=ventral ramus of dentary, dv=ventral process of dorsal ramus of dentary, pa=prearticular, pc=coronoid process, pm=medial process, pr=retroarticular process, rl=lateral ridge, rm=medial ridge, sa=surangular.)

thids (Figure 5), oviraptorids (Barsbold, 1983b, fig. 13), at least in *Garudimimus* among the ornithomimosaurs (Barsbold and Osmólska, 1990, fig. 8.3.D), the paleognaths (Müller, 1963; pers. obs.), the remaining neognaths, and probably *Gobipteryx.*

MANDIBULAR SYMPHYSIS.—The symphysis is unfused in *Archaeopteryx,* although the rostral tips of the rami are connected very tightly. Among the theropods, the ends of the mandibular rami are fused only in the oviraptorosaurs and are fused even in the smallest caenagnathid specimens (Currie et al., 1993), but they remain unfused in the oviraptorid embryo (Norell et al., 1994), suggesting that fusion occurred at or soon after hatching, as in *Gobipteryx* (Elzanowski, 1981). The symphysis is fused in *Confuciusornis,* which combines an *Archaeopteryx*-like postcranial skeleton with a *Gobipteryx*-like skull (Hou et al., 1995), *Gobipteryx* (Elzanowski, 1977), and other ornithurines except for the odontognaths (Marsh, 1880), teratorns (Campbell and Tonni, 1981), and pseudodontorns (Odontopterygia) (Zusi and Warheit, 1992).

The lack of a symphysis in the odontognaths is most probably secondary because in the hesperornithids and possibly in *Ichthyornis,* the tips of the rami were connected by a predentary bone (Martin, 1987), which is definitely a derived character because no other bird or theropod has it. The dentary of birds arises from two centers of ossification (Nemeschkal, 1983b), and the predentary bone most probably ossified from the rostral (mentomandibular) center. Consequently, this bone probably represents the co-ossified symphyseal part that became separated from the remainder of the mandible.

The pseudodontorns are highly specialized, fish-eating neognathous birds related to the pelecaniforms, which makes the lack of mandibular symphysis in these birds unquestionably secondary.

As of now, there is no evidence for multiple origins of the fused symphysis in birds. It may have evolved only once in the ornithurines, and its presence could be another synapomorphy of the oviraptorosaurs and ornithurines.

INTRARAMAL JOINT.—This joint includes the articulations between the dentary and surangular and between the splenial and angular. It permits mediolateral mobility within each ramus of the mandible. The majority of the theropods, including the dromaeosaurids, have an intraramal joint. It is absent in the ornithomimosaurs, *Erlikosaurus,* oviraptorosaurs, and primitive birds, including *Archaeopteryx, Gobipteryx,* and probably *Confuciusornis.* In more advanced birds, there are at least two types of intraramal joints: one in the pelecaniforms (including pseudodontorns) and another in the odontognaths. They are made of different components, which indicates that they evolved independently of each other (Zusi and Warheit, 1992).

Gingerich (1973) proposed that the intraramal joints in *Hesperornis* and *Ichthyornis* have been inherited from the theropods and thus represent yet another theropod/avian synapomorphy. Consequently, the similarity between *Ichthyornis* and hesperornithids would be symplesiomorphic. This, however, is inconsistent with the intraramal joint being absent in *Archaeopteryx, Confuciusornis,* and *Gobipteryx* (see also Feduccia, 1996:155). In addition, the two kinds of intraramal joints in birds are more similar to each other (Gingerich, 1972, fig. 1; Zusi and Warheit, 1992, fig. 7) than either of them is to the joint in the dromaeosaurids (Currie, 1995, fig. 7). In the odontognaths, the hinge is formed primarily by the splenial and angular, and these bones articulate at an angle of ~45° to the long axis of the ramus. In the dromaeosaurids the hinge, reinforced by bony knobs, is primarily between the dentary and surangular, whereas the splenial and angular seem to form a gliding articulation that is oriented much more horizontally than the splenio-angular hinge of the odontognaths. In all probability, birds started their evolution with a rigid mandible, and detailed similarity of the intraramal joints in *Ichthyornis* and hesperornithids is synapomorphic.

JUGAL BAR.—*Confuciusornis* and probably all the ornithurine birds have a thin, rod-like jugal bar that is formed in substantial part, and in some neognaths exclusively, of the quadratojugal. In the oviraptorids and *Avimimus* (Kurzanov, 1987), the bar is thin, as it is in the ornithurines. The slender jugal bar stands out in an otherwise massive oviraptorid skull adapted for durophagy.

In *Archaeopteryx* and the remaining known theropods, the jugal bar is a robust slat. It is formed almost exclusively of the jugal in most of the theropods. In *Archaeopteryx,* the quadratojugal may have extended far rostrally on the medial side of the jugal (Elzanowski and Wellnhofer, 1996, fig. 7).

The postorbital process of the jugal is in the terminal caudal position, and the infratemporal fossa is reduced in the ornithomimosaurs, the troodontids, and *Archaeopteryx. Erlikosaurus* is unique among the theropods in having two ascending processes of the jugal: a postorbital process one-fourth the length from the caudal end, and a terminal process overlying the quadrate and approaching the squamosal. The latter corresponds in position to the postorbital process of the ornithomimosaurs and *Archaeopteryx.* This unique jugal morphology raises the possibility of a secondary enlargement of the infratemporal fossa, accompanied by the division of the initially terminal postorbital process. Although the rostral position of the postorbital bar in the oviraptorids looks like a symplesiomorphy with the majority of theropods, it is conceivable that this position is secondary and that the postorbital process of the jugal corresponds to the rostral, possibly secondary, process in *Erlikosaurus.*

INTERDENTAL PLATES AND TEETH.—The presence of interdental plates is a primitive archosaurian character (Elzanowski and Wellnhofer, 1993). Among the theropods, inderdental plates are known to be absent in troodontids (Currie, 1987), *Archaeornithoides* (Elzanowski and Wellnhofer, 1993), *Baryonyx* and *Spinosaurus* (Buffetaut, 1992), and ornithomimosaurs (Perez-Moreno et al., 1994). Separate interdental plates are present in juvenile dromaeosaurids (Norell et al., 1994) and seem to be replaced by porous interdental bone in adults (Currie, 1987).

The discovery of interdental plates in *Archaeopteryx* (Wellnhofer, 1993) makes it clear that their absence in *Hesperornis* and *Ichthyornis* is secondary, as probably are other aspects of their tooth implantation, such as the expanded dental roots and the equal height of the lingual and buccal margins of the dentary (Elzanowski and Wellnhofer, 1995). The teeth of *Ichthyornis* are usually anchored in separate alveoli, whereas those of the hesperornithids are in a common groove; however, Martin and Stewart (1977) described a mandible of *Ichthyornis* with teeth in a groove.

Avian teeth do not show any close similarity to any known theropod teeth except for the early juvenile teeth of *Archaeornithoides* (Elzanowski and Wellnhofer, 1993). The teeth of *Archaeopteryx* and *Ichthyornis* are similar in having the crowns divided into a straight base and a recurved tip. On the other hand, the teeth of *Ichthyornis* were reported to have the roots distinctly expanded, as in the hesperornithids (Martin and Stewart, 1977). Unfortunately, the radiographs on which this observation is based have never been published. Dental roots are not expanded in *Archaeopteryx* (Howgate, 1984; Elzanowski and Wellnhofer, 1996).[1]

Entirely toothless jaws evolved independently in the oviraptorosaurs, advanced ornithomimosaurs, *Confuciusornis* and *Gobipteryx* (these two genera were included in the Enantiornithes by Hou et al., 1995), and the advanced neornithines. An edentulous premaxilla coexists with a dentigerous maxilla and dentary in the therizinosauroids and hesperornithids. It is clear that the reduction of teeth occurred several times independently within the analyzed set of taxa.

Discussion

Some of the avian characters, such as the toothless beaks of the oviraptosaurs and advanced ornithomimosaurs, are certainly convergent and evolved more than once within the set of taxa under comparison. Reduction of teeth is a recurrent theme in vertebrate evolution.

There is, however, no reason to expect a pervasive convergence on birds in the cranial morphology of the ornithomimosaurs, therizinosauroids, and oviraptorosaurs because their skulls are unlike any avian skull. This is what one could expect as a result of turning a primitive, perhaps *Archaeopteryx*-like cranial morphology into several highly specialized kinds of jaw apparatus of the gigantic descendants of the ancestors of birds. In terms of jaw function, the oviraptorids are comparable to the dicynodonts (Osmólska, 1976), and the therizinosauroids are convergent on the ornithischians in having cheeks (Clark et al., 1994). It seems reasonable, therefore, to suspect that the unique cranial similarities of birds, oviraptorosaurs, therizinosauroids, and ornithomimosaurs (Table 1, characters 1–6) are synapomorphic and thus indicative of the monophyly of a clade composed of these taxa and probably troodontids (Figure 6). This would agree with the phylogeny reconstructed from 20 cranial and 39 postcranial characters by Russell and Dong (1993), who subdivided the tetanurans into two groups: one that included the dromaeosaurs and carnosaurs and one that included the ornithomimosaurs, troodonts, therizinosauroids, and oviraptorosaurs.

Most intriguing are four characters (Table 1, characters 10–13) that are shared by the oviraptorosaurs and the ornithurine birds but are absent in *Archaeopteryx.* These suggest that the oviraptorosaurs branched off after *Archaeopteryx* and thus represent the earliest known flightless birds. Except for the elongate forelimbs (which become shortened in all flightless forms), the postcranial skeleton of *Archaeopteryx* does not have any avian traits that would be absent in the oviraptorids (Barsbold 1983a, 1983b). Therefore, if flightlessness had evolved at a stage of avian evolution close to *Archaeopteryx,* this would be extremely difficult to distinguish from the primary flightlessness of the theropods.

