Ursula B. Göhlich &
Andreas Kroh (Eds)

Paleornithological Research 2013

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SAPE

Proceedings of the 8th International Meeting
of the Society of Avian Paleontology and Evolution

Paleornithological Research 2013

Proceedings of the 8th International Meeting of the
Society of Avian Paleontology and Evolution,
Vienna, 2012

URSULA B. GÖHLICH & ANDREAS KROH (EDS)

Naturhistorisches Museum Wien
2013

Imprint

Publisher: Naturhistorisches Museum Wien

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10 December 2013

ISBN 978-3-902421-82-1

Layout by Andreas Kroh
Cover design by Josef Muhsil
Printed by Holzhausen Druck GmbH

Cover: A skeleton and reconstruction of a Dodo (*Raphus cucullatus* LINNAEUS, 1758), a flightless bird from Mauritius Island, which went extinct in historic times. This skeleton on display in the Natural History Museum of Vienna, is one of few preserved examples of this species. Photograph by Josef Muhsil (Vienna).

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Paleornithological Research 2013: Proceedings of the 8th International Meeting of the Society of Avian Paleontology and Evolution, Vienna, 2012

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Natural History Museum Vienna, Department of Geology & Palaeontology, Vienna, Austria

Dedicated to Cécile Mourer-Chauviré

Table of contents

Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

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Paleornithological Research 2013 — Preface

URSULA B. GÖHLICH & ANDREAS KROH

Naturhistorisches Museum Wien, Vienna, Austria

The "8th International Meeting of the Society of Avian Paleontology and Evolution" took place from 11th to 16th June 2012 at the Natural History Museum Vienna, Austria, and was organised and hosted by Ursula Göhlich (NHMW, Vienna). Fifty-two participants from 19 countries attended the quadrennial meeting and presented 40 oral talks and 10 posters covering a wide range of topics in paleornithology. The abstract and programme volume of the meeting is available as pdf on the SAPE homepage.

The SAPE meeting 2012 and the present proceedings volume are dedicated to Cécile Mourer-Chauviré, in order to honor her outstanding paleornithological contributions and her long-lasting, active commitment for the Society. A special tribute session was performed by the former president Per Ericson (NRM, Stockholm), Ursula Göhlich, and Kenneth Campbell (LACM, Los Angeles), who held a laudation.

Li Ping, Olivier Maridet, and Thomas Neubauer (all NHMW) acted as organisation-assistants during the meeting and Hilde Adamek (NHMW) took care of the coffee breaks. Peter Sziemer (NHMW) kindly acted as guide for an early morning bird watching tour through the Park of the Imperial Schönbrunn Palace and guided one of the tours through the exhibition of the NHMW. Anita Gamauf (NHMW) received several participants of the meeting in the ornithological collection. Martin Riesing (Vienna) co-guided an ornithological excursion to the National Park Lake Neusiedl-Seewinkel and to Marchegg in the National Park March-Zaya-flood plains. Mathias Harzhauser, Director of the Department for Geology and Paleontology, and several colleagues of the department assisted in the organization of the welcome reception.

Christian Köberl, Director General and CEO of the NHMW, and Herbert Kritscher, Vice Director and CFO of the NHMW, are thanked for the possibility to hold the meeting at the Natural History Museum Vienna and for funding of this volume.

The editors gratefully acknowledge the effort by the reviewers Federico Agnolin (Argentina, Buenos Aires), Peter Ballmann (Germany, Cologne), Zbigniew Bocheński (Poland, Kraków), Zlatozar Boev (Bulgaria, Sofia), Walter Boles (Australia, Sydney), David Burney (Kalahao, Hawai), Kenneth Campbell (USA, Los Angeles), Adrian Casinos Pardos (Spain, Barcelona), Luis Chiappe (USA, Los Angeles), Joanne Cooper (United Kingdom, Tring), Pietri, De Vanesa (Germany, Frankfurt), Andrzej Elzanowski (Poland, Warsaw), Růžena Gregorovà (Czechia, Brno), Antoine Louchart (France, Lyon), Gerald Mayr (Germany, Frankfurt), Hanneke J. M. Meijer (USA, Washington), Colin Miskelly, (New Zealand, Wellington), Cécile Mourer-Chauviré (France, Lyon), Jorge Noriega (Argentina, Diamante), Marco Pavia (Italy, Turino), Adam Smith (USA, Durham), Claudia Tambussi (Argentina, Buenos Aires), Alan Tennyson (New Zealand, Wellington), Allison Tumarkin-Deratzian (USA, Philadelphia), Trevor Worthy (Australia, Adelaide), Nikita Zelenkov (Russia, Moscow), Andrei V. Zinoviev (Russia, Tver), and numerous anonymous colleagues.

All articles of this peer-reviewed volume are freely available as pdfs via the NHMW hompepage.

published 10 Dec. 2013

FIGURE 1. Participants of the 8th International Meeting of the Society of Avian Paleontology and Evolution, held 11th–16th June 2012 at the Natural History Museum in Vienna (Photo: A. SCHUMACHER, NHMW)

Participants of the 8th International Meeting of the Society of Avian Paleontology and Evolution, held 11th–16th June 2012 at the Natural History Museum in Vienna

1 ELZANOWSKI Andrzej (Poland, Warsaw)
2 MANEGOLD Albrecht (Germany, Frankfurt)
3 PAVIA Marco (Italy, Turino)
4 SCOFIELD Paul (New Zealand, Christchurch)
5 HUME Julian (United Kingdom, Tring)
6 VAN TUINEN Marcel (USA, Wilmington)
7 COOPER Joanne (United Kingdom, Tring)
8 ZELENKOV Nikita (Russia, Moscow)
9 ATTERHOLT Jessie (USA, Albany)
10 HAARHOFF Philippa (South Africa, Langebaanweg)
11 MICHAILIDIS Dimitrios (Greece, Athens)
12 WALSH Stig (United Kingdom, Edinburgh)
13 TYRBERG Tommy (Sweden, Kimstad)
14 SERRANO-ALARCÓN Francisco J. (Spain)
15 WANG Min (China, Beijing)
16 WATANABE Junya (Japan, Kyoto)
17 CAMPBELL Kenneth (USA, Los Angeles)
18 MARIDET Olivier (Austria, Vienna)
19 TORRES Chris (USA, Wilmington)
20 ZINOVIEV Andrei V. (Russia, Tver)
21 BOCHEŃSKI Zbigniew (Poland, Kraków)
22 WALSH Maureen (USA, Los Angeles)
23 MARJANOVIĆ David (Germany, Berlin)
24 PANDIT Meelyn (USA, Noblesville)
25 WORTHY Jennifer (Australia, Adelaide)
26 WORTHY Trevor (Australia, Adelaide)
27 CHIAPPE Luis (USA, Los Angeles)
28 TENNYSON Alan (New Zealand, Wellington)
29 HU Dongyu (China, Schenyang)
30 O'CONNOR Jingmai (China, Beijing)
31 DE PIETRI, Vanesa (Germany, Frankfurt)
32 CANOVILLE Aurore (South Africa, Cape Town)
33 MEIJER Hanneke J.M. (USA, Washington)
34 MAYR Gerald (Germany, Frankfurt)
35 SMITH Adam (USA, Durham)
36 ERICSON Per (Sweden, Stockholm)
37 KAISER Gary (Canada, Victoria)
38 KESSLER Eugen (Hungary, Szigetszentmiklós)
39 ANGST Delphine (France, Lyon)
40 BUFFETAUT Eric (France, Paris)
41 GÖHLICH Ursula (Austria, Vienna)
42 MOURER-CHAUVIRÉ Cécile (France, Lyon)
43 BOURDON Estelle (France, Paris)
44 NGUYEN Jacqueline (Australia, Sydney)
45 CHINSAMY-TURAN Anusuya (South Africa, Cape Town)
46 LI Ping (Austria, Vienna)
47 SHUTE Elen (Australia, Adelaide).

Registrants not shown:

GAMAUF Anita (Austria, Vienna)
GREGOROVÁ Růžena (Czechia, Brno)
GOEDERT James (USA, Wauna)
SZIEMER Peter (Austria, Vienna)
ZHOU Shuang (China, Beijing)
NEUBAUER Thomas (Austria, Vienna).

Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

Cécile Mourer-Chauviré
Life and works

URSULA B. GÖHLICH

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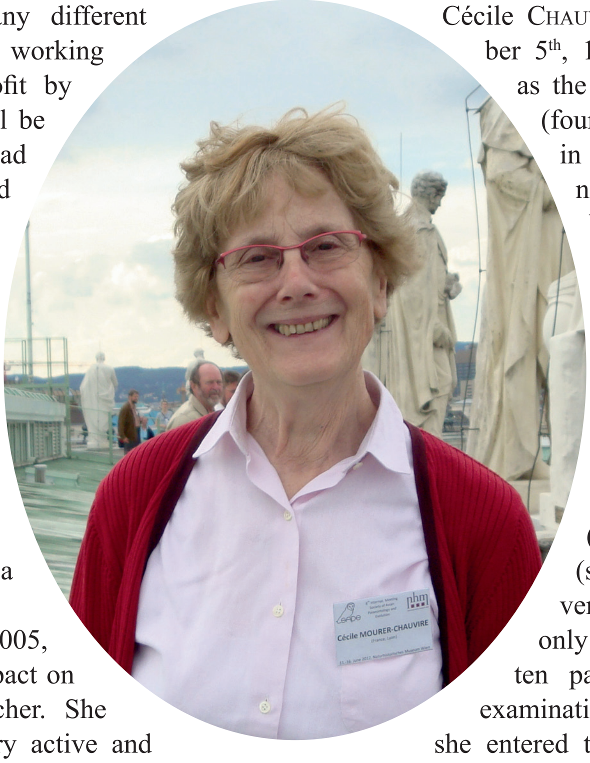
When meeting Cécile Mourer-Chauviré for the first time, one might get the impression that she is a very shy and diffident person. After knowing her a little bit better one will be surprised by her splendid humor as well as her directness and will be fascinated by her outstanding educational background in so many different kinds of topics. When working with her one will profit by her collegiality and will be impressed by her broad paleontological and extraordinary osteological knowledge – and this not only in avian anatomy. And one would wonder how this apparently shy and cautious woman can be combative in professional discussions when disagreeing. She is always good for a surprise.



Cécile retired in 2005, but this had no real impact on her activity as researcher. She remains unfailingly very active and productive, publishing scientific articles, reviewing a vast quantity of manuscripts per month, and participating annually in paleontological as well as archaeological field campaigns.

Cécile can look back to an eventful and highly productive scientific career. She significantly impacted paleornithological research in and outside of Europe for the last 50 years and is in high demand as an expert and favored collaborator for researchers all over the world, but especially for the next generation of paleornithologists.

Cécile Chauviré was born November 5th, 1939 in Lyon (France), as the second of six children (four sisters and 1 brother) in a well-known Lyonnais family, her father being a reputable ophthalmologist.

She went to primary and secondary school in Lyon. The latter was a very strict neighboring school, from which she received the Baccalauréat in 1955 (first part) and in 1956 (second part). After a very hard selection, with only one candidate out of ten passing the competitive examination at the end of the year, she entered the University of Lyon and oriented towards natural sciences with different diplomas in Zoology, Botany and Geology. Since that period she acquired a degree of fame among the students, not only because of her excellent results, but also for her significant

FIGURE 1. A) Roland Mourer and Cécile Mourer-Chauviré in 1967 in their rickety straw hut close to Laang Spean cave (Cambodia) (photo by self-timer), where they had discovered a prehistoric settlement and performed annual archaeological excavations for several years. B) Back again at the Laang Spean cave locality in 2012, Roland (2.f.l.) and Cécile (r) together with Heng Sophady (left) and Hubert Forestier (2.f.r.), the responsible khmer and french researchers, respectively, for the resumed excavations.

repertoire of bawdy songs ("Qu'y a t-il dans le grenier de ton grand-père?" [What's in your grandfather's attic?]) – an unexpected knowledge for a mannerly bachelor girl of that time, as remembered by Marguerite Hugueney, a long-time friend and colleague at Lyon University. However, Cécile explains that she came by the songs honestly while listening to her father sing them in the morning while shaving.

The beginning of Cécile's scientific career did not immediately reveal that she would become one of the most important paleornithologists, as she started with a "thèse de 3ème cycle de Géologie du Quarternaire" on a fauna of large Quarternary mammals from the locality of Châtillon-Saint-Jean, (Drôme, France), that she finished in 1962. Due to this topic she initially acquired a certain fame as a "quarternarist", for which she is still consulted nowadays.

Professor Henri Gauthier, the then director of the laboratory in the University in Lyon, proposed Cécile to be candidate for a position in the CNRS (Centre National de la Recherche Scientifique), with a doctoral thesis subject on Pleistocene birds. At that time almost no one was working on fossil birds in France, and there were not many of them in the rest of Europe either.

Cécile succeeded in securing the CRNS position in 1961 and began her research on fossil birds. She started to gather as many fossil and extant birds as possible in order to create a comparative collection. She visited different collections in France and abroad, and took advantage of the knowledge of Prof. D. Janossy in Budapest (Hungary), one of the few specialists at that time in Europe. Between 1961 and 1964 she was first "Stagiaire", then "Attachée de Recherche au CNRS" at the University of Lyon.

In 1964, Cécile married Roland Mourer, an ethnologist, whom she had met during excavation campaigns during her 3rd cycle thesis. The same year she left with her husband, who was sent to Cambodia for his military service as "coopérant", to the small city of Kompong Chhnang. The sojourn was originally supposed to last one year, for which Cécile had received permission from the CRNS for unpaid leave, but finally they decided to stay longer. She quit her post at the CNRS and in the end remained six years in Cambodia, during which her two sons, Alexis and Ivan, were born. During the first year in Cambodia (1964-1965), Cécile worked as a French teacher at the Lycée Preah Bat Suramarit in Kompong Chhnang. In 1965, she obtained a post as a Professor in Geology at the Université Royale of Phnom Penh where she taught for five years until 1970, when the civil war began in Cambodia.

During their time in Cambodia, Roland Mourer and Cécile went archaeological prospecting in the limestone massifs of the Battambang province, in northwestern Cambodia. Already in 1965, they had discovered a prehistoric settlement in the Laang Spean cave on top of a phnom [mountain, hill] between Battambang and Païlin. They started excavating there and because the location was out of range of any infrastructure, they spent all week there, just the two of them,

FIGURE 2. A) Cécile Mourer-Chauviré in August 1983 working in the office of Prof. Pierce Brodkorb during her second research sojourn in Gainsville at the Zoological Department of the University of Florida and B) in 1981 in the garden of P. Brodkorb (2.f.r.) with her sons Ivan (2.f.r., 12 years old at that time) and Alexis (r., 16 years old at that time), who came to visit Cécile during their school holidays (photo: R. Mourer).

sleeping on straw mats on the ground under a mosquito net and under the stony arches of the partly collapsed cave roof. In the following years and excavation periods, they slept in a tiny rickety straw hut on stilts at the foot of the phnom that local farmers had built for them. One morning Roland and Cécile detected a carnivore's paw print in the dust close to their hut, the size of a plate. A tiger had come along while they were sleeping in their shaky hut. "We never told this story because we did not want people to think we were mad" remembers Cécile. But the presence of a tiger that used to come to drink in a nearby waterhole was confirmed much later by the local people. Forty-four years after they stopped excavating in this cave, Roland and Cécile were invited in 2012 to come back to Cambodia and to visit "their" cave to contemplate new important discoveries that have been made since 2009, when a Khmero-French team had resumed excavations in Laang Spean. They were surprised to see that local people had put a small propitiatory altar in the cave, with small wooden tiger statuettes, where they intended to placate the spirits of the tigers.

In 1970, during vacation back in France, the situation in Cambodia worsened as the Viet Nam War expanded; Cécile decided not to return to Cambodia and instead remained in France with the two children, while her husband Roland spent two more years in Cambodia.

Back again in France, she again succeeded in obtaining a position in the CNRS at the Université Claude Bernard – Lyon 1 in 1971, first as "Attachée" and then until 1984 as "Chargée de Recherche au CNRS". During this period she finished her "Thèse d'Etat" (a long and important diploma that no longer exists) in 1975, which instated her as *the* specialist in fossil birds in France and even in Europe at that time. She followed up with a "Habilitation à diriger des recherches (HDR)" in 1984 and subsequently became "Directeur de Recherche" at the CNRS in 1985 until her retirement in 2005 and has been emeritus "Directeur de Recherche" at the CNRS since then. During all this time and until today (and hopefully for the years to come) she devoted herself to avian research. She was always willing to assist geologist colleagues in identifying fossils they found, she warmly received paleornithologists coming to see her, and took under her wing numerous students and young academics from France and abroad, who came to be trained under her care. I had the pleasure to be among these fortunate individuals. All of us profited from her generosity in sharing her immense paleornithological and paleontological knowledge, by her warm reception and hospitality – among the many reasons she is so popular among a group of younger palaeornithologists such as Gerald Mayr (Frankfurt), Marco Pavia (Torino), Antoine Louchart (Lyon), Estelle Bourdon (Paris), and myself (Vienna). She warmly welcomed me in her lab for a Postdoc sojourn in spite of the fact that a few years earlier I had accidentally dropped a drawer full of fossil holotype bird bones in her office – one of the blackest and most awkward days of my career. But my 15-month postdoc sojourn in Lyon, with Cécile as my host, is one of my highlights and most wonderfully remembered times of my career. PhD students supervised or co-supervised by Cécile Mourer-Chauviré are: Jacques Cheneval, Joëlle Pichon, Philippe Vilette, Christine Lefèvre, and Antoine Louchart.

During her scientific career Cécile herself also took advantage of experience gained abroad. In each of the years 1981 and 1983 she spent six months in the lab of Prof. Pierce Brodkorb at the University of Florida at Gainsville (USA). The latter welcomed her kindly in his house-aviary, which, if you were not afraid of guano accumulation, was an ideal observatory of the life of parrots, budgerigars and allies … in wild conditions. Cécile had started to study the Paleogene birds from the famous Quercy localities in France, but in France the required comparative material of extant bird skeletons was insufficient. The extensive bird collection of Pierce Brodkorb allowed these necessary comparative works. Cécile Mourer-Chauviré and Pierce Brodkorb also collaborated on several studies on fossil birds (Anhingas, Cormorants, Strigiformes) from Olduvai, Tanzania, that he kept in his collection. From 1983 to 1984, Cécile became Adjunct Professor of Zoology at the University of Florida, Gainesville, Florida.

Later, in 1993 and in 1996, she again enjoyed stays of two months and one month respectively at the Smithsonian Institution, in Washington, D.C., where she was warmly welcomed and hosted by Storrs Olson and Helen James.

In 1985, Cécile organized, with the help of Jacques Cheneval, the international meeting "Table ronde internationale du CNRS" under the title "L'évolution des oiseaux d'après le témoignage des fossiles" [evolution of birds based on fossil evidence]. This meeting was held in Lyon-Villeurbanne, from September 18th to 21st, 1985. It was during this meeting that an informal society called the "Society for Avian Paleontology and Evolution" was initiated, and would meet every four years. Cécile was elected Secretary of the SAPE with the task of gathering information and sending a newsletter each year. The first "Information Letter" was sent in September 1987, and from 1987 to 1999, she has taken care of this time-consuming task as the secretary of the SAPE.

Almost annually she participated and still participates in paleontological or archaeological excavations. One of the most outstanding of these was on Réunion Island, where excavations in a swamp, the "Marais de l'Ermitage", were carried out with the aim of finding any evidence of the so-called Réunion White Dodo. Standing in the swamp that was made up of about 80 cm of organic soil, overlying a fossiliferous layer about 40 cm deep, the only way to find the bone remains was to explore the mud in the bottom of the swamp with the fingertips. But after four excavation campaigns, as they kept finding Réunion Ibis bones and no Dodo bones, they finally realized that the Réunion Solitaire, described by early travelers, was not a White Dodo but an Ibis.

Cécile has worked on a wide array of avian groups, periods, and geographic regions. During her entire career she continued to work on Paleogene birds, mainly from the "Phosphorites du Quercy", but also studied Neogene and Quaternary birds. Among the latter, her bibliography indicates a noticeable interest in insular avifaunas from the Balearic Islands, Corsica, Sardinia, Cyprus, La Réunion, and New Caledonia. Antoine Louchart, a former PhD student, points to the fact that she pioneered the revival of the study of extinct birds of the Mascarene Islands, with a special effort to integrate data from concomitantly historical and paleontological archives.