Relationships of the oviraptorosaurs have been enigmatic ever since their discovery (Osborn, 1924). The only consensus reached in recent phylogenetic reconstructions is that the oviraptorosaurs belong in the Coelurosauria, a major clade that gave rise to birds, but their placement within that clade varies considerably (Gauthier, 1986; Barsbold et al., 1990; Holtz, 1996). Evidence for their affinities comes almost exclusively from the postcranial skeleton because the oviraptorid skull is difficult to compare with the skull of any other group of theropods. In contrast, even the highly specialized, edentulous skulls of ornithomimosaurs are still clearly identifiable as theropodan. The two cranial characters used by Gauthier (1986) to define the Coelurosauria, namely, the pterygopalatine fenestra and ventral pocket in the ectopterygoid, are absent in the oviraptorids (as well as in the ornithurines).

Several similarities of the jaws of Hesperornithidae and Ichthyornithidae prove likely to be synapomorphies when analyzed against the plesiomorphic background provided by the theropods and *Archaeopteryx.* Wetmore (1930) combined the Hesperornithiformes and Ichthyornithiformes in the superorder Odontognathae, but monophyly of this taxon has never been explicitly suggested because most of their similarities were thought to be primitive. A closer relationship between these two orders is now suggested by the lack of mandibular symphysis, probably due in both taxa to the separation of the tip of the mandible as a predentary bone; the presence and detailed similarities of the intraramal joint; the absence of interdental plates, which is probably correlated with the lingual alveolar margin being flush with the buccal margin; and probably the expansions of the dental roots (fide Martin and Stewart, 1977) and the straight quadrate.

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[1] Editor's Note: This is at variance with Martin and Stewart, elsewhere in this volume, who consider previously published photographs and descriptions to indicate that the teeth of *Archaeopteryx* do have expanded roots.

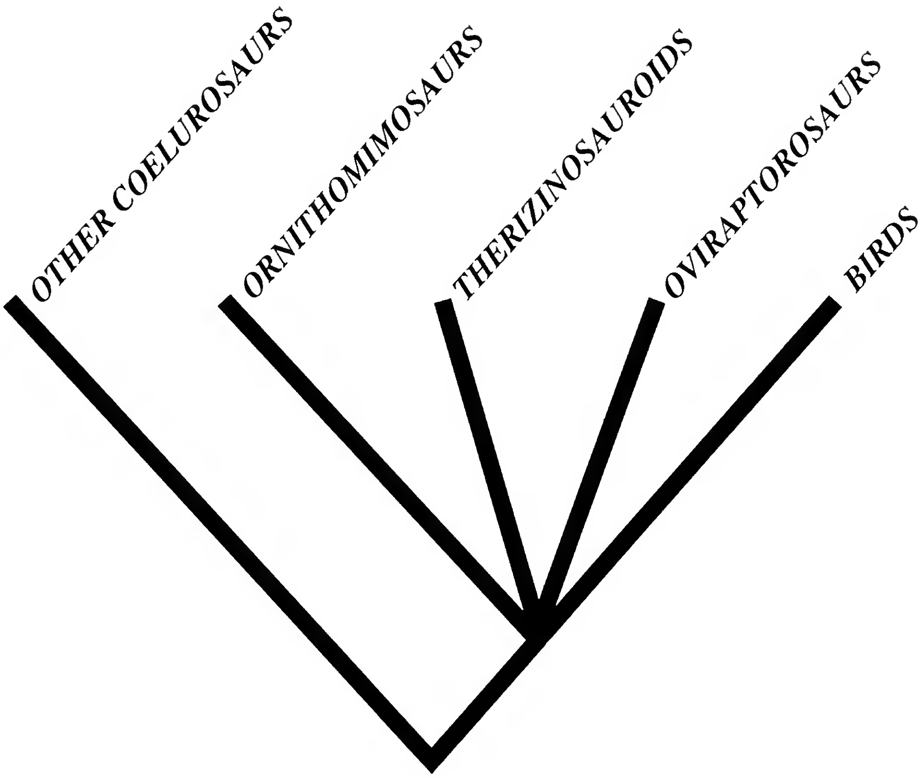

FIGURE 6.—Unresolved polytomy of the avian and three theropod lineages, as suggested by characters 1–6 in Table 1.

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Early Evolution of Birds: Roundtable Discussion

The final day of the Washington, D.C., meeting of the Society of Avian Paleontology and Evolution (7 June 1996) was organized by Peter Wellnhofer and was devoted to Mesozoic birds and avian origins. The morning session consisted of individual paper presentations, some of which appear elsewhere in this volume. The afternoon session was given over to a roundtable discussion in which the participants were gathered in an atmosphere conducive to audience participation. The roundtable consisted of three parts, each with a discussion leader who outlined the problems to be considered and who invited comment. The entire roundtable was recorded on audio- and videotapes, which were later used by the discussion leaders to produce the following partial transcripts and summaries.

There was broad participation in the discussion. Those who are cited directly in the transcripts are listed below in alphabetical order by surname.

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New Aspects of Avian Origins: Roundtable Report

Lawrence M. Witmer

Introduction

The convening of the fourth International Meeting of the Society of Avian Paleontology and Evolution (SAPE) in the year 1996 is significant in that it coincides with the anniversary of several important dates in the history of the debate on the origin of birds. It marks the seventieth anniversary of the publication of Gerhard Heilmann's (1926) *The Origin of Birds,* a volume that established the orthodox view—that birds descended from basal archosaurs in the Triassic—for the next 50 years. Furthermore, 1996 marks the twentieth anniversary of the publication of John H. Ostrom's (1976) magnum opus "*Archaeopteryx* and the Origin of Birds," a comprehensive treatment arguing cogently that *Archaeopteryx* and all other birds are derived from coelurosaurian theropod dinosaurs. Finally, 1996 is the tenth anniversary of the publication of Jacques A. Gauthier's (1986) paper "Saurischian Monophyly and the Origin of Birds," a widely cited work that, among other things, offered critical cladistic support for the theropod affinities of birds.

This paper is not intended as a review of avian origins but rather as a report of the proceedings of an SAPE roundtable discussion organized by Peter Wellnhofer and moderated by myself on 7 June 1996. I was charged by Dr. Wellnhofer to provide the roundtable discussants with a brief overview of current notions on the origin of birds and then present several topics for discussion. I will first expand somewhat on the overview of current opinion to enable readers with less background to follow the discussion. Then the discussion topics will be introduced and their rationale presented. The relevant portion of the ensuing roundtable discussion will be reported after the introduction of each topic. The discussion itself was fairly wide-ranging, and participants often commented on more than one discussion topic. As a result, I will not present the report in its strict chronological order, but rather in the order of the discussion topics. Participants were aware that the proceedings were being recorded on audio- and videotape for subsequent report in this volume. Quotes herein are direct transcriptions from the audiotape, with trivial editing (e.g., deletion of false starts or midstream rephrasing) to enhance flow. Paraphrasings also derive from the audiotape.

Overview of Current Opinion on the Origin of Birds

As mentioned, it is beyond the scope of this report to review the history of the debate. I previously provided a summary up through the late 1980s (Witmer, 1991), and Feduccia (1996) brought the review up to the present. The modern debate is typically characterized as a trio of hypotheses—the "pseudosuchian thecodont" hypothesis, the crocodylomorph hypothesis, and the theropod hypothesis—with theropod relationships holding sway and the other views decreasing somewhat in popularity. Several important developments have arisen in the intervening years, however, suggesting that opinion has not fully consolidated around the conventional theropod hypothesis. It is not the intent herein to provide a critical evaluation of these hypotheses but rather simply to present a thumbnail sketch and provide references.

1. Relationships with basal archosauriforms ("pseudosuchian thecodonts," to use the old paraphyletic taxonomy) were suggested originally by Broom (1913), and this was the idea popularized by Heilmann (1926). The basic premise is that Triassic archosauriforms, such as *Euparkeria,* are "sufficiently primitive" to have been ancestral to birds (and to other groups of archosaurs, as well). Although revived by Tarsitano and Hecht (1980; see also Tarsitano, 1991), the idea was widely criticized, particularly by supporters of theropod relationships (e.g., Thulborn and Hamley, 1982; Gauthier and Padian, 1985), for being uninformative and for offering few or no supporting synapomorphies. It had seemed that this view had passed away—principally because it was so nonspecific—until a recent paper by Welman (1995), who proposed numerous synapomorphies from the basicranial region of the skull, suggesting that *Euparkeria* is closer to avian ancestry than anyone ever thought.

2. A close relationship with crocodylomorphs, such as the Triassic form *Sphenosuchus,* was originally proposed by Walker (1972) and was supported by L.D. Martin (e.g., 1991) and

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his students (see Witmer, 1991, for references). Supporting characters included aspects of tympanic pneumaticity, cranial circulation, and dental morphology and replacement. The crocodylomorph hypothesis was challenged on a number of counts (Gauthier, 1986) and received an apparent deathblow when Walker (1985) himself apparently recanted. Interestingly, Walker (1990, pers. comm., 1995) essentially recanted his recantation and offered renewed support for avian relationships with crocodylomorphs.

3. Nonarchosauriform archosauromorphs, such as the Triassic form *Megalancosaurus,* have been suggested to be close to avian ancestry by a number of authors (e.g., Hecht and Tarsitano, 1982; Martin, 1983; Tarsitano, 1985, 1991), most forcefully by Feduccia (1996; see also Feduccia and Wild, 1993). In all formulations, the origin of birds is tightly linked with the origin of flight, which is presumed to have required an initial arboreal phase. Therefore, it is reasoned, because avian ancestors must have been small and quadrupedal, bird-like forms, such as *Megalancosaurus* (and also *Longisquama, Cosesaurus,* or *Scleromochlus*), make good models for avian ancestors (Feduccia and Wild, 1993; Feduccia, 1996).

4. Theropod dinosaurs are certainly the group most commonly cited as being involved in the origin of birds (Witmer, 1991; Chiappe, 1995); however, the specific nature of the relationship, that is, which specific group of theropods is closest to birds, remains controversial. Ostrom (1976) proposed that dromaeosaurid coelurosaurs, such as *Deinonychus* and *Velociraptor,* were closest to birds based on a large suite of derived characters, principally from the manus and pelvic limb. This hypothesis received cladistic support from Padian (1982), Gauthier (1986), and Holtz (1994) and is the most commonly encountered version of the theropod hypothesis. Alternate versions differ in which clades are hypothesized to be the sister group of *Archaeopteryx* and/or other birds (see Witmer, 1991, for additional references): coelophysoid ceratosaurians such as *Syntarsus* (Raath, 1985), troodontid coelurosaurs (Currie, 1985, Paul, 1988), bullatosaurs (troodontids+ornithomimosaurs) (Thulborn, 1984), or oviraptorosaurs (Elzanowski, 1995, this volume). Sorting out this confusion will require a comprehensive and up-to-date phylogenetic analysis of Coelurosauria, itself involving a very careful analysis of many characters.

5. Under the broad heading of "the theropod hypothesis" is G.S. Paul's unique formulation (Paul, 1984, 1988). In Paul's view, not only are birds phylogenetically nested within Theropoda, but in fact some forms traditionally interpreted as nonavian theropods are actually secondarily flightless "protobirds." Paul (1988) envisioned a lineage of protobirds beginning in the Jurassic with *Archaeopteryx* and becoming even more bird-like in the Cretaceous, culminating in true birds (Metornithes, to use Chiappe's (1995) terminology). Along the way, the protobird lineage repeatedly gave off clades of terrestrial, secondarily flightless forms, such as Dromaeosauridae, Oviraptorosauria, Ornithomimosauria, and Troodontidae. For support, Paul (1988) cited characters from the skull and pelvic limb and offered additional evidence at the 1996 SAPE conference. This hypothesis has received scant attention in the literature.

6. A related notion is G. Olshevsky's (1994) "Birds Came First" (BCF) theory. This hypothesis suggests that the avian lineage is a truly ancient one. That is, archosaur phylogeny is characterized by a "central line" of persistently arboreal, quadrupedal "dino-birds" that, beginning in the Permian, continuously gave off branches of terrestrial archosaurs throughout the Mesozoic Era. These secondarily terrestrial clades went on to become the various clades of archosauriforms (e.g., proterosuchians, aetosaurs, sauropodomorph dinosaurs, etc.). Forms like *Megalancosaurus* and *Longisquama* are very close to this central line and never left the trees. This central line of arboreal dino-birds became progressively more bird-like through time and thus so did their terrestrial descendants. Theropods are on the central line, and thus, as in Paul's (1988) formulation, the Cretaceous bird-like theropods are deemed secondarily flightless forms. Also like Paul's hypothesis, Olshevsky's ideas have been virtually ignored in the literature.

The Roundtable Discussion

Six major topics were presented at the roundtable for discussion. The topics were chosen to stimulate debate, to examine critical issues, and, it was hoped, to reach agreement on at least some points. Again, each topic is briefly outlined below to set up the ensuing discussion.

1. THE CENTRAL ROLE OF *Archaeopteryx* IN THE DEBATE

The history of the debate on avian origins, almost since its inception, has been focused on *Archaeopteryx.* In fact, *Archaeopteryx* has been the key player in not just the origin of birds but in virtually all ancillary debates: the origin of flight (Rayner, 1988; Feduccia, 1993, 1996; Herzog, 1993), the origin of feathers (Parkes, 1966; Dyck, 1985), the origin of endothermy (Ruben, 1995), and others. An entire conference and the resulting volume (Hecht et al., 1985) were devoted to *Archaeopteryx* and its impact on these questions. Moreover, *Archaeopteryx* has importance beyond its technical significance as a symbol of organic evolution. As Ostrom stated during the roundtable, "the Berlin specimen [of *Archaeopteryx*] is the most valuable and most famous specimen of anything."

Given this historically central role, the discussion topic posed to the roundtable participants was whether or not this role is deserved. The first sentence of Ostrom's (1976:91) paper states, "The question of the origin of birds can be equated with the origin of *Archaeopteryx,*" which clearly articulates the feeling that if we can understand *Archaeopteryx,* we will automatically understand the origin of birds (and the origin of flight, etc.). The avian status of *Archaeopteryx* is an unstated assumption of most analyses. The worry is that if all argumentation is founded on this assumption and this assumption is proved questionable or even invalid, then an enormous amount of scientific discourse will have to be called into question. The stakes are quite high. Interestingly, the history of the debate (Witmer, 1991) shows a persistent minority arguing that *Archaeopteryx* may not be part of the true avian clade but rather is a feathered dinosaur (e.g., Lowe, 1944; Thulborn, 1975, 1984; Thulborn and Hamley, 1982; Barsbold, 1983; Kurzanov, 1985). The intent of raising the issue about the central role of *Archaeopteryx* was to nurture healthy skepticism and to offer the opportunity to reinforce (or dispute) its avian status.

The discussion opened with G.S. Paul taking up the issue he presented in his poster and abstract, namely, that *Archaeopteryx* is skeletally a small dromaeosaurid and perhaps not a true bird at all. Paul began by doubting that *Archaeopteryx* had the features of avian craniofacial kinesis suggested by Elzanowski and Wellnhofer (1996), citing the presence of a complete postorbital bar and a strong maxillary-lacrimal contact, both of which would prevent intracranial mobility; furthermore, Paul questioned their interpretation of bird-like features in the pterygoid. "Years ago when I saw the Eichstätt skull," Paul continued, "I thought that I saw an essentially theropod skull, and I believe that with the newest skull this is, in most ways, truer than I ever thought. ... I don't really see very much evidence of anything avian in the skull of *Archaeopteryx.* Except, as Elzanowski and Wellnhofer [1996] have pointed out, apparently the palatine is fairly avian [in being] triradiate and having a small palatine hook [i.e., the vomeropterygoid or choanal process]. But even there, some theropods get very close to that. For example, dromaeosaurs have virtually no fourth process, the maxillary process of the palatine. Postcranially, again, *Archaeopteryx* is very, very similar to dromaeosaurid theropods. The main features that are avian are in the forelimb and, as pointed out today [in Zhou and Martin's talk], particularly in the wrist and hand—and those are features associated with flight. I hadn't really realized until very recently how extremely similar *Archaeopteryx* is to dromaeosaurs in very detailed characters." To illustrate this point, Paul distributed handouts derived from his poster and led the participants through the intricacies of a single character, the twisting of the paroccipital process, which is very similar in *Archaeopteryx* and dromaeosaurids like *Velociraptor* and is unlike other archosaurs, with perhaps the exception of *Mononykus.* "This is what we're getting down to now," Paul continued. "We're getting down to little tiny details shared by dromaeosaurs and *Archaeopteryx.*"

L.M. Witmer suggested that Paul's comments primarily provided "further evidence, I think many of us would say, supporting that birds are related to small theropods, in particular dromaeosaurs. [But the issue is] not necessarily what are the features that *Archaeopteryx* shares with dromaeosaurs, but what are the features that *Archaeopteryx* shares with other birds?" A. Elzanowski responded that *Archaeopteryx* has "very well-defined avian characters in the skull," such as those associated with the palatine and pterygoid. He went on to enumerate features in *Archaeopteryx* that are unique and that set it apart from dromaeosaurids. For example, the pterygoid of *Archaeopteryx* is "so different from a typical theropod or dromaeosaurid pterygoid that we [he and Wellnhofer] had problems, I admit, in identifying what is the left and what is the right element. No one would have any problems of this sort with [theropods given] John Ostrom's excellent documentation of dromaeosaurids.... The [pterygoid] wing that Greg [Paul] wants to see as an ectopterygoid process is certainly not an ectopterygoid process.... The quadrate part of the pterygoid is radically, dramatically different from the dromaeosaurids.... The skull is in many characters dramatically different from any known theropod.... The nasal cavity has very peculiar structures that are very difficult to compare with anything known so far. The pterygoid has an absolutely peculiar longitudinal division which is very hard to interpret and to compare with anything else." Elzanowski argued that molecular systematics provides insight into the importance of weighing characters, such that "characters like bending of the paroccipital process are simply not comparable, and can never outweigh a radical, dramatic difference in, for example, the palatine bone, which is definitely avian in *Archaeopteryx* and is clearly theropodan in dromaeosaurids." Furthermore, he suggested that the presence of an avian palatine reflects significant transformation of the skull and evolution of an avian kinetic apparatus.

J.H. Ostrom argued passionately for the significance of the specimens of *Archaeopteryx,* yet he also noted that "the magnitude of Earth's history is enormous. With a handful of specimens, you think you're going to draw conclusions about who evolved from whom?" In a similar vein, K.C. Parkes offered, "With *Archaeopteryx* we have a snapshot—a snapshot of a brief moment in time.... A hell of a lot of things must have happened between the time of our still arguable ancestral form [and *Archaeopteryx*]. ... We have absolutely no evidence of what happened up to the point of that snapshot in time, which means we have to take *Archaeopteryx* for what we have.... The argument back and forth—is it a bird or not—seems to me almost fruitless because we don't know what came [even] half a million years before *Archaeopteryx.* So that to some extent, all of the conjecture as to where *Archaeopteryx* came from is going to be very fruitless until we can find something that's a lot closer to *Archaeopteryx* in time than anything we have now."

The role of *Archaeopteryx* continued to be debated by the participants but as part of other discussion topics, which appear in their appropriate contexts.

2. THE ROLE OF THE CRETACEOUS AVIAN RADIATIONS IN THE DEBATE

Certainly part of the reason *Archaeopteryx* has been so important is that for very many years it had been almost the only relevant Mesozoic bird (*Hesperornis* was too aberrant and *Ichthyornis* was too "modern" to be pertinent). With the numerous new discoveries of Early Cretaceous (perhaps even Late Jurassic) birds in Spain and China, the database has changed dramatically. Because most analyses (e.g., Chiappe, 1995; Sanz et al., 1995) suggest that these birds are more closely related to modern birds than is *Archaeopteryx,* what relevance do these new discoveries hold for the debate on avian origins?