Finally, in most recent years, Cécile studied many African avifaunas from the Paleogene of Algeria, Tunisia, Morocco, and Namibia, and the Miocene to Pliocene of Namibia, Kenya, and Morocco.

Cécile's longtime friend and colleague, Marguerite Hugueney (Lyon), witnessed that, in addition to Cécile's research work, she contributed actively to the life of the lab at the Université Claude Bernard, Lyon 1, taking on a large part of the syndical and administrative responsibilities; she continued managing the lab during very difficult times for her, when a series of great misfortunes entered her life: illness, the death of her younger sister, and, above all, that of her elder son Alexis in 1996, in whose memory she dedicated the species *Ameripodius alexis*. She thrived

FIGURE 3. Cécile Mourer-Chauviré at different occasions. A) on excavation in Céreste (France) in 2004, B) together with Gerald Mayr (Frankfurt, left) and Marco Pavia (Torino, middle) during the SAPE meeting 2012 in Vienna, C) together with Bernard Sigé (Lyon, left) and Evgeny Kurochkin (Moscow, middle) during the field trip of the SAPE meeting 2004 in Quillan, D) during the field trip of the SAPE meeting 2004 in Quillan, E) with Ursula Göhlich (Vienna, left) during the SAPE meeting 2012 in Vienna, and F) with Pippa Haarhoff (Laangebanweg, left), Ursula Göhlich (Vienna, 2nd from right), and Anusuya Chinsamy-Turan (Cape Town, right) during the SAPE meeting 2012 in Vienna.

to overcome all these events by her dedication to all her family (with four grandchildren, including triplets), to her numerous friends, and to her work.

Several colleagues have expressed their respect for Cécile and her work by naming bird-taxa after her. So far eight fossil bird species or genera carry her name: *Aythya chauvirae* Cheneval, 1987, *Cypseloides mourerchauvireae* Mlíkovský, 1989, *Chauvireria* Boev, 1997, *Pica mourerae* Seguí, 2001, *Oligosylphe mourerchauvireae* Mayr & Smith, 2002, *Tyto mourerchauvireae* Pavia, 2004, *Afrocygnus chauvireae* Louchart *et al*., 2005, *Asphaltoglaux* nov. spec. (named after Cecile*)* Campbell & Bochenskí, in press.

In order to honor Cécile Mourer-Chauviré's outstanding paleornithological contribution and her long-lasting, active commitment as co-founder and as secretary for the "Society of Avian Paleontology and Evolution", the "8th international meeting of the SAPE" held in 2012 in Vienna was dedicated to her, including a special tribute-session and a laudatio by Ken Campbell during the meeting. Subsequently, a new fund was also established by the Executive Council of the SAPE, "The Cécile Mourer-Chauviré Travel Grant", a travel fund supporting graduate students and other scholars presenting papers at future SAPE meetings.

And, last but not least, the present proceedings volume is dedicated to you, Cécile, accompanied by the warmest wishes for the years to come and with the hope that you enjoy this volume, that you continue enriching paleontological research with your contributions, and with the sincerest hope that there will be many additional occasions for colleagues and me to collaborate with you.

With admiration and sympathy,
Ursula

Acknowledgements

Cécile Mourer-Chauviré (Université Claude Bernard, Lyon) kindly provided all necessary data of her biography, a complete bibliography and some photos. I am grateful to Marguerite Hugueney (Université Claude Bernard, Lyon), who shared her memories with me and contributed several additional data and anecdotes. Antoine Louchart (École Normal Supérieur, Lyon) also provided some information. I thank Gerald Mayr (Forschungsinstitut Senckenberg Frankfurt a. M.) for delivering the list of bird taxa named after Cécile and him and Marguerite Hugueney for comments on this manuscript, Anusuya Chinsamy-Turan (Cape Town) for the photoraph shown in Fig. 3F, and Rich Mooi (California Academy of Sciences, San Francisco) for improving the English.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

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ZooBank LSID: urn:lsid:zoobank.org:pub:86C1ED2B-C74F-4624-BE10-1CA9D0EF0C77

A new taxon of stem group Galliformes and the earliest record for stem group Cuculidae from the Eocene of Djebel Chambi, Tunisia

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Abstract — A distal tarsometatarsus and a fragment of carpometacarpus of a small galliform, the size of a recent quail, have been found in the late Early or early Middle Eocene of Chambi, in Tunisia. Although a large number of stem group representatives of Galliformes are known from the Eocene of the Northern Hemisphere, and one from the middle Eocene of Namibia, the taxon from Chambi differs from them and is described as a new genus and species. A very small zygodactyl form, represented by three distal tarsometatarsi, is also present in the same locality. This form, described as a new genus and species, is a stem group representative of the recent family Cuculidae. It shows a plesiomorphic morphology compared to the recent members of the Cuculidae, but it is, however, more derived than the younger genus *Eocuculus*. It is the earliest Cuculidae known so far.

Key words: fossil bird, Eocene, Djebel Chambi, Tunisia, Galliformes, Cuculiformes

Introduction

The Djebel Chambi in central Tunisia is famous for having yielded a rich faunal and floral assemblage (Hartenberger *et al.* 2001), including indeterminate amphibians and squamates, a peradectid marsupial, and several eutherians among which there are chiropterans, a putative erinaceomorph, a strepsirhine primate, a zegdoumyid rodent, a stem macroscelidid, a hyracoid, and charophytes. Hartenberger *et al.* (2001) have proposed that the fauna is Early Eocene in age, roughly contemporaneous with that of the Glib Zegdou in Algeria. However, the age of Chambi and Glib Zegdou faunas have long remained a matter of discussion, and current data rather indicate a late Early or early Middle Eocene age, unfortunately without more precision (e. g. Adaci *et al.* 2007; Seiffert 2010). Recent fieldwork on the Djebel Chambi has led us to the recovery of a new vertebrate locality (Chambi 2) in the same lacustrine limestone strata as the former site (here named Chambi 1) (Fig. 1). Careful acid etching of the fossiliferous limestone from Chambi 1 and 2 has yielded numerous vertebrate elements, among them the few avian elements described here.

Material and methods

The anatomical terminology follows Baumel & Witmer (1993), and when necessary Howard (1929). The fossil material is deposited in the

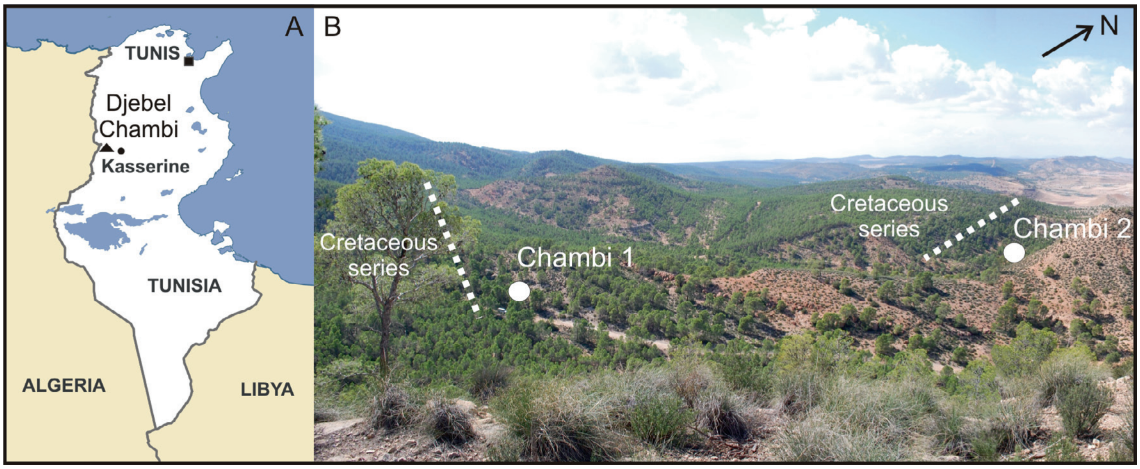


FIGURE 1. A, Map of Tunisia, showing the location of the Djebel Chambi Mountain near the city of Kasserine. **B**, Northern flank of the Djebel Chambi outcrops, section to the northwest, showing the sites of Chambi 1 and Chambi 2. The site of Chambi 1 corresponds to the locality of Harten-berger *et al.* (2001, and references therein) (see also Ravel *et al.* 2013, and Benoit *et al.* 2013); Chambi 2 was discovered in 2009. Only 650 m separate the two sites; both are located in the same stratigraphic position and have delivered the same mammalian assemblage, indicating a late Early or early Middle Eocene age.

collection of the "*Office National des Mines de Tunis*", Tunisia. Acronyms: UCBL, Université Claude Bernard, Lyon 1, France; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington D.C.; ONM, Office National des Mines de Tunis, Tunisia.

Systematic Paleontology

Aves Linnaeus, 1758
Order Galliformes Temminck, 1820
Family incertae sedis

***Chambiortyx* nov. gen.**

Type species: *Chambiortyx cristata* nov. spec.

Diagnosis: Distal part of tarsometatarsus with trochlea met. IV extending distally to about the half of trochlea met. III; trochlea met. II slightly shorter than trochlea met. IV; presence of a ridge starting from trochlea met. II and extending proximally along the boundary between the dorsal and medial sides of the shaft; foramen vasculare distale wide and not situated at the end of an outer extensor groove; trochlea met. II slightly plantarly deflected; trochleae arranged along a weakly arched curve in distal view.

Derivatio nominis: Chambi, from Djebel Chambi in Tunisia, and *ortyx*, Greek word for a quail.

***Chambiortyx cristata* nov. spec.**
(Figs 2A–D)

Holotype: CB1-548 left tarsometatarsus, distal part.

Paratype: CB1-549 left carpometacarpus, fragment of distal part.

Type locality: Chambi 1, Central Tunisia, Kasserine district.

Age: Late Early or early Middle Eocene.

Diagnosis: As for the genus.

Derivatio nominis: *cristata*, Latin word indicating the presence of a characteristic ridge.

Measurements: Tarsometatarsus, holotype: Length as preserved, 7.6 mm; width of shaft at the level of the break, 2.8 mm; depth of shaft at the same level, 1.3 mm; distal width, 5.3 mm; distal depth, 3.7 mm; width of tr. met. III, 2.0 mm; depth of tr. met. III, 2.3 mm. Carpometacarpus, paratype: Length as preserved, 8.7 mm; dorsoventral dimension of the major metacarpal at the level of the break, 1.8 mm; craniocaudal dimensions of the major metacarpal at the same level, 1.5 mm; dorsoventral dimension of the distal end, 1.8 mm; craniocaudal dimension of the distal end, 3.1 mm.

Description and comparisons — Tarsometatarsus (Fig. 2A–C)

On the distal part of the tarsometatarsus, trochlea met. III is relatively elongate, trochlea met. IV extends distally to a little less than the middle of trochlea met. III, and trochlea met. II is slightly shorter than trochlea met. IV. Trochlea met. II is slightly plantarly displaced. The foramen vasculare distale is wide and elongate. There is no visible outer extensor groove (Howard 1929). Proximally compared to the opening of the distal foramen, the dorsal face of the shaft is practically flat. On the medial side of the shaft, proximally compared to trochlea met. II, there is a longitudinal ridge situated at the boundary between the cranial and the medial faces.

On the plantar side, although the lateral rim of trochlea met. III is incomplete; it is possible to see that it extends proximally farther than the medial rim. The fossa supratrochlearis plantaris is relatively narrow and shallow. It is included between two ridges, a medial one which prolongs the proximal part of trochlea met. II, and a lateral one which prolongs the proximal part of trochlea met. IV. The wings of both trochleae met. II and IV are incompletely preserved. The distal vascular foramen is widely open and is situated close to the incisura intertrochlearis lateralis. The canalis interosseus distalis is absent.

In distal view the trochleae are arranged along a weakly arched curve. The medial rim of trochlea met. III advances more dorsally than the lateral rim, and the lateral rim advances more plantarly than the medial rim.

Comparisons with recent galliforms

Chambiortyx differs from the Phasianidae because in this family trochlea met. II is always more strongly plantarly displaced. In the Megapodiidae, the trochleae are more splayed. In *Megapodius* there are also two ridges on the plantar face, but it differs in the morphology of trochlea met. II, which appears very globular on the dorsal face and extends farther distally than trochlea met. IV. In the Cracidae, trochlea met. II extends slightly farther distally than trochlea met. IV; the distal part of the tarsometatarsus is rather flat; on the plantar face, the two ridges, medial and lateral, are present but they are only slightly raised; the fossa supratrochlearis plantaris is wide and shallow; the distal vascular foramen is small.

Comparisons with fossil galliforms

1. Austinornis — Clarke (2004) has attributed to the "Pan-Galliformes" a distal tarsometatarsus from the upper Cretaceous of Texas, which was the holotype of the species *Ichthyornis lentus* (Marsh, 1877), and created for it the new generic name *Austinornis.* This genus differs from *Chambiortyx* in having the distal vascular foramen very small and situated at the distal extremity of a distinct outer extensor groove. In *Austinornis* a "slight groove extends proximally from the juncture of metatarsals II and III on the dorsal surface of the tarsometatarsus" (Clarke 2004: p. 53). This groove is very short in *Chambiortyx* and its characteristic ridge, on the cranial face, medial side, proximal to trochlea met. II, does not exist in *Austinornis*. Lastly, in *Austinornis*, trochlea met. II is more plantarly displaced than in *Chambiortyx*.

2. Gallinuloididae — The Gallinuloididae were present in the early Eocene of North America and in the Early and Middle Eocene of Europe, with the two genera *Gallinuloides* and *Paraortygoides* (Mayr 2009). In both genera the metatarsal trochleae are splayed (Mayr & Weidig 2004). The relative extension of trochleae met. II and IV compared to trochlea met. III is different in these two genera (Mayr 2000a; Weidig 2010). In *Paraortygoides messelensis* Mayr, 2000a the crista medianoplantaris forks and splits into two ridges which reach the wings of trochleae met. II and IV (see Mayr 2000a: fig. 9A). In *Chambiortyx* the two ridges do not meet. In *Paraortygoides radagasti* Dyke & Gulas, 2002 from the Early Eocene of England, there are two ridges on the plantar face, and these two ridges do not meet. These two ridges are not situated on the medial and lateral borders of the bone, but closer to its median axis. There is no ridge on the dorsal surface, proximal to trochlea met. II, and this trochlea is more plantarly displaced than in *Chambiortyx* (see Dyke & Gulas 2002: fig. 2B and F; Mayr 2009: fig. 6.4i).

3. Paraortygidae — The Paraortygidae are known in the Late Eocene and Early Oligocene of the Phosphorites du Quercy, France, and in the

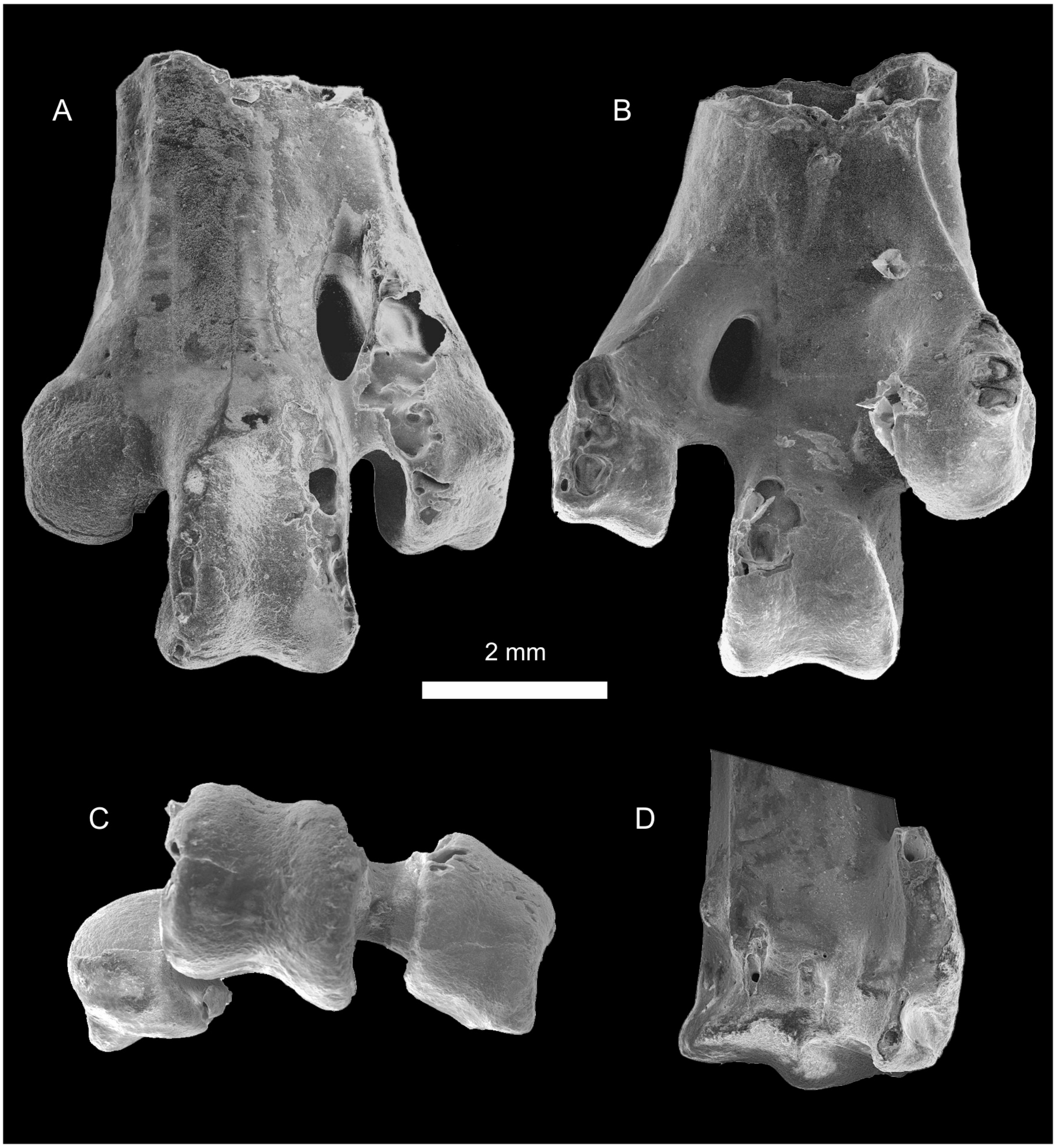


FIGURE 2. *Chambiortyx cristata* nov. gen., nov. spec. from the late Early or early Middle Eocene of the locality Chambi 1, Central Tunisia. **A–C**, holotype, left tarsometatarsus (CB1-548), distal part, dorsal view (A), plantar view (B), distal view (C). **D**, paratype, left carpometacarpus (CB1-549), fragment of distal part, dorsal view.

Early Oligocene of Germany (Mourer-Chauviré 1992a; Fischer 1990, 2003). They were also probably present in the Late Eocene and Early Oligocene of the United States (Mayr 2009). In this family trochlea met. IV extends farther distally than in *Chambiortyx* and reaches the middle of trochlea met. III. Trochlea met. II is more plantarly displaced and, in distal view, the trochleae are more dorsoplantarly elongate. The dorsal surface is more convex, the outer extensor groove is well marked, and there is no ridge proximal to trochlea met. II. However, on the plantar face, there are two well marked ridges, one starting from trochlea met. II, and the other one starting from trochlea met. IV. These two ridges run in proximal direction along the plantar surface and do not meet.

4. Quercymegapodiidae — The Quercymegapodiidae are known in the Middle Eocene (Le

Bretou, see MOURER-CHAUVIRÉ *et al.* 2011a) and the Late Eocene of the Phosphorites du Quercy, France, with the genus *Quercymegapodius*, in the Late Oligocene or Early Miocene of Brazil, and finally in the Early Miocene of France, with the genus *Ameripodius* (ALVARENGA 1988, 1995; MOURER-CHAUVIRÉ 1992a, 2000). In *Quercymegapodius* trochleae met. II and IV are splayed, and trochlea met. II is very globular on the dorsal face. The relative length of the trochleae is the same as in *Chambiortyx*, but in *Quercymegapodius* the dorsal surface of the shaft, proximal of the trochleae, is convex, and the outer extensor groove is deeper. The ridge starting from trochlea met. II and situated on the boundary between the dorsal and medial faces is absent. On the plantar face the ridge starting from trochlea met. IV is present but not the ridge starting from trochlea met. II. In *Ameripodius* the trochleae are less splayed than in *Quercymegapodius*, and, in distal view, trochleae met. II and IV are more plantarly displaced than in *Chambiortyx*. In *Ameripodius*, the dorsal face, proximally to the trochleae, is strongly convex, thus differing from *Chambiortyx*, but the ridge starting from trochlea met. II is present. This ridge first follows the boundary between the dorsal and medial faces, then continues on the dorsal face and finally merges into the surface of the shaft. On the plantar face, the ridge starting from trochlea met. II is absent in *Ameripodius*, while it is present in *Chambiortyx*.

5. Megapodiidae — A small fossil megapode, *Ngawupodius minya* has been described from the Late Oligocene of Australia (BOLES & IVISON 1999). It differs from *Chambiortyx* by the following characteristics: trochleae met. more splayed; trochleae met. II and IV with the same distal extension; trochlea met. II more plantarly displaced; on the dorsal face no ridge starting from trochlea met. II.

6. Namaortyx — Namaortyx sperrgebietensis, from the Middle Eocene, (probably early Lutetian, about 47 to 49 million years ago), of Namibia, was described as the first Paleogene galliform from Africa (MOURER-CHAUVIRÉ *et al.* 2011a). It is only known by a tarsometatarsus and has been left in family incertae sedis. *Namaortyx* resembles *Chambiortyx* by the relative length of the trochleae, and their arrangement along a weakly arched curve in distal view. But it differs from it by its wide and flattened shaft, the strongly developed wing of trochlea met. IV, and the oblique orientation of the trochlea met. III in distal view, compared to the dorsal surface of the shaft. On the dorsal face there is no ridge starting from trochlea met. II.

7. Nanortyx — Nanortyx inexpectatus WEIGEL, 1963, from the Late Eocene (Chadronian) of Canada, is a very small form, described from a distal part of a tarsometatarsus and an omal part of a coracoid. This genus has been attributed to the family Odontophoridae, which itself is part of the family Phasianidae s. l. (MAYR 2009: fig. 6.1). Although it is poorly preserved, the coracoid is more similar to the Quercymegapodiidae than to the Phasianidae (MOURER-CHAUVIRÉ 1992a). These elements, as well as a distal tarsometatarsus from the early Oligocene of Colorado, assigned to the Odontophorinae by TORDOFF (1951), are insufficient to confirm the presence of crown group Galliformes in the Eocene (MAYR 2009). The *Nanortyx* tarsometatarsus differs from that of *Chambiortyx* in the following characteristics: trochlea met. IV extending farther distally; trochlea met. II extending less far distally and more plantarly deflected; presence of an outer extensor groove; on the dorsal surface, absence of the ridge starting from trochlea met. II.

8. Comparisons with members of other orders — The genus *Coturnipes* HARRISON & WALKER, 1977 was described from a distal tarsometatarsus from the Early Eocene of the London Clay, England. This taxon was classified in the order Galliformes, and included in the family Phasianidae, but MAYR (2006a) suggested that this genus could be closely related to the genus *Masillaraptor* from the Middle Eocene of Messel, which is classified in the "Falconiformes". The genus *Coturnipes* has also been reported from the Early Eocene of the Nanjemoy Formation, Virginia, United States (OLSON 1999), and from the Middle Eocene of the Geiseltal, Germany (MAYR 2002a). The different distal parts of tarsometatarsus of *Coturnipes* differ from that of *Chambiortyx* by the following characteristics: large and elongate distal vascular foramen; well defined outer extensor groove; dorsal surface of the shaft proximal to the trochleae convex; trochlea met. II strongly plantarly deflected (see Harrison & Walker 1977: pl. 8, fig. T); no ridge starting from trochlea met. II; trochleae met. III and IV dorsoplantarly elongate in distal view. Among the buttonquails (Order Charadriiformes, family Turnicidae), the tarsometatarsus of the genus *Turnix* looks very similar to that of the galliforms. On the plantar face of this tarsometatarsus, the lateral rim of trochlea met. III extends farther proximally than the medial rim. This feature is present in all Galliformes, but occurs also in other avian clades (Mayr 2000a; Ksepka 2009). Compared to *Chambiortyx* the tarsometatarsus of *Turnix* differs in the following characteristics: articular parts of the trochleae shorter; dorsal surface of the shaft, proximally to the trochleae, strongly convex; distal vascular foramen situated at the end of a well marked outer extensor groove; trochlea met. II more plantarly displaced (Bock & McEvey 1969). In the genus *Ortyxelos*, the tarsometatarsus is more different from that of galliforms, because its trochleae are strongly splayed, and the articular parts of these trochleae are very short. Fossil Turnicidae have been described from the Middle Eocene of Germany, and from the Early Oligocene of France and Germany, but when this detail can be observed, trochlea met. II is more plantarly deflected than in *Chambiortyx* (Mayr 2000b; Mayr & Knopf 2007).

Description and comparisons — Carpometacarpus (Fig. 2D)

The fragment of left carpometacarpus only includes the os metacarpale majus. It shows a well marked sulcus tendineus on the dorsal face. At the level of the symphysis metacarpalis distalis, on the dorsal face, there is a small groove for the tendon of the musculus interosseus distalis, but no osseous arch. This osseous arch is present in *Paraortygoides messelensis* (Mayr 2000a: text-fig. 5E). The morphology of this fragment resembles that observed in Gallinuloididae, Paraortygidae, and Quercymegapodiidae by the fact that the articular surface for the minor digit of the wing is situated at the same level as the articular surface for the major digit, while in the recent galliforms this articular surface extends farther distally. The size of this fragment of bone is compatible with the size of the tarsometatarsus.

Remarks concerning the size of *Chambiortyx cristata* nov. spec.

The size of *Chambiortyx cristata* nov. spec. (distal width of tarsometatarsus 5.3 mm) is slightly larger than that of the recent Common Quail (*Coturnix coturnix*, distal width 4.8 mm) and larger than that of the smallest recent galliform, the Asian Blue Quail (*Coturnix chinensis*, distal width 3.7–3.8 mm). Among the stem group fossil galliforms the smallest known so far are *Quercymegapodius* cf. *brodkorbi*, Middle Eocene (distal width 3.8 mm) (Mourer-Chauviré 1992a; Mourer-Chauviré *et al.* 2011), and *Nanortyx inexpectatus*, Late Eocene (distal width 5.2 mm) (Weigel 1963). The other fossil stem galliforms are larger: *Austinornis lentus*, Late Cretaceous, distal width ca. 10 mm (Clarke 2004); *Gallinuloides wyomingensis*, Early Eocene, distal width ca. 7.1 mm (Weidig 2000); *Paraortygoides messelensis*, Middle Eocene, distal width ca. 7.6 mm (Mayr 2000a); *Namaortyx sperrgebietensis*, Middle Eocene, distal width 11.9 mm (Mourer-Chauviré *et al.* 2011); *Quercymegapodius depereti*, Late Eocene, distal width 5.5–6.1 mm (Mourer-Chauviré 1992a).

Order Cuculiformes Wagler, 1830
Family Cuculidae Leach, 1820

Chambicuculus nov. gen.

Type species: *Chambicuculus pusillus* nov. spec.

Diagnosis: Small zygodactyl form with a well-developed trochlea accessoria, separated from the condylus of trochlea metatarsi IV by a clearly expressed notch. Distal extension of trochlea metatarsi IV situated more proximally than the incisura intertrochlearis lateralis. Presence of a canalis interosseus distalis dorsally roofed by an osseous bridge. Trochlea accessoria oriented plantarly and slightly medially.

Derivatio nominis: Chambi from the Djebel Chambi, in Tunisia, and *cuculus*, Latin word for a cuckoo.

Chambicuculus pusillus **nov. spec.**
(Figs 3, 4, 5B, 6A–B)

Holotype: CB1-541, distal part of right tarsometatarsus, well preserved with the exception of a slight erosion of the crest which is situated on the dorsal side of trochlea met. IV.

Paratypes: CB2-1001, distal part of right tarsometatarsus, incompletely preserved on its dorsal side. Trochlea met. IV is incomplete but the sehnenhalter is well preserved and separated from the condylus by a well expressed notch. On this specimen the sehnenhalter is slightly more bulging than on the Chambi 1 specimen. CB1–560, fragment of a left tarsometatarsus, distal part, with only trochlea met. III preserved.

Type locality: Chambi 1, Central Tunisia, Kasserine district.

Age: Late Early or early Middle Eocene.

Diagnosis: As for the genus.

Derivatio nominis: *pusillus*, Latin word meaning tiny, quite small.

Measurements: Holotype, CB1-541, distal width, 2.66 mm; distal depth, 1.60 mm. Paratype, CB2-1001, distal width, 2.70 mm; distal depth, 1.72 mm. Paratype CB1-560, width of trochlea met. III, 1.00 mm.

Description and comparisons

This taxon is characterized by the presence of a sehnenhalter, or trochlea accessoria, on trochlea met. IV, with the shape of a wing-like flange. Trochleae met. II and IV are slightly plantarly deflected. Trochlea met. III shows two parallel rims, which are clearly separated by a deep groove, well visible in distal view. The lateral rim is slightly wider and more developed plantarly than the medial rim. This trochlea is proximodistally short. It bears a protuberance at the base of its lateral face, on the dorsal side. Trochlea met. II is shorter than trochlea met. III and it reaches distally about the mid-length of this trochlea. It is globular on its dorsal face and shows a slight groove and a short wing on its plantar face. Trochlea met. IV is much shorter and its distal end is situated slightly proximally compared to the incisura intertrochlearis. It shows a prominent crest on its dorsal side. On its lateral side it shows a bulging condyle and a thin and elongate sehnenhalter, plantarly and slightly medially oriented. The condyle is separated from the sehnenhalter by a distinct notch. The articular surface of the condyle does not extend on the sehnenhalter. The distal vascular foramen is very large. This is not clearly visible on Fig. 3A, because the orientation of this canal is oblique and medioplantarly directed, but when it is slightly more medially oriented, this foramen appears extremely wide (Fig. 6A). On the dorsal face this opening is not located at the distal extremity of an outer extensor groove. The canalis interosseus distalis is present. On its dorsal side, a thin osseous bridge joins the lateral side of trochlea met. III to the medial side of trochlea met. IV. Trochlea met. IV also shows a groove on its dorsal face, medial side, clearly visible in distal view. This groove is delimited medially by a protuberance which is situated at the base of trochlea met. III, and laterally by the dorsal crest of trochlea met. IV. On the plantar face, there is a short and shallow groove, proximodistally oriented, which ends in the medial intertrochlear notch. The fossa metatarsi I is situated entirely on the plantar face. It is elongate and made up of two lobes.

Comparison with crown group Cuculidae (Cuckoos) (Figs 5A, 6C–D): The morphological characteristics of the recent Cuculidae have been indicated by Hugues (2000). On the distal part of the tarsometatarsus the first characteristic is the distal end of trochlea met. IV which is situated proximally compared to the incisura intertrochlearis lateralis. In some genera, which are relatively primitive, such as *Geococcyx*, *Morococcyx*, or *Centropus*, the distal end of trochlea met. IV is slightly proximal, whereas in some more derived genera, such as *Cuculus*, *Clamator*, or *Coccyzus*, this distal end is highly proximal compared to the incisura intertrochlearis lateralis. The other characteristic is the presence of a prominent sehnenhalter that is strongly inflected medially.

In the recent Cuculidae the canalis interosseus distalis is absent. At its location there is a groove on the dorsal face, between trochleae met. III and IV and the osseous strip (which bridged the canalis interosseus distalis) has disappeared. The condyle of trochlea met. IV is very globular on its lateral side and dorsoplantarly elongate. As in the

Chambi specimens, there is a sharp crest on the dorsal face of trochlea met. IV and a protuberance at the base of trochlea met. III on its lateral side. *Chambicuculus* differs from the recent Cuculidae by the following features: Presence of a canalis interosseus distalis; condylus of trochlea met. IV less globular and less dorsoplantarly elongate; sehnenhalter more distally and plantarly oriented, while it is more medially oriented in the recent Cuculidae (see also Steinbacher 1935: p. 253, figs 15–16; Mayr 1998: p. 48, fig. 28G; Mayr 2002b: p. 724, fig. 7C); more pronounced notch between the condylus and the sehnenhalter.

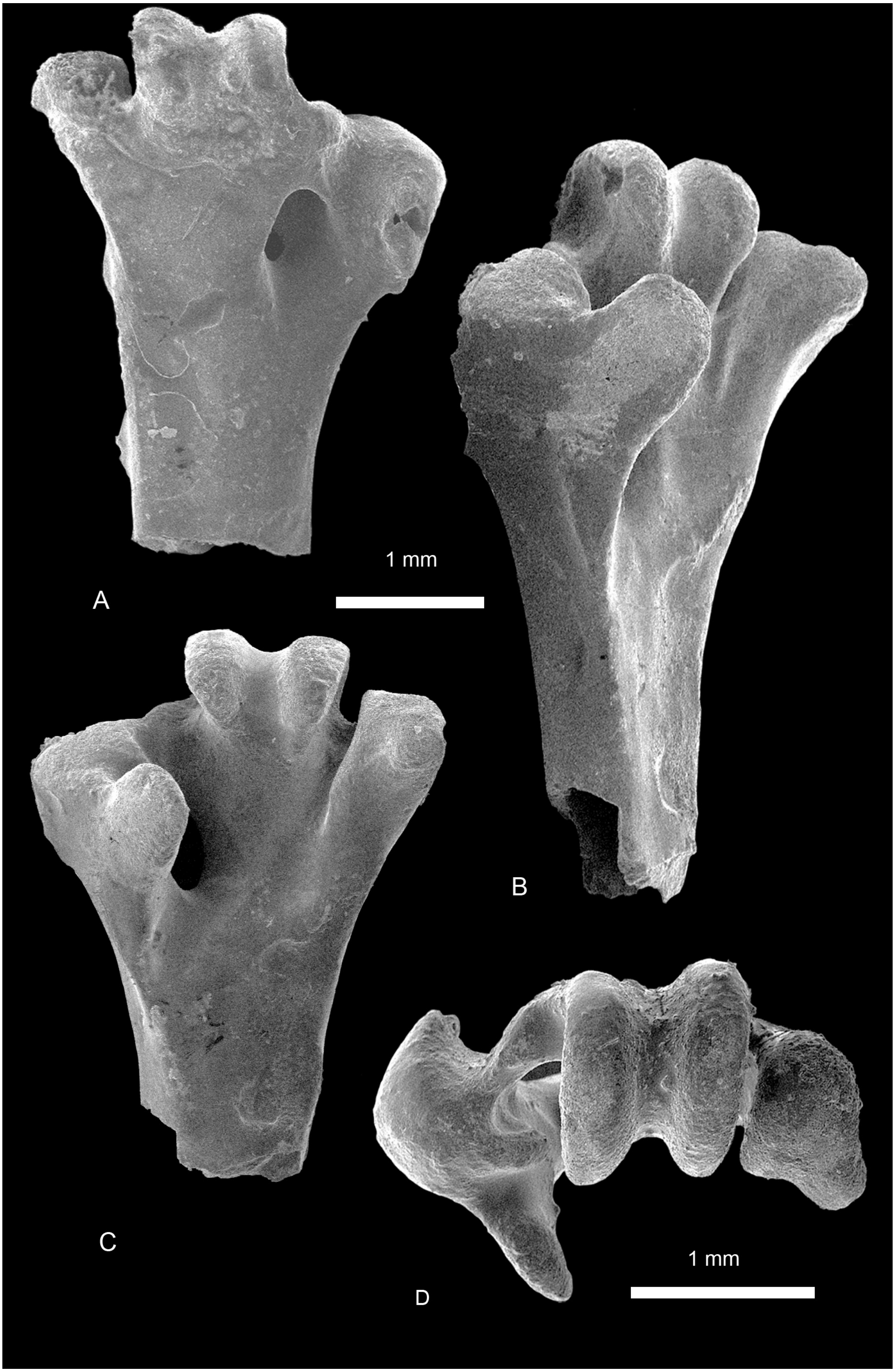
Comparisons with stem group Cuculidae and related forms: The genus *Eocuculus* Chandler, 1999, has been attributed to the Cuculidae by Chandler (1999) and to ?Cuculidae by Mayr (2006b). It is known by the species *Eocuculus cherpinae*, described from the Late Eocene of the United States (Chandler 1999), and by *Eocuculus* cf. *cherpinae*, from the Early Oligocene of France (Mayr 2006b). The skeleton exhibits some derived characteristics of the recent Cuculidae but the tarsometatarsus is quite different. The foot is not zygodactyl but probably only semizygodactyl, and does not show a large trochlea accessoria. Both trochleae met. II and IV are more plantarly deflected than in *Chambicuculus*. Unlike *Chambicuculus*, the foramen vasculare distale is small, the canalis interosseus distalis is absent, and it is replaced by a narrow sulcus. In addition trochlea met. IV extends as far distally as trochlea met. II and it reaches the mid-section of trochlea met. III. Lastly trochlea met. II is wider than in *Chambicuculus*. The presence of a well-developed sehnenhalter in *Chambicuculus* indicates that this new taxon is different from the genus *Eocuculus*.

The other fossil Cuculidae are *Neococcyx mccorquodalei* and *Cursoricoccyx geraldinae*. *Neococcyx mccorquodalei* has been described from the Late Eocene (Mayr 2009) of Canada (Weigel 1963). It is represented by a distal part of humerus, which presents morphological characteristics close to those found in the recent genus *Coccyzus*. *Cursoricoccyx geraldinae* has been described from the Early Miocene of Colorado (Martin & Mengel 1984). It is known by several bone fragments which do not include any distal tarsometatarsus. This fossil is close to the recent genus *Geococcyx* and is placed in the subfamily Neomorphinae.

Pumiliornis tessellatus Mayr, 1999, is a very tiny form, known by two skeletons from the Middle Eocene of Messel, Germany (Mayr 1999; 2008). Its morphological characteristics remind those of *Eocuculus* (Mayr 2008). In *Pumiliornis* trochlea met. IV is oriented plantarly but it lacks a well-developed trochlea accessoria. In addition trochleae met. II and IV have approximately the same length. Both end distally at the level of the base of trochlea met. III. Trochlea met. III shows a well-developed trochlear furrow on its dorsal side and there is a depression at its base. The foramen vasculare distale is small. According to Mayr (2008: p. 251), its foot was at least semizygodactyl. These characteristics are different from those of *Chambicuculus.*

In the Early Eocene of Fur Fm., in Denmark, the partial skeleton of *Morsoravis sedilis* Bertelli *et al.*, 2010, attributed to the Charadriimorphae, has been described. A phylogenetic analysis performed by Mayr (2011) has shown the existence of close relationships between the Early and Middle Eocene *Morsoravis* and *Pumiliornis*, and the Late Eocene and Early Oligocene *Eocuculus*. In *Pumiliornis* and *Morsoravis,* the short and wide proximal phalanx of the fourth toe suggests the presence of a semizygodactyl foot. In *Morsoravis* trochleae met. II and IV have almost the same distal extension and reach about the middle of trochlea met. III (see Bertelli *et al.* 2010: fig. 12), and the foramen vasculare distale is very small. In addition trochlea met. II bears a distinct groove on its medial surface, and it is bilobed (see Mayr 2011: fig. 7D). These morphological characteristics are different from those of *Chambicuculus*.

FIGURE 3. *Chambicuculus pusillus* nov. gen., nov. spec. from the late Early or early Middle Eocene of the locality Chambi 1, Central Tunisia. **A** and **D**, holotype, right tarsometatarsus (CB1-541), dorsal view (A), distal view (D). **B** and **C**, paratype, right tarsometatarsus (CB2-1001), lateral view, slightly plantarly oriented (B), plantar view (C). For figure B the bone has been slightly obliquely oriented in the scanning electron microscope, which gives to the bone a more elongated shape than in figure C. ➤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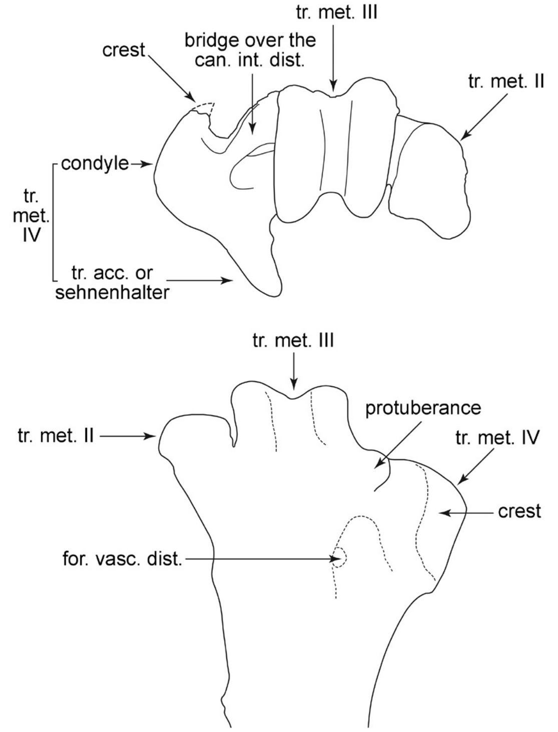

FIGURE 4. Diagrams showing the different parts of the distal tarsometatarsus in *Chambicuculus pusillus* nov. gen., nov. spec., in distal (above) and plantar (below) views. Abbreviations: Bridge over the can. int. dist.: bridge over the canalis interosseus distalis; For. vasc. dist.: foramen vasculare distale; tr. met. II-IV, trochlea metatarsi II-IV; tr. acc. or sehnenhalter: trochlea accessoria or sehnenhalter.