The discussion began with L.M. Chiappe, who suggested that "the role of the Cretaceous avian radiations, in my point of view, is very clear. Without disregarding the data that *Archaeopteryx* provides, I think that we actually don't need *Archaeopteryx* right now, for example, to support the idea that birds are descended from theropod dinosaurs.... We have enormous support from this Cretaceous radiation." Likewise, P.C. Sereno argued for the critical role played by the new discoveries of Cretaceous birds: "Recently, even aside from these possible Late Jurassic–earliest Cretaceous forms, new birds have presented other combinations of characters that include even more advanced avian characters while still retaining things like gastralia and things that we've never seen in bird-like creatures before."

Some participants saw the Cretaceous avian radiations as helping to refine and redefine the role that *Archaeopteryx* plays in the debate. For example, Elzanowski suggested that "barely anything points so much to the central role of *Archaeopteryx*—its central position in [the] evolution of birds—than this record of *Sinornis* and *Confuciusornis.* [*Sinornis* is] perfectly intermediate between *Archaeopteryx* and more modern birds.... So, if let's say *Sinornis* is intermediate between modern birds and *Archaeopteryx,* therefore, by purely logical reasoning, *Archaeopteryx* has to be central to the evolution of birds in morphological terms." For Sereno, the combination of *Archaeopteryx* and the Early Cretaceous birds presents "really a nice phylogenetic situation. I think for a cladist to look at *Archaeopteryx,* it additionally presents a strong argument for the origin of birds because it has so few autapomorphies. When you put it up on a cladogram, you try to see what are the characters that are unique to itself and to help to map its phylogenetic information. There are so few that we almost want to call it a metataxon (something that you can't actually link the specimens together by [apomorphic] features). I think that's the important thing, to reiterate what Luis [Chiappe] is saying, that we've got confirmatory evidence from other animals." G.S. Paul responded that "it is very possible that morphologically *Archaeopteryx* basically is a theropod dinosaur with wings.... It is very possible that *Archaeopteryx* maybe was allied with dromaeosaurs or was a completely independent development from birds. On the other hand, what Paul [Sereno] just said is also true—it's so primitive that it could be at the base of the bird radiation.... In a way, we really don't know whether *Archaeopteryx* has a central role or not—we do not have the information yet."

3. THE THEROPOD HYPOTHESIS AND THE "TIME PROBLEM"

Although the theropod hypothesis has been the most popular one for more than twenty years, it has always faced what may be regarded as "the time problem" (Witmer, 1995; see also Feduccia, 1996), namely, the most bird-like of the nonavian theropods (e.g., dromaeosaurids, troodontids, oviraptorosaurs) are younger in age than *Archaeopteryx.* If the conventional hypothesis is correct, then birds and nonavian coelurosaurs diverged in at least the Jurassic. Where, for example, are the Jurassic dromaeosaurs? How disturbed should we be by this discordance in the fossil record? Does it severely damage the theropod hypothesis, as has been suggested (Tarsitano, 1991; Feduccia, 1994, 1996)?

The discussion of this topic was limited. Sereno, who has studied the temporal ranges of theropod clades in conjunction with the pattern of phylogenetic branching, acknowledged that "there is a time discordance between *Archaeopteryx* and its nearest sister group. But when you look at the overall phylogeny of theropods, there are many time discordances—but also many missing lineages with much greater length than that actually. For example, if we look at the origin of coelurosaurs, we now have radiometrically dated allosaur-like animals for the Lower Jurassic. We know that there was a coelurosaur lineage at the base of that radiation for which we have no evidence for the Jurassic, essentially until the Late Jurassic. So, we're missing maybe 20–30 million years of early coelurosaur evolution before we get to the point where we were talking about *Archaeopteryx* and these other things. So, it's not that unusual. It seems that small theropods in general are your worst case extreme for taphonomists, because you don't have the option usually of lake beds or near-shore marine sedimentary localities, but neither do you have the size that will often carry you through in a fluvial environment. So, you fall in-between the cracks in a very poor record."

4. THE SIGNIFICANCE OF *Protoavis* FOR THE DEBATE

From the time of its discovery, *Archaeopteryx* was regarded as both the oldest and the most primitive bird. Reports of Triassic avian remains from Texas (Chatterjee, 1987, 1991, 1995, this volume) would appear to challenge one or both of these claims. According to Chatterjee's (1991) cladogram (see also Kurochkin, 1995), *Protoavis* is closer to the modern radiation than is *Archaeopteryx.* In other words, *Archaeopteryx* would remain the basal member of Aves, but not the oldest. Thus, what is the significance—even relevance—of *Protoavis* for the debate on avian origins? Obviously it would make the time problem of topic three, above, much worse, telescoping much of theropod cladogenesis into the Norian or even Carnian. Otherwise, *Protoavis* might behave phylogenetically much like the components of the Cretaceous avian radiation (topic two, above).

The discussion began with S. Chatterjee, who saw the time problem as less of an issue, suggesting that "we're caught up in a stratophenetic approach.... We are very content with *Archaeopteryx*—this is the primitive one. You can derive anything from it. When the new evidence comes, look at it. Look at the bones. I think what it tells us is that, like mammals, there was a very bush-like radiation of birds." Chatterjee argued that the real significance of *Protoavis* resides in its prospects for establishing a skeletal definition of birds: "Once you define it, then there is no problem. For *Archaeopteryx* or for birds it is really a circular argument: we are defining on feathers. Do we define mammals on hair? No.... We need some practical, tangible evidence preserved in the fossils so that we can call it 'bird.' Once you define it, then you can see whether *Archaeopteryx* falls under the definition or not.... The time has come: we have to give the osteological definition of birds. For that matter, I think *Protoavis* really has a much, much better chance. You can define birds on the basis of the quadrate. You can define birds on the basis of the cheek region.... If you can document that the orbit and the two temporal openings are confluent, it *is* a bird."

Sereno stated that the significance of *Protoavis* cannot be adequately assessed until the professional community takes a serious approach to the fossils: "It seems that most people ignore *Protoavis,* and I think that this is a sad situation. I think there's a lot of very different opinions about what *Protoavis* is, and some of these have been aired. [But] if we're going to move on the significance of *Protoavis,* it probably would be in having some type of a consortium with the fossil material, with people actually commenting on what they think it is in a serious-science forum."

5. THE ORIGIN OF BIRDS VERSUS THE ORIGIN OF FLIGHT

In some formulations (Tarsitano, 1991; Feduccia, 1993, 1996; Feduccia and Wild, 1993), the origin of flight and the origin of birds are inextricably united: flight "from the ground up" with the theropod hypothesis and flight "from the trees down" with more basal archosaurs. The protocol appears to be to develop a concept of the hypothetical proavis based on one's notion of the origin of flight and then survey the animal kingdom for a match; that is, the functional inference precedes the phylogenetic inference. The intent of this topic is not to examine the origin of flight, but rather to discuss the necessity of coupling these two issues. In other words, what is the relationship of phylogenetic inference to functional inference?

The discussion began with Elzanowski, who proposed, "the strict coupling of theropod/'from-the-ground-up' and alternative-hypotheses/'from-the-trees-down' is not really warranted. I think that the discussion of the taxonomic origin of birds should be decoupled from the mechanics—the evolutionary mechanism—of the origin of flight. As all of us probably agree, we really don't know, in a strict sense, the ancestor of birds—we can't agree which are the closest theropod relatives of birds. We have no idea [of their] size or what those ancestors looked like. We know that they certainly were smaller than basically all the dinosaurs we have fossils of." Elzanowski argued that, as observed in mammals, small theropod dinosaurs would have had much more "flexible ankles" than large dinosaurs. This is "a known generalization.... There is no reason to question that there were arboreal or slightly arboreal theropods that would just climb on the tree or run on the tree trunk and [then] just jump and glide from the tree trunk."

Chiappe agreed that the two should be decoupled, saying, "The kind of data that we have is completely different. For the origin of birds, [it] is exclusively phylogenetic. We have a lot of data. We have fossils we can measure, look at, and examine. The origin of flight is a totally different question—a very interesting one, but the kind of data that we have is certainly ten times more speculative.... First, we should come up with an idea, a notion, about the origin of birds,... and then try to see how we can explain the origin of flight within the framework of that particular idea." Sereno likewise argued "that the two are very separate, because when you start looking at the problem phylogenetically, only some of the characters that are linking these animals together into an evolutionary sequence actually are related to flight. Some of the most interesting things are the characters that were co-opted but were not evolved for flight in the first place. We have the extraordinary opportunity, with the great functional work that's being done and a series of fossils, to go at this functional transformation like we cannot in the case of bats and pterosaurs. We can actually tease apart the functional sequence, but all of the characters are not related to that functional sequence, so the two are pretty separate."

P. Wellnhofer provided some important cautionary remarks about, again, over-reliance on *Archaeopteryx,* commenting that "we have to be careful in our conclusions. I think it's not so important what lifestyle *Archaeopteryx* as an animal really had. Maybe [it] could even climb or sit on a tree or on a tree branch or something like that. I think what's more important is the general architecture of the skeleton. The lifestyle of *Archaeopteryx* [itself] can be quite different from what we suggest."

6. THE VALIDITY OF "NONSTANDARD" HYPOTHESES

As in probably all areas of human endeavor, science tends to eschew the iconoclastic in favor of familiar things from familiar sources. In the present case, the "nonstandard" views of Paul and Olshevsky seem to be examples of this phenomenon in that they reverse the typical ancestor-descendant relationship, derive from individuals that are outside the "fold" of university and museum professionals, and have not been published in the conventional outlets. As mentioned, these views have been almost totally ignored. Ironically, both views agree with the current orthodoxy that birds and theropods are very closely related and, moreover, present the advantage that the time problem disappears. The intent of this topic is to examine the status of these views in the current debate.

The discussion was limited to a statement by L.D. Martin: "One of the things about this conference that I've found extremely interesting is how many of the papers that were presented today could be taken to support Gregory Paul's so-called 'nonstandard' hypothesis. I would say he's getting so much support that we can view it as a school—'the Paulian

School of Bird Origins.' The only thing I see that it lacks for a confirmation would be the discovery of a Cretaceous dinosaur with enlarged feathers... and I would really think that we would have very strong support for Paul's viewpoint."

Recapitulation and Conclusions

Perhaps the best quote from the roundtable came from S.L. Olson: "There is no hypothesis involving the origin and evolution of birds that's too ridiculous that somebody won't propose it." This sentiment was shared by many of the participants, although—and this is the interesting part—there would not be much agreement as to which hypotheses were the ridiculous ones. The goal of the roundtable was not to establish winners and losers, or to be able to come away with a broad consensus on avian ancestry. The goal was to raise issues, discuss them openly, and establish some common ground, and in this the roundtable was very successful.

The role of *Archaeopteryx* received a rare critical appraisal. There was general agreement that *Archaeopteryx* will continue to merit a crucial role in not only this debate but in all the debates associated with the early radiation of birds. In an important departure from the past, however, *Archaeopteryx* may slowly be heading toward a more appropriate position as only one of a number of important fossil taxa. The rapidly growing number of Early Cretaceous (and perhaps even Late Jurassic) discoveries, some species of which are represented by dozens of complete skeletons with feathers, are tremendously helpful in reducing the weight of inferences that *Archaeopteryx* must bear. Furthermore, these Cretaceous fossils provide important corroborating information with regard to the origin of birds such that *Archaeopteryx* apparently could be dropped from many analyses with little resultant change in the phylogenetic pattern of avian ancestry. Several synapomorphies of *Archaeopteryx* and "true" birds were discussed. Nevertheless, the status of *Archaeopteryx* as a true bird was challenged by other participants, and, given the controversial status of a number of taxa discussed at the conference (e.g., "protobirds," *Mononykus,* oviraptorosaurs, new Malagasy fossils), perhaps it is indeed prudent to exercise caution about all taxa positioned phylogenetically near that transitional nexus. For many participants, it is likely that the roundtable ultimately did little to diminish either the avian status or the importance of *Archaeopteryx*. For others, the phylogenetic position of at least *Archaeopteryx* remains somewhat more uncertain. As for myself, I continue to regard *Archaeopteryx* as the basal member of Aves, while at the same time recognizing that I have been wrong before.

As mentioned above, the recent discoveries of indisputable Cretaceous birds were widely seen as contributing very important new data for the origin of birds. They confirm findings previously based solely on *Archaeopteryx* and provide new insights as well. The time problem facing the theropod hypothesis was discussed, and it was pointed out that the fossil record is rife with similar (and even worse) time discordances and that a stratophenetic approach is inappropriate. Perhaps the broadest level of agreement was that the functional issue of the origin of flight needs to be clearly separated from the phylogenetic issue of the origin of birds, although the discussion perhaps was hampered by the absence of several of the chief proponents of the linkage of these issues. Nevertheless, several participants voiced strong opinions that the issue of phylogenetic origin logically and methodologically precedes the exploration of models on the origin of flight. There was little focused discussion on what we should do with nonstandard hypotheses such as those of Paul and Olshevsky, although it was clear that Paul's ideas received an open hearing with perceptions ranging from receptive to skeptical.

In general, there was virtually no discussion of any hypotheses other than the theropod hypothesis, which received strong support from several participants. This situation probably genuinely reflects the broad acceptance that this notion has, but it probably also reflects the fact that several key proponents of alternative views were not in attendance, whereas most of the theropod principals were present. There was only passing discussion of the alternate versions of the theropod hypothesis with the only notable outcome being the survival (even thriving) of Paul's protobird hypothesis.

Finally, it is worth reporting that the roundtable was remarkably noncontentious. Participants listened patiently to the views of others, offered their responses with often amiable good humor, and generally seemed receptive to different ideas. That is not to say that strong views were not expressed, but only suggests that the tenor of the debate has moderated and moved onto a more professional and thoughtful level.

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Early Avian Evolution: Roundtable Report

Luis M. Chiappe

Introduction

Few areas of vertebrate paleontology have advanced more over the last few years than that of the early evolution of birds. Recent findings of primitive, non-neornithine birds have been so numerous that we have more than doubled the number of valid taxa described between 1861, when the first early bird, *Archaeopteryx lithographica* von Meyer, was reported, and 1990. Thus, to address the plethora of new ideas and discussions that all these new findings have triggered, in the single hour of roundtable discussion that I had been assigned to moderate, was a daunting, if not impossible, task. With this in mind, and after discussing possible topics of debate with other colleagues, I decided to center the discussion on only three topics within this new profusion of evidence.

The aim of this report is not to provide a review of the new data on early bird evolution, nor is it to defend my own views over those of others. Much of the new evidence has already been reviewed, and a variety of choices are available for the interested reader. Wellnhofer (1994) and Feduccia (1996) provide reviews based on a traditional "evolutionary" approach, whereas I have reviewed the new data from a strict cladistic perspective (Chiappe, 1995a).

Discussion Topics

Before going into the actual debate at the roundtable, it would be helpful to provide a general overview of the three topics that were discussed.

1. PHYLOGENETIC RELATIONSHIPS AND SIGNIFICANCE OF *Mononykus.—Mononykus olecranus* was first reported by A. Perle, M. Norell, L. Chiappe, and J. Clark on the basis of a partial specimen from the Late Cretaceous Nemegt Formation of southern Mongolia (Perle et al., 1993). This flightless, turkey-sized animal, with short, stout forelimbs instead of wings, was regarded as phylogenetically closer to modern birds than is *Archaeopteryx,* and it was thus interpreted as a bird (Perle et al., 1993, 1994; Norell et al., 1993; Chiappe, 1995a; Chiappe et al., 1996a). Placement of the bizarre *Mononykus* within birds raised significant debate. Opponents expressed their views both in scientific journals and books (e.g., Patterson, 1993; Ostrom, 1994; Wellnhofer, 1994; Martin, 1995a; Zhou, 1995a; Feduccia, 1996) and in popular magazines and newspapers (e.g., Feduccia, 1994; Martin and Rinaldi, 1994; see also Norell et al., 1993; Chiappe et al., 1995, 1996, 1997, for responses to these criticisms), but with the exception of L. Martin, who regarded *Mononykus* as a bizarre ornithomimid (Martin and Rinaldi, 1994; Martin, 1995a), critics of the avian hypothesis have not proposed an alternative, specific hypothesis of relationships. Moreover, proponents of the avian relationship of *Mononykus* found additional support for their views in enlarged cladistic analyses (Chiappe et al., 1996; Forster et al., 1996a) that include data on new specimens (some preserving nearly complete skulls) from the Mongolian Djadokhta-like beds of Ukhaa Tolgod (Dashzeveg et al., 1995) and from close relatives of *Mononykus* found in southern South America (Novas, 1996). In addition, this hypothesis received support from the work done by colleagues performing independent cladistic analyses (e.g., Chatterjee, 1995; Novas, 1996).

Another topic of discussion surrounding *Mononykus* concerns its life style, namely, whether its short, robust forelimbs were used for digging (e.g., Ostrom, 1994; Zhou, 1995a) or for other activities (Norell et al., 1993; Chiappe, 1995b). Although this appears to be a more trivial issue, it has been used as an argument against the hypothesis of avian relationships. For example, Z. Zhou interpreted several of the characters used to support the placement of *Mononykus* within birds as the result of digging adaptations (Zhou, 1995a), concluding that a digging animal cannot be a bird.

2. THE AGE OF *Confuciusornis.*—For more than a century, and with the only exception being a "feather" of controversial origin (see Bock, 1986), *Archaeopteryx lithographica* stood alone as the oldest and only known Jurassic bird (*Protoavis* is left outside this discussion because its avian nature still needs to be confirmed; see Ostrom, 1987, 1996; Chiappe, 1995a). In 1995, L. Hou, Z. Zhou, L. Martin, and A. Feduccia reported on a Chinese bird, *Confuciusornis sanctus,* from lacustrine deposits of the Yixian Formation in the northwestern Liaoning Prov-

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ince (Hou, Zhou, Martin et al., 1995; see also Hou, Zhou, Gu et al., 1995; Hou et al., 1996). Although these authors pointed out that the chronology of the Yixian Formation was far from being settled, their paper was entitled "A Beaked Bird from the Jurassic of China," and thus *Archaeopteryx's* "new partner" was heralded as such by the press. Doubtless, in combining a modern-looking, toothless snout with short wings bearing massive, large claws, *Confuciusornis* is of extreme relevance. Yet whether it compares in age with *Archaeopteryx* or not is an issue that still needs to be analyzed, especially now that new radiometric dates have placed the Yixian Formation in the Early Cretaceous, with dates of roughly 121 million years (Smith et al., 1995, 1996).

3. THE PHYLOGENETIC POSITION OF THE ENANTIORNITHES AND THE MONOPHYLY OF "SAURIURAE."—Many of the new early fossils show a number of derived features that were first reported in an array of mostly disarticulated elements from the Late Cretaceous of Argentina, which C. Walker named Enantiornithes (Walker, 1981). The new cohort of fossils has shown not only that the Enantiornithes are true birds (confirming the perceptiveness of Walker's early observations), but that they formed a large and diverse clade of Mesozoic fliers as well.

In his original paper, Walker (1981) regarded the Enantiornithes as phylogenetically intermediate between *Archaeopteryx* and modern birds. In 1983, L. Martin proposed a basal avian dichotomy leading to modern birds on the one hand, and to *Archaeopteryx* and the Enantiornithes on the other (Martin, 1983). Martin's characters in support of the close relationship of *Archaeopteryx* and the Enantiornithes, a group for which he rescued Haeckel's term "Sauriurae," ranged from being regarded as "not one" (Steadman, 1983:342), to "cannot be shown to exist" (Olson, 1985:94), to "either plesiomorphic or uncertain" (Chiappe, 1995b:60). At the same time, the nonmonophyletic status of the Sauriurae has been broadly disregarded in numerous cladistic analyses (e.g., Cracraft, 1986; Chiappe, 1991, 1995b, 1996; Sanz and Buscalioni, 1992; Chiappe and Calvo, 1994; Sanz et al., 1995, 1996; Forster et al., 1996a). Yet in recent years, Martin's hypothesis has been renewed with the addition of more characters and defenders (e.g., Hou, Zhou, Martin et al., 1995; Kurochkin, 1995; Martin, 1995b; Zhou, 1995b; Feduccia, 1996; Hou et al., 1996). What does not seem to emerge from the discussions of these authors is the realization of the fact that an enormous amount of convergence (and its corollaries) has to be explained for the hypothesis of the monophyly of the Sauriurae to be seriously entertained (see below).