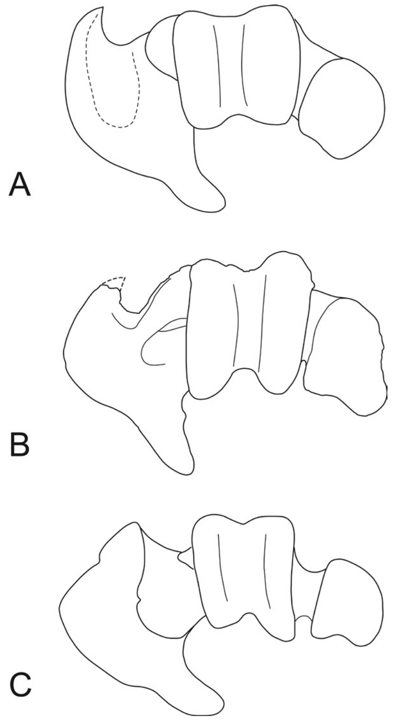

FIGURE 5. Distal views of the right tarsometatarsus (not to scale). **A**, Recent Cuculidae, *Centropus senegalensis*, coll. UCBL. **B**, *Chambicuculus pusillus* nov. gen., nov. spec., Eocene of Tunisia, coll. ONM, CB1-541. **C**, Recent Bucconidae, *Monasa nigrifrons*, coll. USNM 612064.

Eutreptodactylus itaboraiensis, from the Late Paleocene of Brazil, was initially attributed to the Cuculidae (Baird & Vickers-Rich 1997), but its morphological characteristics are different from those of the Cuculidae. Mayr (2005) has placed the genus *Eutreptodactylus* in the extinct family Gracilitarsidae that he considers related to the Piciformes. *Eutreptodactylus* differs from *Chambicuculus* by the following characteristics: trochlea met. II strongly projecting medially; trochlea met. IV ending more distally than incisura intertrochlearis lateralis; trochlea met. IV with a wide and short, plantarly directed, sehnenhalter; canalis interosseus distalis absent; foramen vasculare distale situated at the distal end of the outer extensor groove.

Comparison with crown group Galbulae (Jacamars and Puffbirds) (Figs 5C, 6E–F): Both Chambi specimens show similarities with the tarsometatarsus of the recent Galbulae, particularly in distal view. The Galbulae belong to the order Piciformes and include two families, the Galbulidae (Jacamars) and the Bucconidae (Puffbirds). Their distribution is restricted to the Neotropical zone, ranging from Southern Mexico to Southern Brazil for the Galbulidae (Tobias 2002), and from Southern Mexico to Northern Argentina for the Bucconidae (Rasmussen & Collar 2002). The distal extremity of the tarsometatarsus has been described in detail by Steinbacher (1935). In these two families the foot is zygodactyl and trochlea met. IV bears a trochlea accessoria or sehnenhalter. In the Galbulidae, trochlea met. IV shows two articular facets for phalanx 1 of posterior digit IV. The first one is found only on the condylus itself of the trochlea, and the second one is on the sehnenhalter. Both articular facets are equivalent in size and are separated by a well marked groove (see Steinbacher 1935: p. 256, fig. 18–19; SIMPSON & CRACRAFT 1981: p. 484, fig. 2B; MAYR 1998: p. 48, fig. 28E; MANEGOLD 2005: p. 124, fig. 39C-D).

In the Bucconidae, the articular facet for phalanx 1 of posterior digit I extends also on the sehnenhalter, but the two parts are not so clearly separated. In *Notharchus* the two articular surfaces are separated by a clearly expressed groove, visible in both lateral and distal views of the tarsometatarsus. In *Hypnelus* the articular surface situated on the condylus is larger than that situated on the sehnenhalter, and both surfaces are separated by a faintly visible groove. In *Monasa* and *Chelidoptera* both parts form an inflated and elongate surface, which is perpendicular to the long axis of the bone, and there is no visible groove between them. In the Bucconidae trochlea met. IV is very broad dorsoplantarly and the sehnenhalter is relatively short and thick (see also FEDUCCIA & MARTIN 1976: p. 103, figs 2g-l; HOUDE & OLSON 1992: p. 145, figs 15–16; MAYR 1998: p. 48, fig. 28F; MAYR 2002b: p. 724, fig. 7E).

Chambicuculus differs from the Galbulae by the fact that the articular surface for phalanx 1 of posterior digit IV is situated only on the condyle and not on the sehnenhalter. In addition the distal end of trochlea met. IV is situated slightly proximally compared to the incisura intertrochlearis, while in the Galbulae it is situated slightly distally. *Chambicuculus* also differs from the Galbulae in the strong development of a crest on the dorsal face of trochlea met. IV. This strongly prominent crest seems to be characteristic of the Cuculidae (see STEINBACHER 1935: fig. 16 for *Centropus,* and MAYR 2002b: fig. 7C for *Coua*).

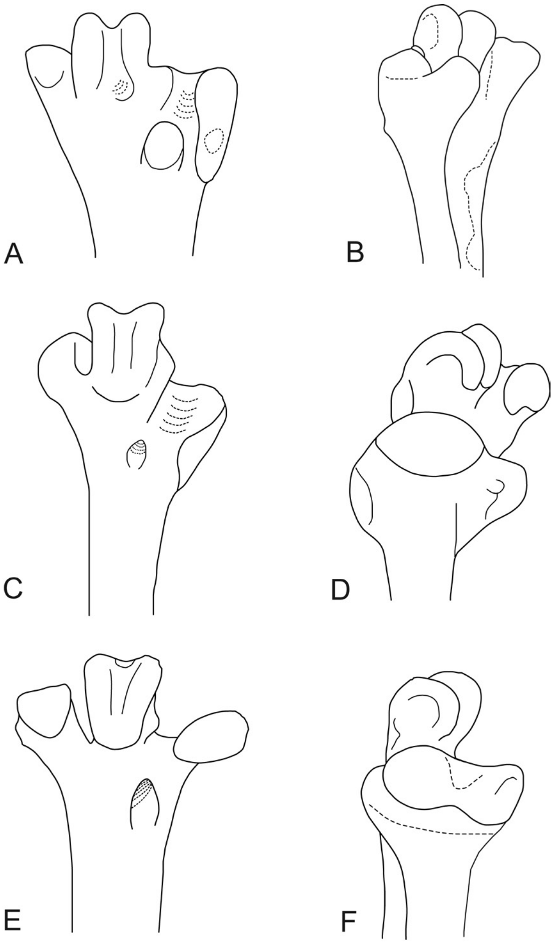

FIGURE 6. Dorsal and lateral views of the right tarsometatarsus (not to scale). **A–B**, *Chambicuculus pusillus* nov. gen., nov. spec.; A: dorsal view; B: lateral view slightly plantarly oriented. **C–D**, Recent Cuculidae, *Centropus senegalensis*, coll. UCBL; C: dorsal view; D: lateral view slightly plantarly oriented. **E–F**, Recent Bucconidae, *Monasa nigrifrons*, coll. USNM 612064; E: dorsal view; F: lateral view.

Comparison with putative stem group Galbulae: A large number of small forms from the Early Eocene of North America and Europe were attributed first to the family Bucconidae, then to the family Primobucconidae, but these Primobucconidae are now considered as ancestral forms of the Coraciiformes sensu stricto (MAYR 2009). Other forms previously attributed to Primobucconidae have been transferred to the family Sandcoleidae (HOUDE & OLSON 1992), which are stem group representatives of the Coliiformes. The only Paleogene form which can be attributed to ?Galbulae is "*Neanis*" *kistneri* (FEDUCCIA, 1973), represented by two almost complete skeletons from the Early Eocene of the Green River Formation in the United States (WEIDIG 2010). On the holotype it is possible to see that the foot is zygodactyl and shows a sehnenhalter but no more details are available. However "*Neanis*" *kistneri* shares morphological characteristics with the Galbulae in the skull, the coracoid, and the humerus. *Chambicuculus* is probably different from "*Neanis*" *kistneri* since its morphological characteristics are closer to the Cuculidae than to the Galbulae.

Comparisons with Quercypsittidae: The tarsometatarsus of *Chambicuculus* looks superficially similar to that of the Quercypsittidae, stem group representatives of the Psittaciformes (see Mourer-Chauviré 1992b and Mayr *et al.* 2010). However it differs from them by the following characteristics: in *Chambicuculus* the distal part of the tarsometatarsus is constricted (more splayed in *Quercypsitta*); trochlea met. II more elongate (it reaches only the basis of trochlea met. III in *Quercypsitta*); trochlea accessoria oriented plantarly and slightly medially (oriented more medially in *Quercypsitta*); distinct notch between trochlea accessoria and trochlea met. IV (more strongly expressed furrow in *Quercypsitta*); canalis interosseus distalis covered by a bony bridge (dorsally open in *Quercypsitta*); groove in the middle of trochlea met. II slightly indicated on the plantar face (present and well visible in distal and plantar views in *Quercypsitta*). In *Chambicuculus* a prominent crest is present on the dorsal face of trochlea met. IV. This part is incompletely preserved on all the specimens of *Quercypsitta*, but it is a characteristic of the Cuculidae and it is absent in the other stem group representatives of the Psittaciformes (Mayr *et al.* 2010).

Remarks concerning the size of *Chambicuculus pusillus*: In *Chambicuculus* the only measurement which can be compared with other forms is the distal width of the tarsometatarsus which is about 2.7 mm. In *Pumiliornis tessellatus*, which resembles the genus *Eocuculus*, this distal width can be estimated at 2.3 and 2.4 mm after the illustrations given by Mayr 1999 and Mayr 2008; this form is thus still smaller than *Chambicuculus*. In *Morsoravis sedilis* the distal width is 3.0 mm (Bertelli *et al.* 2010). In *Eocuculus cherpinae* it is 4.2 mm (Chandler 1999) and in *Eocuculus* cf. *cherpinae* it can be estimated at 4.3 mm (Mayr 2006b). Recent Cuculidae are generally middle- to large-sized, but there are a few very small forms, such as *Chrysococcyx minutillus*, the Little Bronze-cuckoo, which measures 15–16 cm and weights 17g (Payne 1997). The size of *Chambicuculus* was probably comparable to that of the smallest recent Cuculidae.

Discussion

The early evolutionary history of birds in Africa is still poorly known. Their Paleogene fossil record is limited to a handful of localities. Marine forms have been described in the Late Paleocene and Early Eocene of Morocco, and also in the Middle Eocene of Nigeria and Togo (Bourdon *et al.* 2010, and references therein). Among the terrestrial birds only a galliform in the early Middle Eocene of Namibia, and a phororhacoid in the early Middle Eocene of Algeria, are known (Mourer-Chauviré *et al.* 2011a, 2011b). The other Paleogene African forms come from the Late Eocene and Early Oligocene of the Fayum, in Egypt (Rasmussen *et al.* 1987, 2001).

According to the fossil record of the Northern Hemisphere, the Galliformes seem to have been abundant and diversified during the Paleogene. Several stem group families have been found in the Early Eocene (Mayr 2009). However their record is not limited to the Paleogene but it extends back to the Late Cretaceous (Hope 2002). In the Southern Hemisphere, until recently, they were only known from the Late Oligocene, with a Quercymegapodiidae in South America (Alvarenga 1995) and a Megapodiidae in Australia (Boles & Ivison 1999). The presence of two galliforms in Africa, one in the late Early or early Middle Eocene of Tunisia, and the other in the Middle Eocene of Namibia, shows that this group was also present and diversified in this landmass during the Paleogene. *Namaortyx*, from Namibia, and *Chambiortyx*, from Tunisia, do not belong to the same families as those recorded in the Northern Hemisphere. They probably belong to stem group families but, for confirmation, it would be necessary to have some other elements of the postcranial skeleton. Recent African galliforms belong to the family Phasianidae s. l., which are crown group representatives of the Galliformes, and which are only known since the second part of the Oligocene (Mourer-Chauviré 1992a; Mayr 2009).

Concerning the Cuculiformes, a large number of semizygodactyl or zygodactyl forms have been described in the Paleogene of Eurasia and North America, and also in South America

(Mayr 2009), but for Africa, this group was so far undocumented in the Paleogene. The new taxon described here, *Chambicuculus*, represents therefore the first and oldest occurrence of this group in Africa. Another zygodactyl form, *Miopico benimellalensis* Mayr, 1998, family Miopiconidae, was described from the Middle Miocene of Beni Mellal, Morocco. According to Mayr (1998), the Miopiconidae are the sister-group of the Pici, and thus *Chambicuculus* is not related to it.

Chambicuculus is older than the other fossil Cuculidae known so far. In this taxon the presence of a canalis interosseus distalis is a plesiomorphic condition for birds (Mayr *et al.* 2003). By the presence of this canal, *Chambicuculus* could appear somewhat more primitive than *Eocuculus* from the Late Eocene and Early Oligocene. However in *Chambicuculus*, the presence of a well-developed sehnenhalter, which is a derived condition indicating that this taxon was fully zygodactyl, and the lesser distal extension of trochlea met. IV suggests that *Chambicuculus* was morphologically more derived than *Eocuculus*.

Acknowledgments

We thank AnneLise Charruault, from UM2–CNRS, for technical assistance, Arlette Armand, from UCBL, for the scanning electron microscope pictures, James P. Dean, Christina A. Gebhard, from the USNM, and Christine Lefèvre, from the Paris NMHN, for the loan of comparative material. We also thank Gerald Mayr and an anonymous reviewer for their useful comments.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

naturhistorisches museum wien

The tarsometatarsus of the Middle Eocene loon *Colymbiculus udovichenkoi*

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Abstract — We describe the previously unknown tarsometatarsus of the earliest unambiguously identified loon, *Colymbiculus udovichenkoi*, from the Middle Eocene of the Ukraine. Except for being more elongate and apart from details of the hypotarsus morphology, the bone resembles the tarsometatarsus of the Early Miocene *Colymboides minutus*. We consider the hypotarsus morphology of *Colymbiculus* to be plesiomorphic for Gaviiformes. *Colymboides* and crown group Gaviiformes are each characterized by an autapomorphic hypotarsus morphology, which precludes the former from being directly ancestral to the latter. The similarities shared by *C. udovichenkoi* and *C. minutus*, including their small size, are likely to be plesiomorphic for Gaviiformes. Although the disappearance of small stem group Gaviiformes may be related to the retreat of loons to cold Northern latitudes, more data are needed to firmly establish this hypothesis. We finally note that early Paleogene stem group Gaviiformes markedly differ from putative Late Cretaceous loons, whose identification needs to be verified by further fossil specimens.

Key words: *Colymbiculus*, *Colymboides*, fossil birds, Gaviiformes, Eocene, Lutetian, Ukraine

Introduction

Loons (Gaviiformes) have a fairly comprehensive Neogene fossil record (Olson 1985; Mayr 2009a), but the early evolutionary history of these foot-propelled diving birds is still incompletely known. The first fossil loon recognized as such, and also one of the best-represented species, is *Colymboides minutus* Milne-Edwards, 1867 from the Early Miocene of France and the Czech Republic (Milne-Edwards 1867–71, Storer 1956; Cheneval 1984; Mlíkovský 2002). Other species from the Neogene of Europe were assigned to *Gavia*, the taxon that includes the four extant species, with *Gavia egeriana* Švec, 1982 from the Early Miocene of the Czech Republic (Švec 1982), the earliest stem lineage representative, being distinctly smaller than its modern congeners. Disregarding the poorly known *Gaviella pusilla* (Shufeldt, 1915), whose exact age is uncertain but possibly Oligocene (Wetmore 1940), loons first appear in North America in the Early Miocene (Rasmussen 1998). All Neogene North American species were classified in the taxon *Gavia* (Olson 1985; Olson & Rasmussen 2001).

Pre-Miocene Gaviiformes are morphologically clearly distinguished from their extant relatives. Most of the fossils were, at least tentatively, assigned to *Colymboides*, and the two named Paleogene species of this taxon are *Colymboides anglicus* Lydekker, 1891 from the Late Eocene of England (Harrison 1976; Harrison & Walker 1976) and ?*Colymboides metzleri* Mayr, 2004 from the Early Oligocene of Germany and Belgium (Mayr 2004, 2009b). Contemporaneous with the latter species there was also a large gaviiform species of undetermined affinities in the Early Oligocene of Belgium (Mayr & Smith 2002). A *Colymboides*-like loon of uncertain species identity was further reported from the Late Oligocene of Germany (Mayr & Poschmann 2009), and undescribed remains of *Colymboides* were also found in the Late Oligocene of Kazakhstan (Kurochkin 1976).

Putative Upper Cretaceous records of Gaviiformes were described from Chile (*Neogaeornis wetzeli* Olson, 1992) and Antarctica (*Polarornis gregorii* Chatterjee, 2002), but these are based on a single bone and a very fragmentary partial skeleton, respectively, and their identification needs to be corroborated with more material (see also below). The earliest well-documented stem group representative of Gaviiformes is *Colymbiculus udovichenkoi* Mayr & Zvonok, 2011, which occurs in Middle Eocene (about 48 million years ago) marine sediments of the eastern Tethys Sea in Ukraine (Mayr & Zvonok 2011, 2012). *Colymbiculus udovichenkoi* is quite abundant at the type locality, but up to now the material assigned to this small species consisted only of four skeletal elements, *i.e.*, the humerus, ulna, radius, and tibiotarsus. In light of the fact that loons are highly specialized foot-propelled diving birds, one of the most significant bones of *C. udovichenkoi* – the tarsometatarsus – remained thus unknown. This bone was found in the 2012 excavation campaign at the type locality and is described in the present study.

Material and methods

Osteological terminology follows Baumel & Witmer (1993). Measurements are in millimeters. The fossils are deposited in Naturhistorisches Museum Basel, Switzerland (NMB) and Forschungsinstitut Senckenberg, Frankfurt am Main (SMF).

Systematic Paleontology

Gaviiformes Wetmore & Miller, 1926

Gaviidae Allen, 1897

Colymbiculus udovichenkoi Mayr & Zvonok, 2011

Referred specimen: SMF Av 592 (complete left tarsometatarsus).

Locality and horizon: Ikovo sand quarry, about 1 km west Novopskov, Luhansk Province, Ukraine (49°31′42″N, 39°3′59.5″E); Middle Eocene (Lower Lutetian).

Measurements: Length, 39.4; proximal width, 7.0; distal width, 6.0; minimum mediolateral width of shaft, 2.9.

Description and comparisons: The tarsometatarsus of *Colymbiculus udovichenkoi* resembles that of *Colymboides minutus*, but is proportionally longer relative to the humerus (the tarsometatarsus of other *Colymboides* species is unknown or too poorly preserved for detailed comparisons): Whereas the lengths of humerus and ulna of *Colymbiculus* correspond with the lower size range of *C. minutus* (~63.3 and 49.1 versus 62.0–66.0 and 49.8–56.0, respectively; Storer 1956, Mayr & Zvonok 2011, 2012), that of the tarsometatarsus is distinctly larger (39.4 mm versus 30.8-32.8 mm; Storer 1956). Further unlike *C. minutus*, the hypotarsus of *C. udovichenkoi* does not exhibit a canal for the tendon of musculus flexor digitorum longus (Fig. 1E, I). Instead, there are three well-developed sulci for, from medial to lateral, musculus flexor digitorum longus, m. flexor perforatus digiti II, and m. flexor hallucis longus. The lateral surface of the crista medialis hypotarsi bears a shallow furrow for the tendon of musculus flexor perforans et perforatus digiti II. The small foramina vascularia proximalia are closely adjacent. The distal end of the bone corresponds well with *Colymboides minutus*, and as in the latter and modern loons the trochlea metatarsi II is short and plantarly deflected. The foramen vasculare distale is situated farther distally than in extant loons. The canalis interosseus distalis is dorsally open. A fossa metatarsi I is absent.