The Roundtable Discussion

THE PHYLOGENETIC POSITION OF *Mononykus*.—The debate was opened by L. Martin asking A. Elzanowski "whether *Mononykus* can be embedded somewhere in the same scheme where we have *Oviraptor* and ornithomimids." At one of the regular presentations of the Symposium on Mesozoic Birds that morning, Elzanowski had presented a cladogram, based on cranial data, supporting the idea that *Oviraptor* was closer to modern birds than is *Archaeopteryx*. In other words, *Oviraptor* was regarded as a flightless bird. In responding to Martin, Elzanowski posited that *Mononykus* "would be on an earlier branch than *Archaeopteryx*," but added, "I would easily agree that *Mononykus* is closer to birds than a typical theropod... [yet] I cannot provide evidence in support of *Mononykus* [having] been related to birds." Martin then asked, "Do you think it [*Mononykus*] is related to *Oviraptor?*" Elzanowski disregarded that alternative, saying he could not think of any potential synapomorphy between *Mononykus* and *Oviraptor*. Martin asked, "Do you think [*Mononykus*] is a more advanced bird than *Oviraptor?*" Elzanowski replied, "I don't think so."

This initial exchange between Martin and Elzanowski was followed by J. Ostrom who, with intense democratic spirit, inquired, "How many people here believe *Mononykus* is a bird, and why?" The almost palpable hesitation of the audience was broken by L. Witmer who, after acknowledging that he had reviewed some of the papers defending the hypothesis of avian relationships (and had seen the material as well), asserted that "they [A. Perle, L. Chiappe, M. Norell, and J. Clark] have argued appropriately with the data they have. ... I think they have scored the specimens honestly and put them into their analysis, and they [the specimens] fell out between *Archaeopteryx* and modern birds." Put another way, Witmer was taking up the issue that part of the disagreement, as L. Chiappe put it, "is more related to methodological issues."

The atmosphere of hesitation evolved into one of critical, scientific evaluation of the available data when P. Sereno surmised that there could be "crucial data from the skull of the excellent specimens, and perhaps that would be the decisive data." Chiappe then projected the slides of two new, nearly complete skulls of *Mononykus* from Ukhaa Tolgod (collected in 1994 and 1995, and still unpublished), pointing out that "the jugal bar is rod-like... there is not even a slightly ascending process for its contact to the postorbital [bone]... [yet] there is a postorbital like in *Archaeopteryx*." The audience followed up with numerous questions about specific anatomical features. P. Bühler inquired about the relationships of the two heads of the quadrate to other bones, which articulated with both the braincase and the squamosal, and was puzzled by the fact that the external nares open at the tip of the snout, saying, "It looks like a kiwi." S. Chatterjee asked about the shape of the orbital process of the quadrate, which is broad as in other basal birds (e.g., *Archaeopteryx*, Enantiornithes, *Patagopteryx*) and, as Chiappe remarked, "not a pointy, typical ornithurine quadrate." Elzanowski and S. Olson followed with questions about the condition of the dentition, to which Chiappe responded, "there are teeth in the mandible and those are set in a groove... their crowns are not serrated... they look quite like those of birds. ... [There] may be a few teeth [in the maxilla], but those would be in the very anterior tip." P. Wellnhofer commented that "*Archaeopteryx's* teeth are not serrated, but they have a sharp edge that runs to the tip," and he asked Chiappe, "can you see anything like this in *Mononykus?*" Chiappe agreed that in *Mononykus,* as in *Archaeopteryx,* "there is a carina going throughout the edge." Martin, however, disagreed with this, and showed slides of the teeth of both the Aktien-Verein and London *Archaeopteryx* specimens, pointing out that "the base of the [tooth] of *Archaeopteryx* is as broad as or broader than the crown itself. ... This is the antithesis of what we see in *Mononykus.* ... *Mononykus'* teeth are identical to the teeth of *Pelecanimimus* [see Pérez-Moreno et al., 1994], the Spanish Lower Cretaceous ornithomimid." Although Martin was correct in that the dentition of *Pelecanimimus* is very bird-like, with teeth lacking serrations, his remarks on the teeth of *Archaeopteryx* satisfied neither Elzanowski, who pointed out that "most of the other teeth [of *Archaeopteryx*] don't show any indication of expansion of the roots," nor *Archaeopteryx* expert Wellnhofer, who concurred with Elzanowski's viewpoint.

The issue of the life style of *Mononykus* was not discussed, although after noting that its hyoids were very well developed, Olson pointed out, "so this [*Mononykus*] is a termite eater." This was an interesting observation because it matches the suggestion made by Norell et al. (1993) that *Mononykus* may have used its forelimbs to tear apart insect nests, and it also coincides with ideas suggesting digging activities for the forelimbs of this animal, although not implying that it was fossorial.

Sereno wondered about the "other related material from Argentina" and its implications for the phylogenetic placement of *Mononykus.* Chiappe stated that "there are some relatives of *Mononykus* in the Upper Cretaceous of Argentina [see Novas, 1996],... [but] those are more primitive forms,... and these new findings have demonstrated that some of the characters [used by Perle et al., 1993] are independently derived between *Mononykus* and more advanced birds,... but even including those taxa, the results are exactly the same" (see Chiappe et al., 1996; Novas, 1996). Chiappe remarked that "[this] is the way we can set this issue, finding new primitive members of this very weird and peculiar lineage,... [but] unfortunately the Argentine forms are very incomplete."

AGE OF *Confuciusornis.*—This section of the debate began with Martin discussing the accuracy of the absolute dates provided by Smith et al. (1995; see also Smith et al., 1996), stating, "We were familiar with the results of the Canadian team and received a copy of the dates before publication." Martin then read the dates from the "lower part of the section [Yixian Formation]. ... Remember that there [are] over 1500 meters of section involved ...[the dates are] 119.5, 119.2, 121.8, 123.1, 120.8. ... These are argon-argon [dates], which means that they can have very high precision;... it does not mean they have very [high] accuracy. ... Now I will read to you [the dates of] the top of the section, which is 1500 meters above: 120.2, 121.8, 122.7. ... There is more variability in any of the sets of dates they got than they have for the entire section. ... They may be very accurate dates, but they behave as the dates of one unit, not a section. ... This could happen if you have an intrusive event; in other words, these are all of the same event." Later on he stated that "at least some of these [basalts] are intrusive." It must be said, though, that the 1500 meters of thickness mentioned by Martin are not for the Yixian Formation but for the entire Jehol Group, which includes three additional formations (see Smith et al., 1995:1427), and that glaucony dates from the sedimentary rocks in between these two basalt levels also provided comparable dates (Smith et al., 1995, 1996).

Martin made a valid point by questioning the accuracy of the Ar-Ar dates provided by Smith et al. (1995, 1996), yet that did not address the main point, which was, as Chiappe argued, "what is the data supporting a Late Jurassic age?" Martin continued: "If you look at our paper very carefully, you will see that we said that we felt that the ages were controversial," although this consideration was omitted in the title. Z. Zhou followed up, saying, "I don't know if this is Late Jurassic or Early Cretaceous. ... The reason we thought it could be Late Jurassic is based on absolute dating, potassium-argon [dates] from a different area supposed to be the same formation... not from the same locality." Sereno rightly argued that "having argon-argon dates from basalts, you could not ask for anything more, that's the best. ... I think that great attention should be paid to these basalts."

The discussion branched off to the ages of *Archaeopteryx* and *Sinornis* (Sereno and Rao, 1992) relative to *Confuciusornis.* Wellnhofer stated that "the correlation [between the Solnhofen limestones and the Yixian Formation] may not be possible on biostratigraphic evidence. ... We rely on the absolute dating that can be applied in China but cannot be applied in Solnhofen." Martin agreed and argued that "even if we were sure that we have dated the unit [Yixian Formation] correctly,... we may still not know what the relative age is to *Archaeopteryx.*" There was, however, a clear agreement that *Confuciusornis* is younger than *Archaeopteryx* and, on stratigraphic grounds, is older than *Sinornis.*

THE MONOPHYLY OF "SAURIURAE."—The discussion started with Sereno, who inquired as to whether this hypothesis "has been seriously entertained... after decent skeletons of Enantiornithes [have been found]." The answer is yes. G. Paul cheered up the Sauriurae affair with his statement that "it is possible... though very remote... that dromaeosaurs, *Archaeopteryx,* and troodontids formed a clade with the Enantiornithes, separated from *Mononykus* and other birds. ... A few characters may suggest that that may be true, but it requires massive convergence in the flight apparatus and also in the skull, [which] may be more serious." His remarks on convergence were reiterated by Chiappe, who stated that "[if Sauriurae is going to be accepted,] there are a number of characters, certainly flight correlated, that have to be assumed to have evolved independently twice." Martin expanded on his thesis that the structure of the metatarsals and distal tarsals was essentially different in Enantiornithes and Ornithurae: "In *Archaeopteryx* and the enantiornithine birds, the proximal end of the tarsometatarsus fuses; the distal end, however, does not. This is true even of Maastrichtian Enantiornithes." Chiappe pointed out that this was true "except for *Avisaurus gloriae* [see Varricchio and Chiappe, 1995] from the [Campanian] Two Medicine Formation, which has some fusion [distally]." Martin continued, "In all modern birds without exception, the metatarsal bones begin to fuse distally, and this fusion then moves forward to the proximal articulation. ... Modern birds built an epiphysis; that epiphysis is created by one or more distal tarsals,... but it makes a cap.... The proximal end of metatarsal III is wedge shaped. ... In *Archaeopteryx* and Enantiornithes the metatarsal bones are together in a row, and they don't build a tarsal cap;...you can literally follow the metatarsals up, look at the proximal end of the articulation and see the ending.... So my argument is that indeed *Archaeopteryx* and the enantiornithine birds and modern birds all have fused metatarsal bones, but the way they put together the ontogenetic constraints are different." He then added with emphasis, "I would call this a fundamental way to discover convergence," and continued, "In all modern ornithurine birds...there is a single prominence from the ischium.... In *Archaeopteryx* and all the enantiornithine birds you get a double prominence,...a little square thing that comes up...and then there is a little triangular process behind that. ... The triangular process is homologous with the structure in ornithurine birds, the other structure is not found in ornithurine birds, it is found in all enantiornithines."