The tarsometatarsus of *Colymbiculus* is less mediolaterally compressed than that of extant

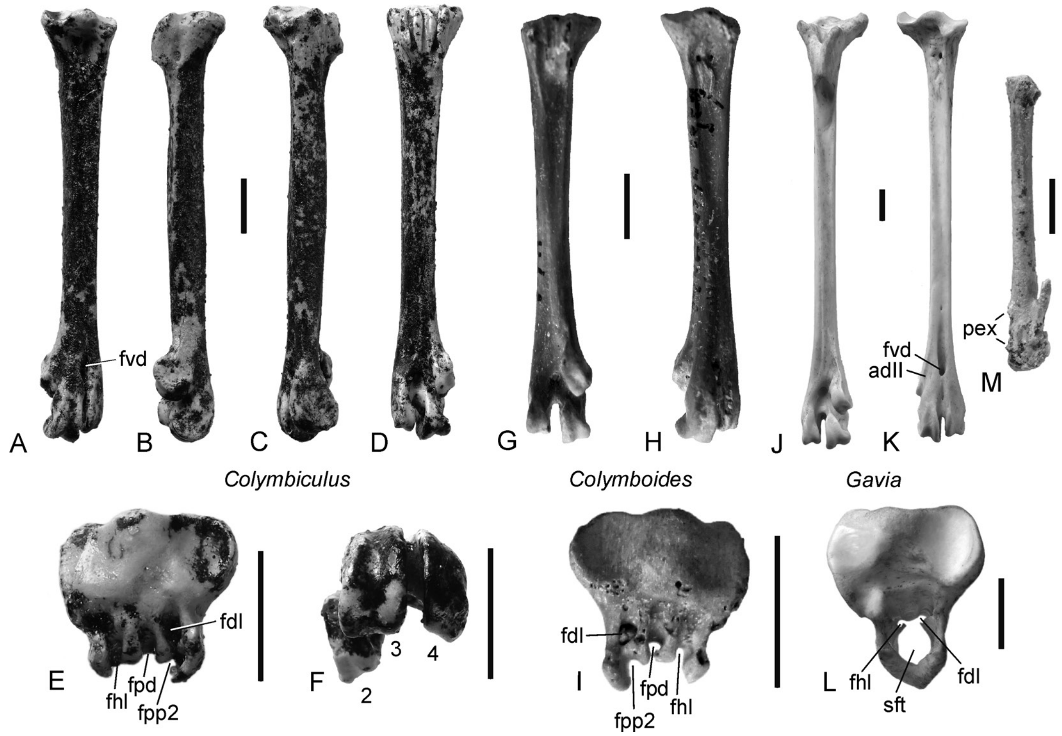

FIGURE 1. Tarsometatarsus of **A–F**, *Colymbiculus udovichenkoi* from the Middle Eocene of Ukraine in comparison with **G–I**, the Early Miocene *Colymboides minutus* and **J–L**, the extant *Gavia stellata*. **A–F**, left tarsometatarsus (SMF Av 592) in dorsal (**A**), medial (**B**), lateral (**C**), plantar (**D**), proximal (**E**), and distal (**F**) view. **G**, **H**, left tarsometatarsus (NMB MA. 2668) in plantar (**G**) and dorsal (**H**) view. **I**, right tarsometatarsus (NMB S.G. 20829) in proximal view. **J–L**, left tarsometatarsus in plantar (**J**), dorsal (**K**), and proximal (**L**) view. **M**, left carpometacarpus (SMF Av 593, ventral view) of an unidentified small bird from the Middle Eocene of the Ikovo sand quarry. Abbreviations: adII, sulcus for tendon of musculus abductor digiti II; fdl, canal for tendon of musculus flexor digitorum longus; fhl, canal for tendon of musculus flexor hallucis longus; fpd, canal for tendon of musculus flexor perforatus digiti II; fpp2, canal for tendon of musculus flexor perforans et perforatus digiti II; fvd, foramen vasculare distale; pex, base of broken processus extensorius; sft, canal for superficial flexor tendons. In (**F**) the trochleae are numbered. Scale bars equal 5 mm.

Gaviidae. There is further no marked sulcus for the tendon of musculus abductor digiti II. Proximal of the foramen vasculare distale, on the dorsal surface of the bone, the sulcus extensorius is less marked than in extant loons. In the hypotarsus of modern Gaviidae the cristae mediales et lateralis hypotarsi are much better developed and fuse plantarly, thus enclosing a large canal for the superficial flexor tendons (Fig. 1L; Wilcox 1952). There is a marked sulcus for these tendons on the plantar surface of the tarsometatarsus, which is absent in *Colymbiculus*.

Discussion

Like *C. minutus* (Storer 1956), *C. udovichenkoi* was less specialized for foot-propelled diving than extant Gaviiformes, in which the tarsometatarsus is much more mediolaterally compressed and in which the tibiotarsus exhibits much better developed cnemial crests (Mayr & Zvonok 2012). *Colymbiculus udovichenkoi* further distinctly differs from *Colymboides minutus* and extant loons in the much more pronounced crista deltopectoralis of the humerus (Mayr & Zvonok 2012), and reduction of the deltopectoral crest is here considered a synapomorphy of *Colymboides* and *Gavia*. With *Colymbiculus* thus being the sister taxon of the clade (*Colymboides* + *Gavia*), the similar tarsometatarsus morphology shared by *Colymbiculus* and *Colymboides* is likely to be plesiomorphic for Gaviiformes.

We also regard the hypotarsus morphology of *Colymbiculus*, with three plantarly open sulci, to be plesiomorphic for the clade including *Colymbiculus*, *Colymboides*, and *Gavia*. Absence of hypotarsal canals is certainly primitive for Neornithes, the clade including all modern birds, as such canals are absent in non-neornithine Mesozoic taxa close to the crown group as well as in palaeognathous birds. Aequornithes, the "waterbird clade" to which Gaviiformes belong (Ericson *et al.* 2006; Hackett *et al.* 2008; Mayr 2011), includes taxa with and without hypotarsal canals, but in those where canals are present (*i.e.*, Pelecanidae, Scopidae, Balaenicipitidae, Fregatidae, Sulidae, Phalacrocoracidae, Anhingidae) hypotarsus morphology is different from that of loons. Moreover, in the phylogeny of Hackett *et al.* (2008) these latter taxa form a clade within Aequornithes, whereas the basally branching Spheniscidae, Procellariiformes, and Ciconiidae lack hypotarsal canals. We thus conclude that the hypotarsus morphologies of *Colymboides* (closed canal for tendon of musculus flexor digitorum longus; Fig. 1I) and *Gavia* (cristae medialis et lateralis forming large canal; Fig. 1L) constitute two independently acquired derived states, and that *Colymboides* is not directly ancestral to crown group Gaviiformes.

Stem group Gaviiformes were much smaller than their extant relatives for more than 30 million years, from the Middle Eocene (48 mya [*Colymbiculus udovichenkoi*]; Mayr & Zvonok 2012) to the Early Miocene (17 mya [*Colymboides minutus*]; Mlíkovský 2002). Although species with a size approaching that of extant loons did occur in the Late Eocene and Early Oligocene of Europe (Harrison & Walker 1976; Mayr & Smith 2002), the disappearance of small gaviiform species is notable. In the Paleogene and early Neogene loons still inhabited warm tropical and subtropical environments, which is vividly illustrated by the recent discovery of a loon leg in association with a crocodile tooth (Mayr & Poschmann 2009); the remains of *Colymbiculus* were also found in the same horizon as crocodilians (Zvonok & Skutschas 2011). It may thus be near at hand to assume that extinction of small stem group Gaviiformes was related to the retreat of loons to cold environments, where larger-bodied animals have a selective advantage (reduced heat loss) owing to a lower body surface area to volume ratio (Bergmann's rule; *e.g.*, Meiri & Dayan 2003). Still, however, there are many avian species with a small body size, which occur in aquatic habitats of far Northern or Southern latitudes today (*e.g.*, Pelecanoididae, Phalaropidae, and some Alcidae), and more data on the exact correlation between the size, distribution, and extinction dates of stem group Gaviiformes are needed to firmly establish, or refute, this hypothesis.

The two Late Cretaceous putative loons, *Neogaeornis wetzeli* Lambrecht, 1929 and *Polarornis gregorii* Chatterjee, 2002, are larger than *Colymbiculus udovichenkoi* and *Colymboides minutus*. We note, however, that the tarsometatarsus of *N. wetzeli* is very different from that of *Colymbiculus* (the tarsometatarsus of *P. gregorii* is unknown). Instead of four cristae as in *C. udovichenkoi*, the hypotarsus of *N. wetzeli* only exhibits two widely separated ones with a very indistinct sulcus in between (Olson 1992). The shaft is much more mediolaterally compressed in *N. wetzeli* and, most unusually and unlike *Colymbiculus*, *Colymboides*, and extant Gaviidae, the trochlea metatarsi IV reaches farther distally than the trochlea metatarsi III (Olson 1992 considered this to possibly be an artifact of preparation, but this is not evident from the published figures). With regard to the latter feature, the tarsometatarsus of *Neogaeornis* is in fact more similar to the tarsometatarsus of grebes (Podicipedidae) than that of Cenozoic and extant loons. We acknowledge the possibility that there was a derived lineage of gaviiform birds in the Late Cretaceous of the Southern Hemisphere, where Gaviiformes do not occur today. However, we also note that evidence for gaviiform affinities of both, *Neogaeornis* and *Polarornis*, is not yet compelling, and their identification should be regarded tentative until more material becomes available (see also van Tuinen & Hedges 2004).

We finally note that the new material from the Ikovo sand quarry also includes an incomplete carpometacarpus (Fig. 1M). Although the bone resembles the carpometacarpus of *Colymboides minutus* in overall proportions, the (broken) processus extensorius was not proximodistally elongated as in *Colymboides* and extant loons. Moreover, the specimen is significantly short than the tarsometatarsus, whereas carpometacarpus and tarsometatarsus are of equal length in *C. minutus* (Storer 1956). Another, morphologically distinct, carpometacarpus from the Ikovo sand quarry was reported by Mayr & Zvonok (2012), who discussed the possibility that it is from *Colymbiculus udovichenkoi*. This latter specimen likewise significantly differs from the carpometacarpus of *Colymboides* and extant Gaviiformes, and despite the relative abundance of other postcranial bones of *C. udovichenkoi* at the type locality, an unambiguous identification of its carpometacarpus has to await further specimens.

Acknowledgements

We thank Oleksandra Karpiuk (Universitätsmedizin Göttingen) for assisting in the transport of the fossil and Vanesa De Pietri (SMF) for providing pictures of *Colymboides minutus*. All other photos were taken by Sven Tränkner (SMF). We further acknowledge reviews by Claudia Tambussi (CICTERRA, Cordoba, Argentina) and Jorge Noriega (CICYTTP-CONICET, Diamante, Argentina).

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

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Galliformes, Upupiformes, Trogoniformes, and other avian remains (?Phaethontiformes and ?Threskiornithidae) from the Rupelian stratotype in Belgium, with comments on the identity of "*Anas*" *benedeni* Sharpe, 1899

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Abstract — We describe new avian fossils from the Boom Formation of Belgium, which almost double the number of bird taxa known from this part of the Rupelian stratotype. Three galliform species can, at least tentatively, be assigned to the paraortygid species *Paraortyx brancoi*, *P. lorteti*, and *Pirortyx major*. Among the fossils is a partial sternum, which shows that *Paraortyx* lacks a spina interna. The absence of this structure is plesiomorphic for Galliformes and probably related to the absence of a large crop, thus indicating that Paraortygidae were not yet adapted to the regular processing of coarse and dry food. Two distal humeri belong to Trogoniformes (trogons) and Upupiformes (hoopoes, woodhoopoes, and allies), respectively. A femur is tentatively assigned to Phaethontiformes (tropicbirds), and a carpometacarpus is, likewise tentatively, referred to Threskiornithidae (ibises and spoonbills). We finally comment on the affinities of "*Anas*" *benedeni* Sharpe, 1899 and detail that this species most likely belongs to Gaviiformes (loons).

Key words: fossil birds, early Oligocene, Boom Formation, Paraortygidae

Introduction

The Lower Oligocene Boom Formation of the Rupelmonde area in Belgium was deposited in a shallow open sea in the southwestern part of the North Sea Basin, and is part of the Rupelian stratotype (*e.g.*, van Simaeys & Vandenberghe 2006). The formation is exposed at various localities in the Rupelmonde area near Antwerp and has yielded numerous avian remains, most of which were collected in the late 19th and early 20th century.

The majority of the bird fossils belongs to the diomedeoidid procellariiform *Rupelornis definitus* (Mayr & Smith 2012a). Remains of other marine birds are much rarer and were assigned to Diomedeidae (albatrosses; Mayr & Smith 2012b) and Gaviiformes (loons; Mayr 2009a). Lambrecht (1931) reported a large, putatively anseriform bird (*Cygnopterus affinis*), whose affinities are in need of a revision (Mayr 2009b). More recently, Mayr (2009a) identified a new species of Selenornithidae, an extinct and poorly known group of Strigiformes (owls), and fossils of the gruiform taxon Parvigruidae were described by Mayr (2013). Most of these species have been described after Cheneval's (1996) review of the Belgian avifauna, who at that time could mainly list various poorly established and largely incorrectly identified species described by van Beneden (1871).

Despite the progress made in recent years, our knowledge of the Rupelian avifauna of Belgium, and the North Sea Basin in general, is still anecdotal. Because of the marine origin of most fossil deposits the avian record is biased towards aquatic taxa, and very small birds are underrepresented in the old collections due to the fact that most fossils are surface finds. Here we report on further avian remains from the Boom clay, including the first remains of small land birds, and revise the affinities of "*Anas*" *benedeni* Sharpe, 1899, one of the species introduced by van Beneden (1871) under the preoccupied name "*Anas creccoides*".

Material and methods

Osteological terminology follows Baumel & Witmer (1993). Measurements are in millimeters. Institutional abbreviations: IRSNB, Institut royal des Sciences naturelles de Belgique, Belgium; SMF, Senckenberg Research Institute and Natural History Museum Frankfurt.

Systematic Palaeontology

Galliformes Temminck, 1820
Paraortygidae Mourer-Chauviré, 1992
Paraortyx Gaillard, 1908

Taxonomic remarks: Paraortygidae is a taxon of stem group Galliformes, which was established by Mourer-Chauviré (1992) for fossils from the Quercy fissure fillings in France. In these deposits, three species can be distinguished, which occur in Late Eocene/Early Oligocene (*Paraortyx brancoi* and *P. lorteti*) and Late Oligocene (*Pirortyx major*) localities; Fischer (1990) further reported *P. major* from the Lower Oligocene of Germany.

Paraortygidae are distinguished from crown group Galliformes by plesiomorphic features of the humerus (lack of a transverse ridge at the beginning of the incisura capitis) and the coracoid (presence of an excavated cotyla scapularis). The Rupelmonde material includes remains of at least three paraortygid species, which can, at least tentatively, be assigned to the three species reported from the Quercy deposits.

Paraortyx cf. *lorteti* Gaillard, 1908
(Fig. 1A)

Referred specimen: IRSNB Av 115 (proximal end of right humerus; collection Delheid IG 8289, found in 1896).

Locality and horizon: Niel-Boom; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

Measurements: Length as preserved, 22.3; proximal width, 10.2 [9.2–11.2] (dimensions of Quercy specimens of *P. lorteti* in brackets, after Mourer-Chauviré 1992).

Remarks: The specimen is identified as a stem group galliform by the lack of a transverse ridge at the beginning of the incisura capitis. It exhibits a marked second (dorsal) fossa pneumotricipitalis (weakly developed in *Pirortyx*), and closely matches the Quercy specimens of *P. lorteti* in size and morphology (Mourer-Chauviré 1992: fig. 2). Assignment to this latter species is nevertheless tentative because of the fragmentary nature of the fossil.

Paraortyx brancoi Gaillard, 1908
(Fig. 1B–H)

Referred specimens: IRSNB Av 116a–c (cranial portion of corpus sterni, left coracoid, proximal end of right ulna; collection Delheid IG 8289, found in 1891).

Locality and horizon: Steendorp; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

Measurements: Coracoid, maximum length, 35.3; estimated length from processus acrocoracoideus to broken angulus medialis, ~32 [31.0]. Ulna, dorsoventral width across cotylae, 6.8 (dimensions of Quercy specimens of *P. brancoi* in brackets, after Mourer-Chauviré 1992).

Remarks: These three bones are from a single individual. In size and morphology, the coracoid (Fig. 1B) corresponds with that of *Paraortyx brancoi* from the Late Eocene (MP 18/19) of the Quercy fissure fillings in France (Mourer-Chauviré 1992). As in other stem group Galliformes

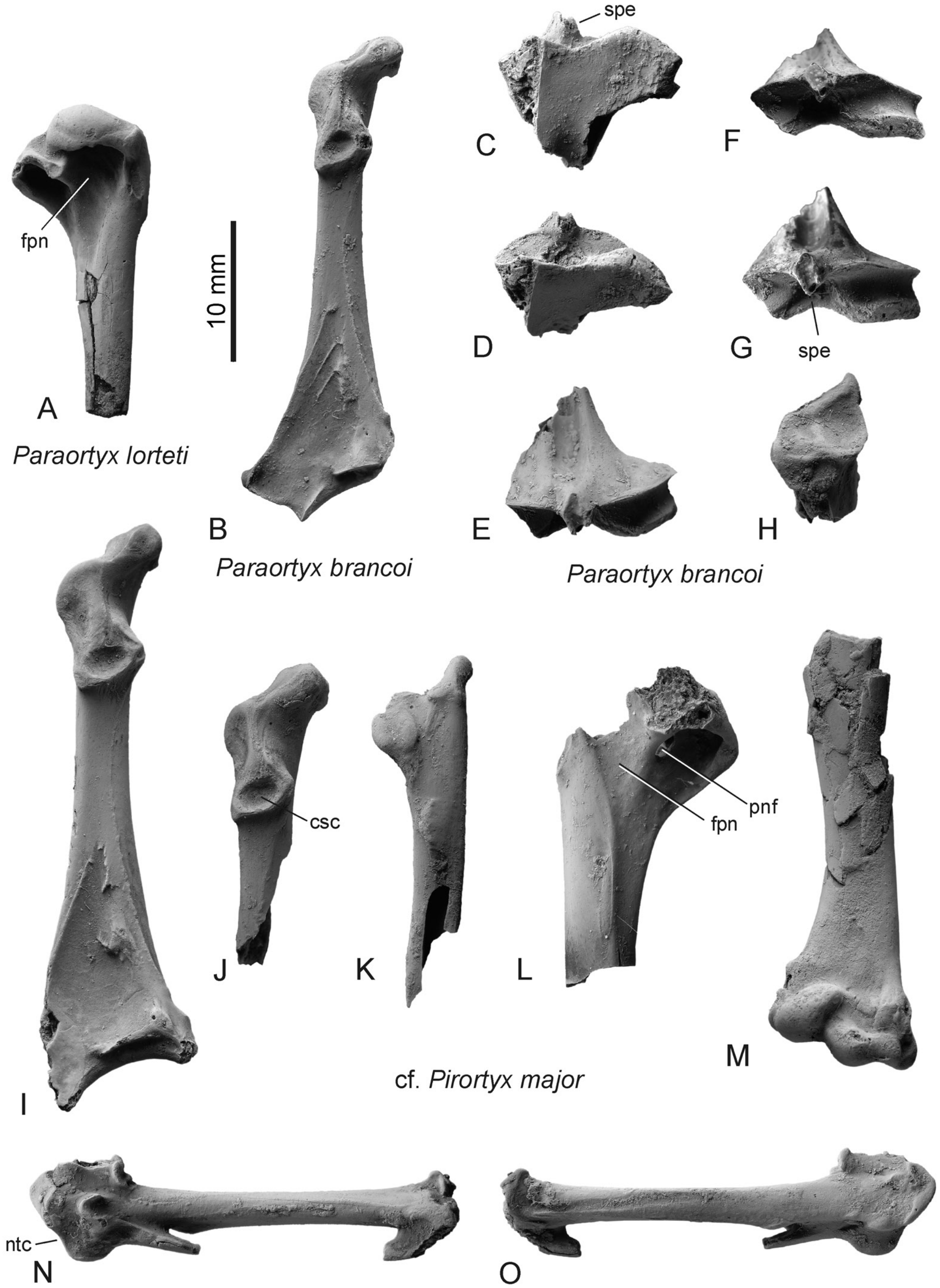

FIGURE 1. Galliformes from the Rupelian of Belgium. **A**, *Paraortyx* cf. *lorteti*, proximal end of right humerus (IRSNB Av 115) in caudal view. **B–H**, *P. brancoi*, **B**, left coracoid (IRSNB Av 116a) in dorsal view; **C–G**, cranial portion of corpus sterni (IRSNB Av 116b) in dorsal (**C**), craniodorsal (**D**), ventral (**E**), cranial (**F**), and cranioventral (**G**) view; **H**, proximal end of right ulna (IRSNB Av 116c) in cranial view. **I–O**, cf. *Pirortyx major*, **I**, left coracoid (IRSNB Av 117) in dorsal view; **J**, extremitas omalis of left coracoid (IRSNB Av 118a) in dorsal view; **K**, extremitas cranialis of left scapula (IRSNB Av 118b) in lateral view; **L**, proximal end of left humerus (IRSNB Av 119) in caudal view; **M**, distal end of right humerus (IRSNB Av 120) in cranial view; **N**, **O**, incomplete left carpometacarpus (IRSNB Av 122) in ventral (**N**) and dorsal (**O**) view. Abbreviations: csc, cotyla scapularis; fpn, second (dorsal) fossa pneumotricipitalis; ntc, notch in rim of ventral portion of trochlea carpalis; pnf, pneumatic foramen; spe, spina externa. Bones were coated with ammonium chloride.

it exhibits a cup-like cotyla scapularis. The ulna of *P. brancoi* has not been described, but, apart from being larger (proximal width 6.8 mm versus 4.4–4.9 mm; Mourer-Chauviré 1992), the Belgian ulna (Fig. 1H) matches that of *P. lorteti* (Mourer-Chauviré 1992).

IRSNB Av 116a–c also includes the cranial portion of a sternum (Fig. 1C–G). This bone was unknown for *Paraortyx* and other Early Oligocene Galliformes before and distinctly differs from the sternum of crown group Galliformes in the absence of a spina interna, which in crown group Galliformes is fused with the spina externa to form a spina communis (see discussion).

?*Pirortyx* Brodkorb, 1964
cf. *Pirortyx major* (Gaillard, 1939)
(Fig. 1I–O)

Referred specimens: IRSNB Av 117 (Fig. 1I; left coracoid; collection Hasse IG 20664, found in 1904). IRSNB Av 118a+b (Fig. 1J, K; extremitas omalis of left coracoid, extremitas cranialis of left scapula; collection Delheid IG 8289, found in 1895). IRSNB Av 119 (Fig. 1L; proximal end of left humerus; collection Delheid IG 8289, found in 1901). IRSNB Av 120 (Fig. 1M; distal end of right humerus; collection Delheid IG 8289). IRSNB Av 121 (extremitas cranialis of right scapula; collection Delheid IG 8289). IRSNB Av 122 (Fig. 1N, O; incomplete left carpometacarpus; collection Delheid IG 8289, found in 1901).

Locality and horizon: Steendorp (IRSNB Av 119, IRSNB Av 118a+b), Niel-Boom (IRSNB Av 117), Rumst (IRSNB Av 120), Terhagen (IRSNB Av 122); all Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

Measurements: Coracoid (IRSNB Av 117), maximum length, 41.0; length from tip of processus acrocoracoideus to angulus medialis, 38.5. Humerus (IRSNB Av 119), proximal width (est.), ~13.5 [13.5]. Humerus (IRSNB Av 120), distal width, 10.8 [9.7]. Carpometacarpus (IRSNB Av 122), length, 30.6 (in brackets the dimensions of Quercy specimens of *Pirortyx major*, after Mourer-Chauviré 1992).

Remarks: *Pirortyx major*, the only species of the taxon *Pirortyx*, is known from the holotype (a complete humerus from an unknown horizon of the Quercy fissure fillings), a referred proximal humerus from the Late Oligocene of the Quercy fissure fillings (Mourer-Chauviré 1992), as well as a proximal and another distal humerus from the Lower Oligocene of the Weißelster Basin in Germany (Fischer 1990). The proximal humerus IRSNB Av 119 agrees with *Pirortyx* and differs from *Paraortyx* in that the second fossa pneumotricipitalis is shallower, less extensive, and bears a pneumatic opening (Fig. 1L; Mourer-Chauviré 1992). The tentatively referred distal humerus IRSNB Av 120 is larger than that of previously reported *P. major* fossils (10.8 mm versus 9.7 mm in the *P. major* holotype and 8.7 mm in a specimen referred to the species by Fischer 1990), but a comparable range of individual size variation is known from humeri referred to *Paraortyx brancoi* (Mourer-Chauviré 1992: tab. 1).

The coracoid and scapula of *Pirortyx* have not been described before, and the above-listed specimens are referred to the taxon based on their large size. We note, however, that if our assignment is correct, *Pirortyx major* had a proportionally shorter humerus than the species of *Paraortyx*, as the ratio humerus length: coracoid length would then be 1.46 for *Pirortyx major* (holotype of *P. major*: IRSNB Av 117), whereas it is 1.62 in *Paraortyx lorteti* and 1.63 in *P. brancoi* (calculated after the mean dimensions given by Mourer-Chauviré 1992: tab. 1). Morphologically, the Belgian coracoids and scapulae closely resemble the corresponding bones of *Paraortyx lorteti*.

The carpometacarpus IRSNB Av 122 is too large to belong to either of the two *Paraortyx* species (the bone measures only 19.5–21.7 mm in the larger *P. brancoi*; Mourer-Chauviré 1992), but would correspond in size to *Pirortyx major*, with the ratio humerus length: carpometacarpus length being 1.84 (*P. major* holotype: IRSNB Av 122) and 1.90 in *Paraortyx brancoi* (calculated after the mean dimensions given by Mourer-Chauviré 1992: tab. 1). IRSNB Av 122 agrees with the carpometacarpus of *Paraortyx* in its proportions, and as in other stem group Galliformes the intermetacarpal tuberosity is only weakly developed. The ventral surface of the proximal portion of the os metacarpale minus does, however, not exhibit a well-developed tubercle, which is found in *Paraortyx* and some other taxa of stem group Galliformes (Mourer-Chauviré

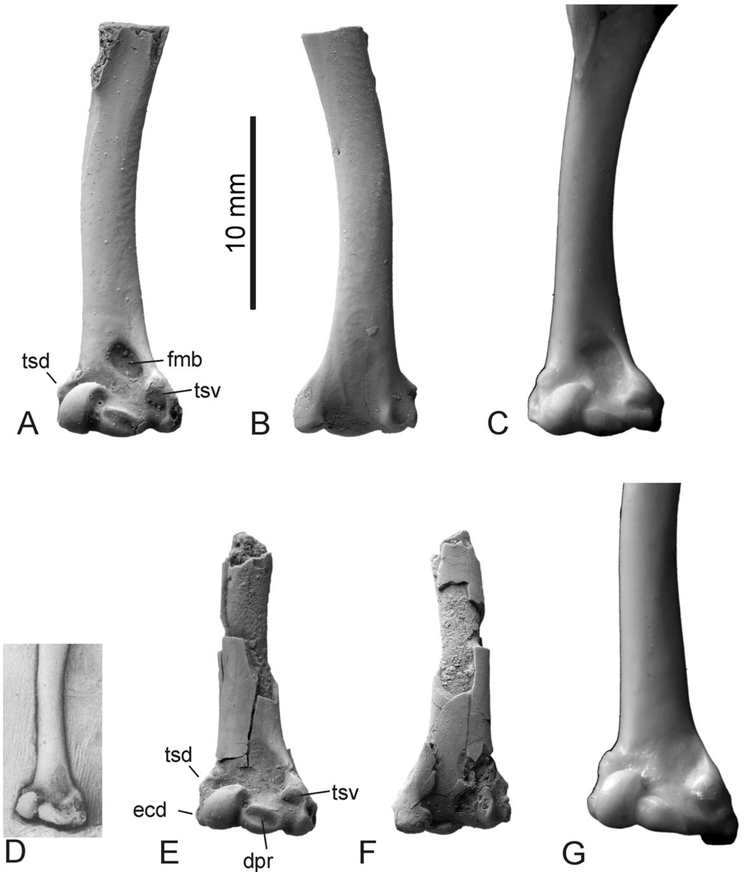

FIGURE 2. Trogoniformes and Upupiformes from the Rupelian of Belgium. **A**, **B**, ?*Primotrogon* sp., distal end of right humerus (IRSNB Av 123) in cranial (**A**) and caudal (**B**) view, in comparison to **C**, the distal humerus of the Orange-breasted Trogon, *Harpactes oreskios* (Trogonidae). **D**, distal end of right humerus of *Messelirrisor halcyrostris* (Messelirrisoridae) from the early Eocene of Messel in Germany (from Mayr 1998: pl. 6). **E**, **F**, Upupiformes, gen. et sp. indet., distal end of right humerus (IRSNB Av 124) in cranial (**E**) and caudal (**F**) view, in comparison to the distal humerus of **G**, the Green Woodhoopoe, *Phoeniculus purpureus* (Phoeniculidae). Abbreviations: dpr, depression on cranial surface of condylus ventralis; ecd, epicondylus dorsalis; fmb, fossa musculi brachialis; tsd, tuberculum supracondylare dorsale; tsv, tuberculum supracondylare ventrale. Fossil bones were coated with ammonium chloride.

1992: pl. 2; Mayr 2006: fig. 5d). Further unlike *Paraortyx*, the caudal rim of the ventral portion of the trochlea carpalis is distinctly notched (Fig. 1N).

Trogoniformes American Ornithologists' Union, 1886
?Primotrogon Mayr, 1999

?*Primotrogon* sp.
(Fig. 2A, B)

Referred specimen: IRSNB Av 123 (distal right humerus; collection Delheid IG 8289).

Locality and horizon: Steendorp; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

Measurements: Length as preserved, 21.9; distal width, 6.5.

Remarks: IRSNB Av 123 is from a species about the size of the extant Orange-breasted Trogon, *Harpactes oreskios*. It is identified as a trogon by its stout overall proportions and by the marked and sharply delimited fossa musculi brachialis; this latter fossa is very distinct in most of the studied species of *Harpactes* (*oreskios*, *diardii*, *ardens*) as well as in *Trogon rufus*, whereas it is shallower in *H. erythrocephalus*, *Apalharpactes reinwardtii*, *Trogon viridis*, and

Pharomachrus spp. The tuberculum supracondylare dorsale of IRSNB Av 123 is more marked and dorsally protruding than in all studied crown group Trogoniformes (specimens of *Apaloderma* were not available for comparisons) (Fig. 2). In this latter, possibly plesiomorphic feature, the Belgian fossil is also distinguished from *Paratrogon gallicus* from the Lower Miocene of France (Milne-Edwards (1869–71: pl. 177). The tuberculum supracondylare ventrale is large as in *Trogon* and *Pharomachrus*, whereas it is proximodistally less elongate in *Harpactes*.

IRSNB Av 123 is tentatively assigned to *Primotrogon*, which is the only trogoniform taxon from the Lower Oligocene of Europe that has been named (Mayr 1999, 2001, 2005, 2009b). It is larger than an Early Oligocene trogon fossil from the German locality Frauenweiler (the distal width of the humerus of SMF Av 498, described by Mayr 2005, is only 4.7 mm), but corresponds well in size with *Primotrogon wintersteini* from the Early Oligocene of the Luberon in southern France (the distal width of SMF Av 423, described by Mayr 2001, is 6.1 mm).

Upupiformes sensu Mayr (2000)

Upupiformes gen. et sp. indet.

(Fig. 2E, F)

Referred specimen: IRSNB Av 124 (distal right humerus; IG 17702).

Locality and horizon: Steendorp; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

Measurements: Length as preserved, 15.9; distal width, 6.3.

Remarks: This specimen is identified as an upupiform bird by the shape of the small condylus dorsalis, which is proximodistally low and oriented at a very oblique angle towards the longitudinal humerus axis, and by the protruding epicondylus dorsalis. In these features it differs from the humerus of the otherwise similar coraciiform Geranopteridae (Mayr & Mourer-Chauviré 2000). The tuberculum supracondylare dorsale is low but distinct. There is a marked depression on the cranial surface of the condylus ventralis. This depression is less marked in crown group Upupiformes, but present in middle Eocene stem group representatives (Mayr 1998: fig. 10A–C). The tuberculum supracondylare ventrale is situated far distally, with its proximal margin being on a level with the proximal margin of the condylus dorsalis. The processus flexorius is not protruding distally and somewhat shorter than in crown group Upupiformes (Fig. 2G); again the shape of this process is more similar to middle Eocene stem group Upupiformes (Fig. 2D; Mayr 1998: fig. 10A–C) than to the extant representatives. The fossa brachialis is shallow and ventrally situated.

Stem group representatives of Upupiformes are already known from the Early Eocene of Europe and were classified in the extinct taxon Messelirrisoridae (Mayr 1998, 2009b). Upupiform birds have not yet been described from lower Oligocene localities, but there exist fossils from the Luberon (southern France) in private collections (Mayr 2009b). An undescribed upupiform species occurs also in the Late Eocene of the Quercy fissure fillings (Mourer-Chauviré 2006). Two upupiform species of the taxon *Laurillardia* were further reported from the Late Eocene of the Paris Basin in France (Mayr 1998, 2009b), but the very poor preservation of the fossils does not allow for closer comparisons with IRSNB Av 124. The latter is slightly larger than the Early Miocene *Phirriculus pinicola* (distal width of humerus 6.3 mm versus 4.9–5.2 mm; Mlíkovský & Göhlich 2000), from which it further differs in the less strongly distally protruding processus flexorius. The small size of IRSNB Av 124, as well as its close similarity to the humerus of messelirrisorids (Fig. 2D), suggest that the fossil is from a stem group representative of Upupiformes.

?Phaethontiformes Christidis & Boles, 2008

?Phaethontiformes gen. et sp. indet.

(Fig. 3A, B)

Referred specimen: IRSNB Av 125 (right femur; collection Hasse IG 20664, found in 1904).

Locality and horizon: Niel-Boom; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

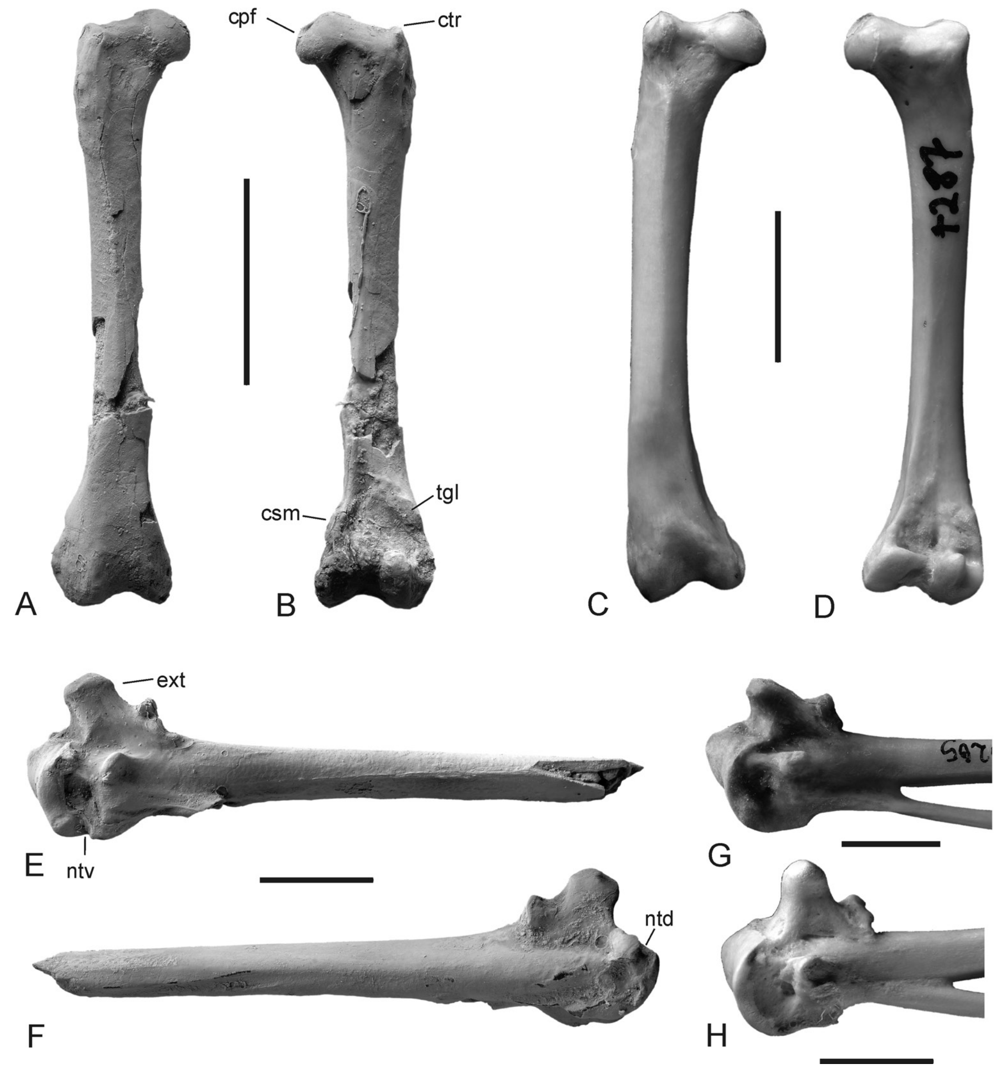

FIGURE 3. ?Phaethontiformes and ?Threskiornithidae from the Rupelian of Belgium. **A**, **B**, ?Phaethontiformes, gen. et sp. indet., right femur (IRSNB Av 125) in cranial (**A**) and caudal (**B**) view, in comparison to **C**, **D**, the right femur of the Red-tailed Tropicbird, *Phaethon rubricauda*, in cranial (**C**) and caudal (**D**) view. **E**, **F**, ?Threskiornithidae, gen. et sp. indet., proximal portion of left carpometacarpus (IRSNB Av 126) in ventral (**E**) and dorsal (**F**) view, in comparison to the left carpometacarpus of **G**, the Northern Bald Ibis, *Geronticus eremita*, and **H**, an immature Madagascar Ibis, *Lophotibis cristata*. Abbreviations: cpf, caput femoris; csm, crista supracondylaris medialis; ctr, crista trochanteris; ext, processus extensorius; ntd, notch in dorsal portion of trochlea carpalis; ntv, notch in ventral portion of trochlea carpalis; tgl, tuberculum musculi gastrocnemialis lateralis. Fossil bones were coated with ammonium chloride. Scale bars equal 10 mm.

Measurements: Length, 29.0; proximal width, 6.2; distal width, 5.9.

Remarks: This femur exhibits a characteristic morphology in that the caput femoris is proximomedially directed, *i.e.*, oriented obliquely to the shaft and not perpendicular as in most other birds. The facies articularis acetabularis is large and globular. The crista trochanteris is very low in proximal direction, but distally continuous with a ridge along the craniolateral margin of the bone. The shaft of the bone is straight and the distal end narrow. At the beginning of its distal third, the bone is broken in two pieces, which were glued together at a slightly inaccurate angle. The crista supracondylaris medialis on the distal end is well-developed (Fig. 3B). The tuberculum musculi gastrocnemialis lateralis is moderately developed, the sulcus patellaris is shallow and wide.

A similar femur morphology is found in some pelecaniform birds, of which only the femora of Phaethontidae are, however, as small as the fossil one, with IRSNB Av 125 being slightly smaller than the femur of the extant White-tailed Tropicbird, *Phaethon lepturus*, which in the one individual available to us measures 32.1 mm. Despite a similar overall morphology, the fossil differs, however, from extant Phaethontidae in the more proximomedially directed caput femoris, the less proximally projecting crista trochanteris, and the more marked fossa poplitea.