After Martin's arguments, E. Kurochkin followed in the same vein, reaffirming the metatarsal thesis as well as arguing that the articulation between the coracoid and scapula is different (reversed) in the Enantiornithes and Ornithurae. Unfortunately, by that point time had run out, and there was no possibility of rebutting on morphological grounds. The interested reader can find a specific analysis of the evidence in support of and against the monophyly of the Sauriurae in Chiappe (1995b), or can simply analyze the character distribution provided in various cladistic analyses (e.g., Cracraft, 1986; Chiappe and Calvo, 1994; Sanz et al., 1995; Chiappe et al., 1996).

The discussion was closed by C. Forster and S. Peters. Forster presented a new, spectacular specimen from the Late Cretaceous of Madagascar that combines an ulna with quill knobs, a long tail, and a typical dromaeosaur/troodontid, sickle-clawed digit II of the foot (see Forster et al., 1996b). Peters showed a specimen of *Confuciusornis* (recently acquired by the Senckenberg Museum in Frankfurt) that proves that the tail of this early bird was not long (as reconstructed by Hou, Zhou, Martin et al., 1995) but short, ending in a pygostyle (see Peters, 1996).

Concluding Remarks

Although the roundtable discussion was played out in an arena of cordiality, it was evident that the different methodological approaches of the participants (cladists versus noncladists) were clouding the debate on the interpretation of the actual evidence.

The methodological miscommunication was more apparent when analyzing the phylogenetic position of *Mononykus* and the monophyletic status of the Sauriurae. A great many of these misunderstandings appeared to center around the criteria used toormulate and test homology and the way in which phylogenetic statements are justified. For example, the hesitation in accepting *Mononykus* as a bird appears to stem more from the fact that its overall aspect (most notably its forelimbs) and its presumed fossorial life style (e.g., Ostrom, 1994; Zhou, 1995a) are at odds with the stereotypical view of a bird than from the critical evaluation of the distribution of anatomical characteristics among taxa. As has been shown by several researchers (e.g., Perle et al., 1993; Chatterjee, 1995; Chiappe et al., 1996; Forster et al., 1996a; Novas, 1996), cladistic analyses that have used complete data sets have concluded that, in contrast to any initial intuition, *Mononykus* is closer to modern birds than is *Archaeopteryx*. Clearly, those arguing against the hypothesis of avian affinities were understanding homology as being validated by overall similarity (both morphological and functional) rather than by congruence of derived characters (see Hall, 1994; Shubin, 1994, for a discussion of the homology concepts). These different approaches to the concept of homology were best portrayed by Martin. After remarking upon the different ontogenetic pathways of *Archaeopteryx* and Enantiornithes (proximal to distal metatarsal fusion) on the one hand and the ornithurine birds on the other (distal to proximal metatarsal fusion) in his defense of the monophyly of the Sauriurae, he emphatically declared, "I would call this a fundamental way to discover convergence." Again, the conflict between different homology concepts ("biological homology" versus "phylogenetic homology"; see Shubin, 1994) becomes apparent. Martin prefers to assume the convergent evolution of the flight apparatus (among other features) in the Sauriurae and Ornithurae over the equally possible alternative of similar developmental constraints evolving independently in *Archaeopteryx* and the Enantiornithes.

We are living in an exceptional period of discovery. With several early birds being described every year, new ideas are being formulated at a pace that exceeds our ability to blend them into a theory structured over this burst of new evidence. Methodological miscommunication stands as another obstacle in this process of assimilation. Clearly, fruitful discussions such as this roundtable, along with a better understanding of the methodological differences between us, can put us one step closer to the most exciting goal of reaching a sound, comprehensive theory of the early evolution of birds.

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The Origin of Bird Flight: Roundtable Report

G.E. Goslow, Jr.

Introduction

Our charge during this roundtable disussion was to consider evidence, old and new, regarding the origin of flight in birds. This topic, one that many of us approach with what seems to be a genetically programmed fascination, had been broached numerous times in both the morning contributed paper session and during the previous two roundtables. To initiate discussion, Sankar Chatterjee kindly agreed to share an illustration summarizing several competing hypotheses regarding the transition from nonflying to flying forms. The ensuing hour focused on four general questions/themes: (1) were theropods capable of climbing; (2) what can claws tell us; (3) what are the limitations of the cursorial theory; and (4) do we have the right perspective?

My first priority in this record is to reproduce the ideas and thoughts expressed by the participants and, whenever possible, to do so by reporting the conversation verbatim (from audio- and videotapes made with the knowledge and cooperation of the participants). In some instances for clarity, I made editorial alterations that are not intended to change the meaning of what was said. I took the liberty to rearrange the order of some comments to group them within logical topical headings.

The Roundtable Discussion

1. WERE THEROPODS CAPABLE OF CLIMBING?—Pondering the various scenarios for the origin of flight, Larry Martin asked Gregory Paul, "Do you think these (theropod) dinosaurs were good climbers or not? I would not have thought so from some of your reconstructions." Paul responded, "A good analogy would be a jaguar. If I were being chased by a jaguar, the jag could catch me on the ground. If I ran to a tree, the jag could climb the tree and catch me there as well. Jags are about the same size as the dromaeosaurs. The jaguar scenario suggests the situation for dromaeosaurs. I think they were very good runners, but I also think they were good climbers, as is true for many of these small theropods. My theory is that there exists a group of small arboreal theropods from the Triassic or perhaps Jurassic that we have not found yet, because they will be very hard to find, that were good climbers. That's where you get *Archaeopteryx* from as well as some of the Cretaceous theropods. I agree with Sankar Chatterjee that overlapping fields of vision and large brains are not necessary for flight because pterosaurs do not have large brains, nor do insects. Nor do pterosaurs have overlapping binocular vision, but primates evolved these things in trees. [There] are other suggestions [that] these theropods were climbing; they had raptorial hands and three-toed feet with reversed hallux trackways, which suggests they could wrap this stucture around. Even *Tyrannosaurus* has a reversed hallux trackway, so yes, I would agree that many of these small theropods could be semiarboreal forms." "So you do not have any problem with these forms being arboreal?" asked Martin. "No, I would agree, the arboreal hypothesis is far superior," responded Paul.

Steve Gatesy raised a cautionary note regarding tracks and a reversed hallux by adding, "We are finding in the Triassic Greenland forms what we are calling a tetradactyl trackway, where we have shown that a 'reversed-hallux' trackway can actually be made by a form without a reversed hallux by plunging the foot into the substrate in a certain way that the toe is not really reversed anatomically. We must be careful about looking for perching feet in Triassic forms from trackways."

Paul expanded further about theropod design by commenting on their shoulder architecture and by referring to a set of reconstructive drawings he provided for the participants. "There have been some misconceptions about the shoulder girdles of dinosaurs. Quadrupedal forms, of course, walked with forelimbs outstretched to the ground and the limbs under the body. In a lot of the theropods, for example *Syntarsus* and other Cretaceous forms, the shoulder glenoid faces laterally so that the humerus can be brought out laterally. When I manipulate the humerus in the shoulder of *Syntarsus,* I can extend the humerus laterally and slightly dorsally as I have illustrated. The range of motion in these theropods is very similar to that of *Archaeopteryx;* there is very little difference. Not until later birds do we see the glenoid facing dorsally so that the wing can be brought higher up over the back. This ability to position the humerus

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laterally and slightly dorsally is evidence for raptorial adaptations early in theropods."

2. WHAT CAN CLAWS TELL US?—Kenneth Parkes precipitated some lively discussion by saying, "I'd like to get back to the previously suggested rejection of trees as a source of gravity. I was very impressed at the *Archaeopteryx* conference with a paper that John will remember, where direct comparisons were made of the claw morphology of bark-climbing and non-bark- climbing organisms—lizards, squirrels, and birds [Yalden, 1985]. He found that the morphology of the claws of the bark-climbing animals differed from the ground-dwelling forms but were exactly like those of *Archaeopteryx.* After that paper, I recall you John [Ostrom] saying, 'I am convinced.' So if *Archaeopteryx* did not go up trees, why did it have tree-climbing claws?" Paul quickly reminded us of the potential flaw in arguments that place *Archaeopteryx* in trees by saying, "There's an alternate hypothesis to trees; there is a scrub cover problem with that hypothesis in that there were no trees. Arid islands with a scrub cover—zero trees."

Paul Bühler, however, pointed out, "The problem is that you can have desert and an inland sea and still have a nice forest not too far away. In the Solenhofen near Eichstätt they have found dragonflies and other aquatic insects. That means that not too far away there must have been a forest present which was denser than the one documented in the fossil record. So you cannot trust the fossil record in the immediate vicinity of the specimen to reflect the ecological situation of the entire surrounding area."

"The claws of *Archaeopteryx* are indeed, in superficial form, similar to something like a woodpecker," added Stefan Peters, "but they are not strong enough. There are claws in animals that do not climb at all; for instance, in some cuckoos you will find claws that look like the claws of climbers. It may be a climber has to have claws similar to this or that, but you cannot reverse this argument. You cannot say, 'If I find an animal with such claws, it must have been a climber.' Lions, for example, have very similar claws but do not climb very often. We published a paper on this; I am not very convinced by this argument. As far as I can see, the claws [of *Archaeopteryx*] are the only argument which remains for the arboreal theory."