The earliest fossils assigned to Phaethontiformes belong to the Prophaethontidae, which occur in the Late Paleocene of Maryland (USA; Olson 1994) and Kazakhstan (Bourdon *et al.* 2008), the Early Eocene of England (Harrison & Walker 1976a) and Morocco (Bourdon *et al.* 2008a), and the Middle Eocene of Belgium (Mayr & Smith 2002a). The earliest unambiguous fossil record of true Phaethontidae dates from the Miocene, with *Heliadornis ashbyi* having been reported from the middle Miocene of Maryland (USA) and Belgium (Olson 1985, Olson & Walker 1997), and *H. paratethydicus* from the Late Miocene of Austria (Mlíkovský 1997). Another record of putative Phaethontidae, *Phaethusavis pelagicus* from the Early Eocene of Morocco (Bourdon *et al.* 2008b), needs confirmation of its affinities within Phaethontiformes by more material (Mayr 2009b).

Among the fossil species, the femur is only known from the prophaethontid *Lithoptila abdounensis* (Bourdon *et al.* 2008a: fig. 2). In this species the crista trochanterica is as low as in IRSNB Av 125, but the caput femoris is not proximally directed, the distal end more medially inflected, the condylus medialis larger, and the crista supracondylaris medialis more prominent.

?"Ciconiiformes" sensu Christidis & Boles (2008)

?Threskiornithidae Richmond, 1917

?Threskiornithidae gen. et sp. indet.

(Fig. 3E, F)

Referred specimen: IRSNB Av 126 (proximal portion of left carpometacarpus; collection Hasse IG 20664).

Locality and horizon: Steendorp; Early Oligocene, between 30.5 and 31.5 Ma (lower part of the Boom Formation, Rupel Group, middle Rupelian).

Measurements: Length as preserved, 54.8; estimated total length, ~65; proximal width, 14.5.

Remarks: This fossil is from a medium-sized bird and, compared to extant taxa, most similar to the carpometacarpus of Threskiornithidae (ibises). The bone is characterized by a distinct notch in the caudal rim of the ventral portion of the trochlea carpalis, and another notch in the proximocranial rim of the dorsal portion of this trochlea (Fig. 3E, F). In these features it differs from extant Threskiornithidae and other taxa with a similar carpometacarpus shape. The processus extensorius is straight and protrudes perpendicular to the long axis of the bone; in most extant Threskiornithidae it is lower and with a more proximally directed tip (Fig. 3G), but a similar shape of the processus extensorius is found in the Madagascar Ibis, *Lophotibis cristata* (Fig. 3H).

In the Paleogene of Europe, Threskiornithidae were reported from the Early Oligocene of the Luberon in France (Roux 2002) and the Late Eocene of England (Harrison & Walker 1976b), but meaningful comparisons with the Belgian fossil are not possible because the carpometacarpus is either poorly preserved (in the case of the Luberon fossil) or unknown (in the case of the Late Eocene *Actiornis anglicus*).

Discussion

By adding six new species to the seven previously described ones, the present study almost doubles the number of bird species known from the Rupelian stratotype (Table 1). Mayr (2009a) already commented on biogeographic affinities between the Rupelmonde avifauna and those of other Lower Oligocene localities in Europe, and Table 2 provides an updated overview of some taxa and localities. In Belgium, Early Oligocene avifaunas are also known from Hoogbutsel and Boutersem, some 60 km southeast of the Rupelmonde area. The fluvio-lacustrine deposits of these fossil sites yielded several taxa so far unknown from the Boom Formation, including duck-like Anseriformes, Charadriiformes, Rallidae, Picidae, and Coliiformes (Mayr & Smith 2001, 2002b). In part this probably reflects different palaeohabitats (marine versus fluvio-lacustrine) and depositional environments, but a collection bias towards larger fossils may have also contributed to the scarcity of very small bird remains in the Rupelmonde avifauna.

Diomedeoidid Procellariiformes and other aquatic birds that occur in the Boom Formation were widespread in the Rupelian epicontinental sea system, which covered Europe in the Early Oligocene (Mayr 2009b). Some of the terrestrial taxa also appear to have had a wide distribution across Europe, and the newly reported fossils add Paraortygidae and Trogoniformes to those avian groups, which are also known from Lower Oligocene localities in southern Europe.

As detailed above, the sternum of *Paraortyx* lacks a spina interna. A spina interna is likewise absent in the Early Eocene Gallinuloididae (Mayr 2006: fig. 3a, 2009b), which further differ from crown group Galliformes in a much more robust furcula and a more cranially prominent apex of the carina sterni. These differences in the morphology of the pectoral girdle bones were ascribed to the presence of a large crop in crown group Galliformes, which, through the shift of the center of gravity and the caudal displacement of the pectoral muscles, led to modifications in the morphology of the pectoral girdle bones (Stegmann 1964; Mayr 2006). The plesiomorphic sternum morphology found in *Paraortyx* indicates that a large crop, one of the key innovations of crown group Galliformes, was not developed in Paraortygidae, and these birds were thus probably not yet adapted to regular processing of very coarse and dry plant matter (Mayr 2006).

Trogons are predominantly frugivorous or insectivorous birds with poor migration capabilities and are today only found in subtropical and tropical regions. However, these birds had a long evolutionary history in Europe (Mayr 2009b), and in the Early Eocene they even occurred in the northern part of Denmark (Fig. 4A; Kristoffersen 2002). The Belgian fossil reported here is the so far northernmost occurrence of trogons in post-Eocene deposits (Fig. 4A), and indicates the presence of forests or at least woodlands in the

TABLE 1. List of avian taxa reported from the Rupelian of the Boom Formation

Order	Family	Species	References
?Anseriformes	family inc. sed.	*Cygnopterus affinis*	Lambrecht (1931)
Procellariiformes	Diomedeidae	*Tydea septentrionalis*	Mayr & Smith (2012b)
	Diomedeoididae	*Rupelornis definitus* (incl. *Vanellus selysii* van Beneden, 1871)	Mayr, 2009b; Mayr & Smith (2012a)
Gaviiformes	Gaviidae	“*Anas*” *benedeni* (= *Anas creccoides* van Beneden, 1871)	Mayr (2009a); this study
Galliformes	Paraortygidae	*Paraortyx* cf. *lorteti*	this study
		Paraortyx brancoi	this study
		cf. *Pirortyx major*	this study
“Gruiformes”	Parvigruidae	cf. *Parvigrus pohli*	Mayr (2013)
		Rupelrallus (?) *belgicus*	Mayr (2013)
Strigiformes	Selenornithidae	*Selenornis steendorpensis*	Mayr (2009a)
Trogoniformes	Trogonidae	?*Primotrogon* sp.	this study
Upupiformes	family inc. sed.	gen. et sp. indet.	this study
?Phaethontiformes	family inc. sed.	gen. et sp. indet.	this study
?“Ciconiiformes”	?Threskiornithidae	gen. et sp. indet.	this study
species of doubtful affinities			
order inc. sed.	family inc. sed.	“*Puffinus*” (“*Larus*”) *raemdonckii*	van Beneden (1871)
order inc. sed.	family inc. sed.	“*Fulica*” *dejardinii*	van Beneden (1871)

palaeoenvironment of the Boom Formation.

We finally comment on the affinities of "*Anas*" *benedeni* Sharpe, 1899, a species originally described by van Beneden (1871) under the preoccupied name "*Anas creccoides*". The original material assigned to "*A.*" *benedeni* includes a humerus lacking the proximal end, a proximal humerus, and two proximal ulnae. Brodkorb (1962) removed the species from Anseriformes, considering its affinities uncertain and designating the more complete humerus as the lectotype. Whereas other material referred to "*A. creccoides*" by van Beneden (1871) belongs to the procellariiform Diomedeoididae (Mayr 2009b; Mayr & Smith 2012a), the lectotype humerus closely resembles a humerus of a gaviiform bird from the Boom Clay, which was assigned by Mayr (2009a) to *Colymboides* (?) *metzleri*, a species originally described from the Early Oligocene Rhine Graben locality Frauenweiler (Mayr 2004) (Fig. 4B, C). Based on the published figure of the lectotype humerus, we consider it most likely that "*Anas*" *benedeni* is a gaviiform bird. However, because the condylus dorsalis shows slight differences to *Colymboides* (?) *metzleri* in size and orientation (Fig. 4B, C), we refrain from any taxonomic action until the "*Anas*" *benedeni* lectotype, which is not in the collection of IRSNB, is located.

Acknowledgements

We thank A. Folie (IRSNB) for assisting in the loan of the fossil birds to GM, and S. Tränkner (SMF) for taking the photographs. We are further

TABLE 2. Comparison of the Rupelmonde avifauna with other early Oligocene (MP 21–23) European localities (after Mayr 2009b and references listed in the reference list); entries for the middle Eocene to late Oligocene Quercy fissure fillings include only records with a proven early Oligocene age (after Mourer-Chauviré 2006).

	Belgium		**Germany**		**France**	
	Rupelmonde	**Boutersem/ Hoogbutsel**	**Weißelster Basin**	**Frauenweiler**	**Luberon**	**Quercy**
Paraortygidae	+	–	+	–	–	+
Diomedeidae	+	–	–	–	–	–
Diomedeoididae	+	–	+	+	–	–
Gaviiformes	+	+	–	+	–	–
Parvigruidae	+	–	+	–	+	–
Selenornithidae	+	–	–	–	–	+
Upupiformes	+	–	–	–	+[b]	–
Trogoniformes	+	–	–	+	+	–
Pelecanidae	–	–	–	–	+	–
Phalacrocoracidae	–	–	–	–	+[b]	–
Anatidae	–	+	–	–	–	–
Charadriiformes	–	+	–	+	+	–
Rallidae	–	+	–	–	–	–
Idiornithidae	–	?[a]	–	–	–	+
Archaeotrogonidae	–	–	–	–	–	+
Coliiformes	–	+	–	+	–	–
Todidae	–	–	–	+	–	+
Sylphornithidae	–	+	–	–	–	–
Piciformes	–	+	–	+	–	–
Passeriformes	–	–	–	+	+	–

[a] a fragmentary distal tarsometatarsus was tentatively identified by Mayr & Smith (2001)

[b] unpublished fossils in private collections (Mayr 2009b)

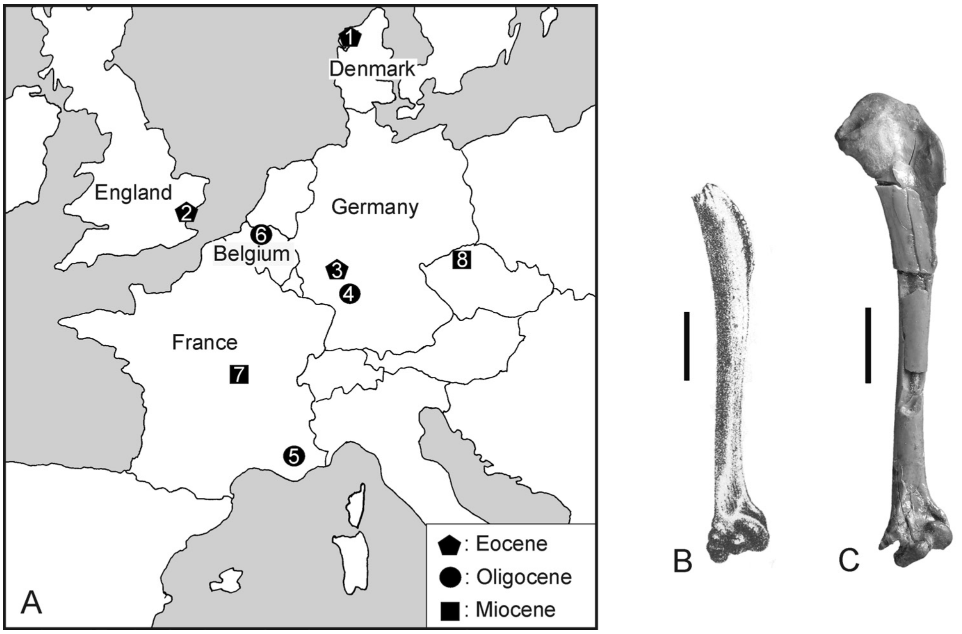

FIGURE 4. A, Map of Central Europe with localities where fossil Trogoniformes were found (after Mlíkovský 2002; Mayr 2009b, 2011): 1 – Fur Formation, Denmark (Early Eocene); 2 – London Clay (Clacton-on-Sea), England (Early Eocene); 3 – Messel, Germany (Middle Eocene); 4 – Frauenweiler, Germany (Early Oligocene); 5 – Luberon, France (Early Oligocene); 6 – Steendorp, Belgium (Early Oligocene); 7 – Saint-Gérand-le-Puy, France (Early Miocene); 8 – Dolnice, Czech Republic (Early Miocene; undescribed record mentioned by Mlíkovský 2002: 227). **B**, **C**, Humeri of loons (Gaviiformes) from the Boom Formation. **B**, lectotype of *Anas benedeni* Sharpe, 1899 (from van Beneden 1871: fig. 3). **C**, right humerus (reversed as to appear from the left side to facilitate comparison) from the Rupelian of Niel-Boom (IRSNB Av 85), which was assigned to *Colymboides* (?) *metzleri* by Mayr (2009a). Scale bar in B and C equals 10 mm; scale for *A. benedeni* based on the assumption that figures in van Beneden (1871) represent the natural size of the bones.

indebted to E. Steurbaut (IRSNB) for information about the age of the Boom Formation, and to the reviewers, C. Mourer-Chauviré and N. Zelenkov, for thoughtful comments, which improved the manuscript. This study is a contribution to project MO/36/020 supported by the Federal Science Policy Office of Belgium.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
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A review of avian remains from the Oligocene of the Outer Carpathians and Central Paleogene Basin

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Abstract — The paper is a brief review of avian specimens that were found in marine deposits of the Paratethys in the Oligocene sites of Poland, Slovakia and Czech Republic. It provides additional information on the localities and comments on their faunas.

Key words: Oligocene, birds, Poland, Slovakia, Czech Republic, Paratethys

Introduction

Several bird specimens were described from the Oligocene of Poland, Slovakia and Czech Republic during the last few years. This paper summarizes our knowledge on the avian specimens from that part of the Paratethys and presents additional information on the sites.

During the Oligocene, large parts of central and eastern Europe were covered by the Paratethys, a northern branch of the Tethys Ocean (Fig. 1). During the Alpine orogeny, the Paratethys was separated from the Tethys by the Alps, Carpathians and other mountains but the separation was not a single event because the Paratethys was at times reconnected with the Tethys. It gradually became shallower and finally disappeared during the Late Miocene, becoming an isolated inland sea. Today's remnants of the Paratethys include the Black Sea, Caspian Sea and Aral Sea (Rögl 1999; Schulz *et al*. 2005).

The Menilite beds of the Carpathian flysch zone (northeastern Czech Republic and southeastern Poland) and the Central Paleogene basin (northern Slovakia) are very rich in Oligocene fish fossils. The ichthyofauna is not only very rich and diverse but also very characteristic for particular strata. Therefore the palaeoecological assemblages are successfully used in biostratigraphy, especially in the Polish part of the Carpathians (Fig. 2). The fish-bearing levels have been assigned to the respective IPM (Ichthyofauna, Paleogene, Menilite-Krosno Series) zones (IPM1 to IPM6) and correlated with the calcareous nannoplankton in the standard zonation (comprising NP22 to NP25 zones) and together they indicate the geological age (Kotlarczyk & Jerzmańska 1976; Kotlarczyk *et al*. 2006). In Poland, many thousand of fish fossils have been recovered mainly during the late 1970s until the mid 1990s from more than 200 outcrops (Kotlarczyk *et al*. 2006). Since that time many of the localities have been overgrown with vegetation and partly or completely destroyed by natural processes or people. The state of preservation of the sites (Fig. 3) that yielded avian remains and

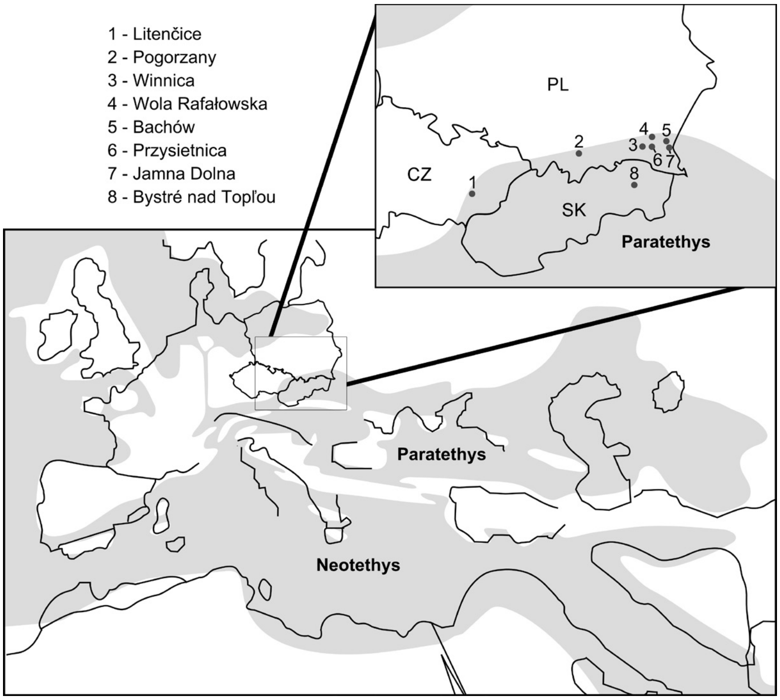


FIGURE 1. Early Oligocene paleogeography, with all known sites with bird remains from Poland, Slovakia and Czech Republic (inlet). Grey areas indicate the extent of the Oligocene sea. Modified from Rögl (1999).

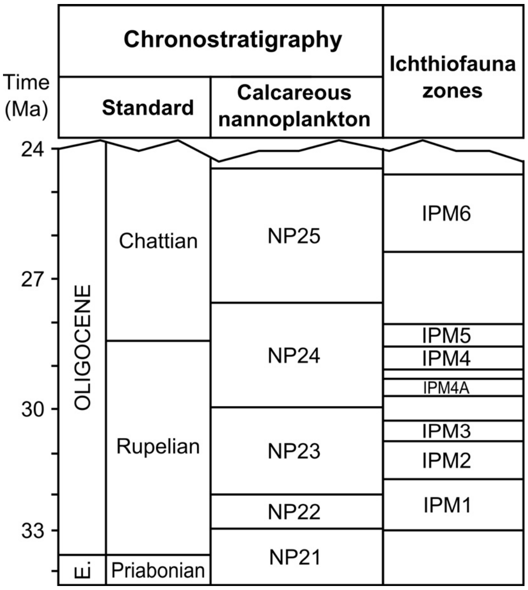
their GPS positions (Tab. 1) were recorded during a survey of Polish sites conducted between 2010 and 2012.

Animal fossils other than fishes are found only sporadically in the Carpathian Flysch. Birds are also extremely rare (Bochenski *et al*. 2012). They are usually preserved as incomplete but articulated imprints on slabs; only on one occasion (?*Diomedeoides lipsiensis* from Pogorzany, Poland) a three-dimensional bone fragment was extracted from a breccia (Tab. 1). Skeletons or their fragments remain in articulation in marine environments only if they reach the burial place soon after death because soft tissues begin to decompose rapidly and skeletal elements disarticulate fast (Schäfer 1972). Therefore, it seems that all but one of the birds must have got into the water, drowned and sank to the bottom rather than being transported in streams or flushed to the sea. This is in agreement with taphonomic studies carried out on fish remains where it was suggested that articulated fish specimens have been preserved due to a quiet environment, pelagic sedimentation and anoxic conditions (Bieńkowska-Wasiluk 2010; Kotlarczyk *et al*. 2006). The single bone from Pogorzany (Poland) was probably deposited as a result of submarine debris flow or turbidity currents (Elzanowski *et al*. 2012).

The avifauna

The nine avian specimens described so far from the marine deposits of eight localities of the Outer Carpathians and Central Paleogene Basin represent taxonomically very diversified groups: Procellariiformes (Elzanowski *et al*. 2012; Gregorová 2006), Apodiformes (Bochenski & Bochenski 2008), Coraciiformes (Kundrat *et al*. in press), Piciformes (Mayr & Gregorová 2012), Passeriformes (Bochenski *et al*. 2011, 2013, in press) and Aves indet. (Bochenski *et al*. 2010). A big taxonomic diversity of fossil birds points to complex habitats and very rich avifauna in that part of the Paratethys which agrees with the fossil records from other parts of Europe (Mayr 2009). It is noteworthy that seven of the nine specimens are land birds that must have lived in the forests near the shoreline and were blown off to sea or perished during migration. The predominance of terrestrial birds in marine deposits is not an

FIGURE 2. Chronostratigraphy of the Oligocene. The characteristic ichthyofaunal zones (IPM) are correlated with the calcareous nannoplankton zonation (NP) and together they indicate the geological age. Modified from Kotlarczyk *et al*. (2006).



unusual phenomenon (Mayr 2009). A similar tendency is also observed in many other Paleogene localities including the Eocene Fur Formation of Jutland in Denmark (Kristoffersen 2002) and London Clay Formation in southern England (Mlíkovský 2002), as well as in the Oligocene Wiesloch-Frauenweiler in southern Germany (Mayr 2009). In addition to skeletal specimens, a number of isolated feather imprints have been found in the Carpathians. These specimens are housed in various collections and are sometimes mentioned in the publications but none of them

TABLE 1. Data on all avian specimens from the Oligocene of the Outer Carpathians and Central Paleogene Basin. Asterisk (*) indicates approximate geographic coordinates.