3. WHAT ARE THE LIMITATIONS OF THE CURSORIAL THEORY?—After discussing the above evidence, which lends some support for the notion that the flight of birds arose from an arboreal ancestor, discussion of evidence in support of the "cursorial theory" was inevitable. Bühler initially asked, "What benefit can you get by running along and getting away from the earth [using wings]? There is a problem—the most probable situation is that the animal is a prey which is running away. In that case, by jumping from the ground the animal will be giving up its energy transformation system. That means it will be getting slower by gliding or flying, and I cannot think of any possibility where running and jumping into the air will be advantageous."

To address the question about possible advantages of leaving the ground through flight, Ted Goslow asked, "Our work on the organization/action of the supracoracoideus in birds has led us to wonder if just the act of getting out of the way, or of taking off quickly, could be reason enough. Could early flight have been an erratic behavior to evade predation by jumping from the ground or from a tree for that matter? Does this make any sense?" Storrs Olson responded by saying, "In the case of flying from trees where you are going into a different medium and you are experiencing an optical change it does, but not in a terrestrial situation."

"Among students of mammalian locomotion," noted Goslow, "the question of why saltation [richochetal locomotion] as a form of locomotion would ever evolve is often asked. Is not one possible selective advantage thought to be predator evasion through erratic movements?"

Virginia Naples indicated that two points need to be considered in any discussion of leaping and its relationship to early flight. "If an animal is running and intends to jump and remain in the air for any length of time, that animal must get high enough to complete a downstroke, an upstroke, and a second downstroke in order to stay in the air. Secondly, I am concerned that if you are leaping into the air to escape a predator or startle a predator, you are only going to be successful if you also change direction. That requires a tremendous level of [neural] sophistication in terms of maneuverability in flight, and I do not know if these early forms were capable of this."

"We have a modern analog," said Sankar Chatterjee, "the kangaroo. They jump, they leap, but they never use their forelimbs in any way suggesting flight. It doesn't matter how far or how long they jump—they never use their forelimbs."

"This brings up another point," said Storrs Olson, "although I do not know how related the origin of flight is to the evolution of bipedality, but when you have bipedal, terrestrial animals, the tendency is always to shorten the forelimbs. You have kangaroos, kangaroo rats, and humans. When animals come down from the trees and assume a terrestrial position, the forelimbs are shortened. This is directly against everything that happens with birds where you have elongation of the forelimbs."

John Ostrom recalled that in 1974, "I wondered why *Archaeopteryx* had hands that were designed like 'flyswatters.' I thought maybe the primaries could be used as flyswatters [Ostrom, 1974]. Critics at the time did not like this, and I do not blame them; now I have a better understanding of powered flight. A former student, Rick Vazquez, described how the hand of a bird is supinated upon the trochlea carpalis and how this supination acts to streamline the upstroke [Vazquez, 1992]. I illustrated this morning in my presentation how this ability was already present in dromeosaurs, such as *Deinonychus* and *Velociraptor.* There is something in the gene pool which allows for this. In modern birds, for example the starling, a wingbeat cycle occurs in just 70 milliseconds. In these small birds at least, the wing must supinate many times per second and it does so automatically. *Archaeopteryx* had this same ability. It had the big primaries, secondaries, modern wing feathers, and the automatic streamlining mechanism. Modern birds lose traction on the ground, but in air they build up the speed of the upstroke to get to the next power stroke—a dozen times a second. When this transition occurred in birds, I do not know. But *Archaeopteryx* had most of the required arm structures necessary for flight. It has been asked, 'Is gliding required or is it more primitive than powered flight?' This group keeps referring to flight by having the animal get up into the trees and gliding down. Why is the elevation in a tree required when the additional lifting power is available by increasing the rate of the wingbeat cycle? Why are those wrists built that way, to climb trees?"

Martin asked, "John, do you think flight got started essentially straight up from a standing start?" Ostrom responded, "No, it has some forward velocity motion by the hindlegs; *Archaeopteryx* is built as a cursorial biped." For clarification, Martin asked, "Do you think the motion of supination enabled the animal to get started right off or are you saying it gained forward velocity from running? My question is, is the supination motion you are describing adequate in and of itself, or does the animal need velocity from some other means? Are we talking once again about cursorial flight?" Ostrom responded, "Most birds can run and take off too. Many birds walk or run into their flight. They do not all begin from a standing start. I am just saying that the modified carpus was doing something. What?"

In response to this question, Olson asked another: " What was it doing in those dinosaurs? They were not flying." To which Ostrom responded, " I do not know. The theropod/bird plan—they all have that carpal plan. Why?"

Gerald Mayr asked, "What was the selective advantage of the ability to supinate to an intermediate stage, i.e., to a creature with small feathers that was running?"

"Birds are bipeds and have long forelimbs," offered Paul, "and early forms have raptorial hands like *Archaeopteryx.* Among archosaurs, the only other forms like that are theropod dinosaurs [Paul, 1988]. The arms of some giant theropods, such as *Deinocheirus,* were about 10 feet long. As far as the lunate carpal block, every single dinosaur that is a theropod has this lunate and some other avian features in other parts of the skeleton and skull that are not present in *Archaeopteryx.* This suggests or implies, but I cannot prove it, that the reason they do have the system is that they are secondarily flightless. A new troodontid from China, *Sinornithoides,* a photo of which I reproduce on my handout, can fold the manus over the radius and ulna well over 90°; it possesses a very good folding mechanism. *Sinornithoides* was described by Russell and Dong in 1993."

Paul Sereno quickly responded, "I disagree with that interpretation. There are different interpretations of the carpi positions on that specimen; one is slightly higher than 90°, the other is about 90°. The specimen is coming at you a little and the photo is deceiving. I have looked at that specimen, and I found evidence it could not retract the manus any more than *Archaeopteryx.*"

Martin noted, "I was recently asked a question about the long forelimbs of dromeosaurs, so I measured the limbs of a few. When I took off the manus and compared the length of the arm to the hindlimb without the foot, I found that the forelimb bones were all significantly shorter than those of the hindlimb. In primitive animals, one expects to find the forelimbs and hindlimbs to be about equal length. In *Archaeopteryx,* if you take the manus off and compare the arm length to the hindlimb length, you will find the forelimb is considerably longer than the hindlimb. So in comparison to the primitive plesiomorphic condition, even the dromeosaurs are shortened and *Archaeopteryx* is elongated like a bird. It seems evolution is going in different directions."

4. DO WE HAVE THE RIGHT PERSPECTIVE?—Through the course of the roundtable, questions regarding the group's perspective or orientation to the question of the origin of flight were expressed. These thoughtful comments do, of course, force us to evaluate our own perspectives and biases and serve to stimulate new lines of investigation. Paul noted, "There is another issue people have not really looked at. I have done calculations on the number of insects a ground-dwelling, insect-eating bird the size of *Archaeopteryx* would have to consume. Flying insects are a very small package of energy so you have to get a lot of them; something like 100 of them per day if the protobird had an overall energy budget similar to modern Aves. And I did the figures to determine how far it would have to run and so on to catch these things and the numbers did not work out very well. The foraging range, running an average of 10 miles per hour, would be far beyond that observed for animals living today. So there are real serious energetic problems with the historic insect-catching hypothesis. Most insectivores the size of *Archaeopteryx* or bigger tend to feed on insect colonies so they can have a concentrated resource. Most insectivores that feed on individual insects are small so they do not have to eat so many each day. The basic insect catching hypothesis is energetically very implausible." A question was raised, "Where did you get the numbers for the insects?" "I just looked them up," Paul responded. He continued by saying, "There exists no animal today that runs around on the ground and gets the majority of its energy from flying insects. Probably energetically this is not a good idea. Plus you are fighting gravity, and the insects are far superior in agility; it is just not a good idea."

Andrzej Elzanowski cautioned the group early in the discussion to be careful about adaptive arguments that simply support either an arboreal theory or cursorial theory for the origin of flight by saying, "I find something in our approach to be very confusing, and I may be speaking for others as well. Today I have heard much about coupling morphology to environmental factors. For example, there is coupling of arboreal adaptations with gliding to support an arboreal origin of flight. I think this linking of one model of the origin of flight with the peculiar ecological conditions of say, an arboreal habitat, is not really justified. It has been pointed out that there are different elevated objects in the environment, not just trees, that can be used to provide gravitation as a source of acceleration for getting up speed and gaining lift. Therefore, I think this dichotomy, this contradistinction, between an arboreal and terrestrial origin of flight is not really justified. I think we should first discuss the gliding model then the cursorial model. These should be considered separately. Following this, if we come to the conclusion, as many have, like Jeremy Rayner [1991], who knows a lot more about this than I do, that the gliding model is aerodynamically much more likely than the cursorial model, we can evaluate the data to see if this model is supported ecologically. But we should not start out with the arboreal versus the cursorial theory per se; this is simply misleading."

Peter Wellnhofer concluded the afternoon's discussion with a plea for putting *Archaeopteryx* into the perspective of an evolved flyer, not as the first bird. His thoughtful comment was: "The focus of our discussion here has centered around the abilities of *Archaeopteryx*—as an animal could it climb, could it run, how fast, et cetera? I think these issues are not so important. The early origin of flight happened well before, much earlier than the evolution of *Archaeopteryx.* We must not compare the life style of *Archaeopteryx*—i.e., the environment, the habitat. It doesn't matter whether there were trees or not; these are absolutely unimportant in the present context. Even if *Archaeopteryx* could climb trees, it doesn't change the general bauplan of the skeleton of *Archaeopteryx,* which is a bauplan for bipedal running. What is displayed in *Archaeopteryx* is a later adaptation in the direction of climbing flight."

Concluding Remarks

While listening to the various points raised and discussed in this roundtable, one could not help but be reminded of the Eichstätt conference on *Archaeopteryx* held 12 years ago in 1984. Have our opinions about the origin of flight changed since then? If so, in what way? In my estimation, some progress has been made in that the participants seemed not only willing to consider views at odds with their own but were anxious to entertain new information and approaches. I believe many of us are guardedly optimistic about the promise of new insights into the question of the origin of flight in birds, aided by the additional specimens of *Archaeopteryx* unavailable to us 12 years ago and by the recent additions to our database of a series of Cretaceous fossil birds (for a review, see Chiappe, 1995).

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