Taxon	Preservation	Coordinates	Age	Publications	Site
Procellariiformes					
?*Diomedeoides lipsiensis* (Fischer, 1983)	isolated coracoid	49°47.06′ N 20°10.49′ E	Rupelian	Elzanowski *et al.* (2012)	Pogorzany*
Procellariidae	part of wing and legs	49°11.56′ N 17°12.16′ E	Rupelian	Gregorová (2006)	Litenčice*
Apodiformes					
Eurotrochilus noniewiczi Bochenski & Bochenski, 2008	nearly complete	49°37.94′ N, 021°40.44′ E	Rupelian, NP23, IPM2	Bochenski & Bochenski (2008)	Winnica
Coraciiformes					
Putative upupiform	articulated leg	49°00.20′ N 21°32.39′ E	Rupelian	Kundrat *et al.* (in press)	Bystré nad Topľou*
Piciformes					
Picavus litencicensis Mayr & Gregorová, 2012	postcranial skeleton	49°11.56′ N 17°12.16′ E	Rupelian, NP23	Mayr & Gregorová (2012)	Litenčice*
Passeriformes					
Jamna szybiaki Bochenski, Tomek, Bujoczek, Wertz, 2011	nearly complete	49°38.67′ N, 022°33.52′ E	Rupelian, NP23,IPM2	Bochenski *et al.* (2011)	Jamna Dolna
Resoviaornis jamrozi Bochenski, Tomek, Wertz, Swidnicka, 2013	nearly complete	49°59.25′ N, 022°09.53′ E	Rupelian, NP24, IPM4	Bochenski *et al.* (2013)	Wola Rafałowska*
Passeriformes indet.	articulated leg	49°43.98′ N, 022°03.02′ E	Rupelian, NP24, IPM4A	Bochenski *et al.* (in press)	Przysietnica
Aves indet.					
Aves indet.	articulated foot	49°46.18′ N, 022°29.52′ E	Chattian, NP25, IPM6	Bochenski *et al.* (2010)	Bachów

FIGURE 3. Photographs of Polish Oligocene sites that yielded avian remains. **A**, Bachów: high bank of a stream (an avian foot of inresolved affinities); **B**, Winnica: high bank of the Jasiolka River (a near-complete hummingbird, *Eurotrochilus noniewiczi*); **C**, Przysietnica: steep slope bordering a dirt road (a passerine leg); **D**, Jamna Dolna: high bank of Jamninka stream, a tributary of the Wiar (a near-complete passerine, *Jamna szybiaki*); **E**, Wola Rafałowska: high bank of a stream, a tributary of the river Strug (a near-complete passerine, *Resoviaornis jamrozi*); **F**, Pogorzany: high bank of a stream (an isolated coracoid of ?*Diomedeoides lipsiensis*).

has been described so far, probably because they are not attributable to particular avian taxa (Bieńkowska-Wasiluk 2010; Boué 1829; Kalabis 1950; personal observations). The fossil record from Poland, Slovakia and Czech Republic increases our knowledge on the Oligocene bird fauna of Europe by at least four new taxa.

Acknowledgments

We thank the reviewers of the manuscript, Andrzej Elzanowski (Museum and Institute of Zoology, Warsaw) and Růžena Gregorová (Moravian Museum, Brno), for their valuable comments.

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Paleornithological Research 2013

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A fossil stone-curlew (Aves: Burhinidae) from the Late Oligocene/Early Miocene of South Australia

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Abstract — *Wilaru tedfordi* nov. gen. et nov. spec. is a fossil burhinid from Upper Oligocene/Lower Miocene sites in northern South Australia. Almost all specimens come from Lake Pinpa, with a few recovered from Lake Palankarinna and Billeroo Creek. Numerous specimens have been recovered, representing most elements of the pectoral girdle, forelimb and hindlimb. This is the oldest known burhinid. It shares several morphological character states with the genus *Esacus* and, like that taxon, had a proportionally long humerus and short tarsometatarsus, although the difference is much more pronounced. Also like species of *Esacus*, and in contrast to those of *Burhinus*, *Wilaru* may have frequented the shorelines of lakes and rivers.

Key words: Burhinidae, stone-curlew, *Wilaru tedfordi*, Late Oligocene/Early Miocene, Australia

Introduction

The Burhinidae is a distinct but low diversity group in the order Charadriiformes. Currently, it includes nine extant species, two named fossil species and one fossil subspecies, found globally in a variety of habitats. These fossil and extant species are placed in two genera, *Burhinus* Illiger, 1811 (containing nine species and the fossil subspecies) and *Esacus* Lesson, 1831 (two species). Colloquially, burhinids are known as thick-knees owing to their prominent ankle joints.

Burhinids are long-legged, terrestrially foraging and breeding birds. They are good fliers, but prefer to spend most of their time on the ground. Most species of *Burhinus* are similar in structure, with moderately long wings and legs (body length 320–480 mm, wing length measured from bend of wrist to longest primary 200–248 mm, mass 290–535 g). The considerably larger *B. grallarius* (Latham, 1802) (body length 540–590 mm, wing length 270–288 mm, mass 580–860 g) has similar proportions except for its markedly elongated tarsometatarsus. The two species of *Esacus* are more stocky birds than those of *Burhinus*. *Esacus magnirostris* (Vieillot, 1818) is of similar general size to *B. grallarius* (body length 530–570 mm, wing length 270–300 mm), but it has proportionally shorter legs and a larger bill and is notably heavier (870–1130 g). *Burhinus* and *Esacus* species also differ in habitat preferences. Modern burhinids occur in temperate and warm zones of the Americas, Africa, Middle East and Indo-Australasia. The species of *Esacus* are found on the shorelines of oceans and rivers, while those of *Burhinus* "tend to frequent a variety of exposed, largely low-lying, flat or rolling landscapes" (Hume 1996) from temperate open woodland to semi-arid to arid country with little vegetation and avoiding forest and heavily vegetated areas.

Two extant species, one from each genus, occur in Australia. *Burhinus grallarius*, the Bush Thick-knee, commonly inhabits grassy woodlands and rarely associates with water bodies (Geering *et al.* 2007). *Esacus magnirostris*, the Beach Thick-knee, is strictly coastal, inhabiting a variety of types of beaches (Geering *et al.* 2007).

There has been limited osteological work on burhinids. Shufeldt (1915) described the skeleton of *E. magnirostris* but did not compare this taxon to other species. Strauch (1978) and Livezey (2010) incorporated all species in larger studies of the Charadriiformes, but detected very little variation in the post-cranial skeletons. Differences were largely confined to the skull, with members of *Esacus* having more massive bills than those of *Burhinus* (Geering *et al.* 2007).

The fossil record of the Burhinidae is sparse. Of reliably identified fossil burhinids, there are two named palaeospecies, *Burhinus lucorum* Bickart, 1981 (Lower Miocene Sheep Creek Formation, late Hemingfordian, Nebraska, United States) and the Late Pleistocene *B. aquilonaris* Feduccia, 1980 (Sanborn Formation, Kansas). Quaternary-aged burhinid fossils (living neospecies and undetermined species *Burhinus* sp.) are known from several continents (Brodkorb 1967; Howard 1971), and a palaeosubspecies of the living *B. bistriatus* (*B. bistriatus nanus* Brodkorb, 1959) has been described from the Bahamas. Baird (1991) noted the presence of *B. grallarius* in Quaternary cave deposits in Australia.

A supposed burhinid from Upper Cretaceous sediments in Antarctica was reported by Cordes (2002) in a conference abstract, but no formal paper on this material has been published. Burhinid-like post-cranials from Eocene of Australia (Boles 1999) were referred to the Graculavidae, a form-family created to accommodate various taxa with similar post-cranial skeletons and for which the cranial material was unknown. The possibility has been raised that these may be anseriform (Elzanowski & Boles 2012). Harrison & Walker (1976) reported a burhinid from the Late Eocene of England, but this was dismissed by Mayr (2006) as not being even assigned to the Charadriiformes with certainty.

Vickers-Rich (1991) cited a large collection of burhinid fossils recovered from several Late Oligocene/Early Miocene-aged sites in the Lake Eyre region of northern South Australia, with most elements of the skeleton represented. This taxon was regarded as "clearly a form distinct from the Australian forms of today, at least rating a new specific recognition" (Vickers-Rich 1991, p. 760). Here, on the basis of this material, the most extensive for any paleospecies in this family, we describe the first burhinid fossil genus and species from Australia.

Study Area

The fossils discussed in this paper were recovered from fluvio-lacustrine sites in two depositional regions of the Lake Eyre Basin in South Australia (Fig. 1). A small number of fossils came from Lake Palankarinna (28°46–47′ S, 138° 24′ E) in the western Tirari Sub-basin (= Lake Eyre Sub-basin) from localities in the Etadunna Formation. Burhinids from the Ngapakaldi Fauna were collected from several sites on the western side of Lake Palankarinna, while a single burhinid bone from the Ngama Local Fauna was recovered from Mammalon Hill at the northern end of the lake.

Lake Pinpa (= Pine Lake) (31°8′ S, 140° 13′ E) and the neighbouring Billeroo Creek (31° 6′ S, 140° 14′ E) in the eastern Callabonna Sub-basin (= Tarkarooloo Sub-basin) contain the Pinpa Fauna, which occurs in sediments that lie near the top of the Namba Formation in the green dolomitic claystones cropping out on the west side of Lake Pinpa. Three bones came from Billeroo Creek, while the vast majority of all specimens were found at Lake Pinpa, in particular, Site C ("an area on the western shore of the lake that extends north from the E-W cross lake track to about the location of the base of my measured section of 1971, *e.g.*, grid coord. 317148, Curnamona [1:250.000] sheet, (R. Tedford, pers. comm., 30 August 2006)", cited by Worthy (2009). Within Site C, almost all were found at a single location, QMAM 47, by two of us (P. Vickers-Rich and T. Rich), who participated in the 1971 joint Queensland Museum–American Museum of Natural History Museum expedition led by R. (Dick) H. Tedford.

A review of the available evidence by Woodburne *et al.* (1994, p.485) concluded "that all of the isotopic, foraminifera and magnetostratigraphic data are consistent with an approximate age of 24–26 my for the Etadunna Formation in the Lake Eyre Basin". Woodburne *et al.* (1994) are followed regarding correlation between the Etadunna and Ngama Formations and nomenclature of local faunas and mammal zones. They correlated Zone A of the Etadunna Formation, the oldest mammal zone, containing the Minkina LF, with the Pinpa Fauna in the Namba Formation and Zone B, containing the Ditjimanka Local Fauna at Lake Palankarinna, with the Ericmas Fauna in the upper part of the Namba Formation. Woodburne (1986) and Woodburne *et al.* (1994) identified the black and brown claystone beds at Mammalon Hill as the youngest part of the Etadunna Formation cropping out at Lake Palankarinna. In sum, the oldest is the Pinpa Fauna, followed by the Ngapakaldi Fauna, with the Ngama Local Fauna youngest. The setting is dominantly lacustrine and partly fluviatile and outcrop sporadic.

The collections have been made through several field visits by various institutions and these often have locality site codes. Most of the specimens were collected during joint Queensland Museum–American Museum expeditions in 1971 and 1973; these have site localities with prefix QMAM (1971: 41, 47, 59; 1973: 125, 133, 151, 199, 243, 264). A few fossils were obtained during fieldwork by the University of California, Museum of Paleontology (site codes V-5375, V-5762, V-5764).

Material and Methods

Anatomical terminology follows that of Baumel & Witmer (1993). Measurements (mm) were generally taken following Steadman (1980) except where explained below. All measurements were taken with electronic digital callipers and rounded to 0.1 mm.

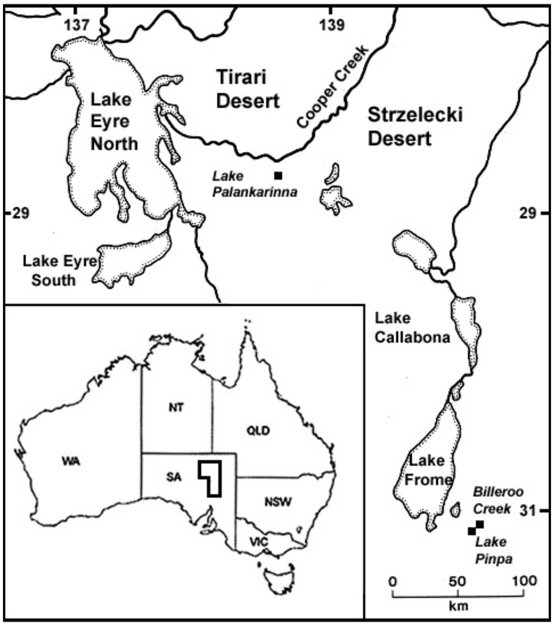

FIGURE 1. Locations in northeastern South Australia, central Australia, at which *Wilaru tedfordi* nov. spec. material was found: Lake Pinpa, Lake Palankarinna and Billeroo Creek.

All major elements of the limbs and pectoral girdle are represented in the fossil collection. The material studied here is housed in several institutions, but the vast majority is in the American Museum of Natural History, New York (specimen registration number prefix AMNH); a few are in the collections of the University of California Museum of Paleontology, Berkeley (UCMP), Museum Victoria, Melbourne (MV) and South Australian Museum, Adelaide (SAM). Representative specimens of the elements were transferred to the South Australian Museum from the American Museum holdings.

Comparative skeletons were made available from the collections of Museum Victoria, Melbourne (MV), Australian Museum, Sydney (AM) and Australian National Wildlife Collection, Canberra (ANWC): *Burhinus grallarius* (MV B20430, B25090, AM O.43444, O.44452, O.63417, O.66366, ANWC B30772, B30774, B30775), *B. oedicnemus* (Linneaus, 1758) (AM O.69165), *B. bistriatus* (Wagler, 1829) (MV B13715), *B. capensis* (Lichtenstein, 1823) (MV B13648, ANWC B23045), *Esacus magnirostris* (MV W6587, B13191, B14255, AM O.65024, ANWC B23052). These were supplemented by images of material of additional species provided by the United States Museum National Museum, Washington (USNM), Los Angeles County Museum of Natural History, Los Angeles (LACM), and Natural History Museum

(British Museum), Tring (BM): *B. senegalensis* (Swainson, 1837) (USNM 553053, 322589), *B. vermiculatus* (Cabanis, 1868) (USNM 291425, 430630), *B. superciliaris* (Tschudi, 1843) (LACM Ecuador 1–6, 9–12) and *B. oedicnemus* (BM A5582). These were used to assist in assessing characters but not for measurements. The extant *Esacus recurvirostris* (Cuvier, 1829) was not represented, but it is similar to *E. magnirostris*. The fossil burhinid species *Burhinus lucorum* and *B. aquilonaris* were represented by a cast (AMNH 10215) and by an image from the University of Kansas Natural History Museum, Lawrence (KNHM 6822), respectively.

Abbreviations: art., articularis; d, distal; L, left; o, omal; lig., ligamentum/ligamentum/ligmentosa; m, musculus/musculi; p, proximal; R, right; s, shaft; tub., tuberculum/tuberculi. For institutional acronyms, see above.

Systematic Palaeontology

Order Charadriiformes Huxley, 1867
Family Burhinidae Mathews, 1912

The characters on which the skeletal elements are referred to the Burhinidae are given in the descriptions below. For those elements for which diagnostic characters could not be identified on the material available assignment to this family was made for those most comparable to modern burhinid morphology.

Genus *Wilaru* nov. gen.

Type and only species: *Wilaru tedfordi* nov. spec.

Diagnosis: *Wilaru* differs from *Burhinus* and *Esacus* by having a unique combination of characters, including the following. Humerus: caput humeri merges with tuberculum dorsale without being separated by a notch; fossa pneumotricipitalis larger and deeper and extends to margo caudalis; fossa m. brachialis extends across proximal sides of condyli to dorsal and ventral borders of cranial face. Scapula: acromion much longer; tub. coracoideum larger and more bulbous. Coracoid: omal half deflected further medially; sulcus m. supracoracoidei with flatter dorsal border; processus procoracoideus short and triangular, lacking cranially-directed strap-like projection; projection on the sternal end of the medial margin more distally located. Carpometacarpus: dorsal and ventral rims of the trochlea carpalis extend caudally to about the same extent; sulcus tendineus deeper. Femur: collum femoris more constricted; facies art. antitrochanterica with more prominent caudally protruding lip. Tarsometatarsus: much shorter in proportion to humerus; proximal and distal ends proportionally wider; apex of the eminentia intercotylaris broader and more rounded; crista lateralis hypotarsi longer and thinner; sulcus extensorius much shallower on distal half of shaft; trochlea metatarsi II with greater medial inflection; trochlea metatarsi II with greater plantar extent. Additional characters are given below.

Etymology: ‘Wilaru’ for ‘stone curlew’ in the language of the Australian Dieri tribe of the Lake Eyre region of South Australia (Blake 1981).

Wilaru tedfordi, nov. spec.
(Figs 2–4, 5A–B)

Holotype (Fig. 3D, E): Left humerus SAM P48925 (formerly AMNH 11442) missing proximodorsal corner of processus deltopectoralis, ventral border of processus bicipitalis, with the shaft fractured and repaired. Collected by T.H. Rich and P. Vickers-Rich in 1971 on joint Queensland Museum-American Museum of Natural History expedition led by R.H. Tedford.

Diagnosis: As for genus.

Etymology: After Richard H. Tedford (1929–2011) of the American Museum of Natural History, who led the 1971 expedition during which these fossils were collected and, who along with R.A. Stirton (University of California, Berkeley), spent many field seasons in South Australia, the first comprehensive surveys of the region for fossil vertebrates.

Type locality: Lake Pinpa, Site C, collection code QMAM 47 (31° 07′ S, 140° 13′ E), South Australia.

Horizon and age: Namba Formation, late Oligocene–early Miocene (24–26 my) (Woodburne *et al.* 1994), Pinpa LF.

Distribution: Late Oligocene (24–26 my), South Australia, Australia: Lake Pinpa and Billeroo Creek, Namba Formation, Pinpa LF; Lake

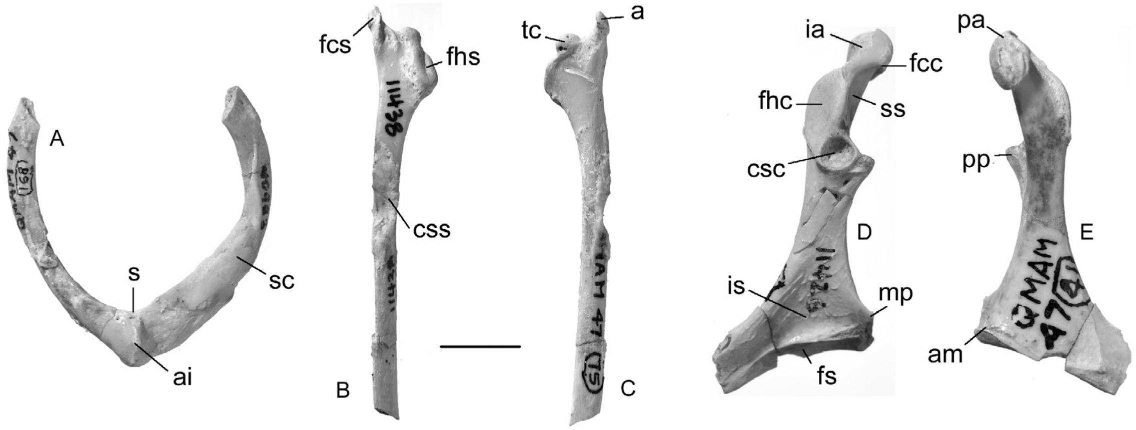

FIGURE 2. Pectoral girdle elements of *Wilaru tedfordi* nov. spec.: **A**, furcula AMNH 11983 (caudal view); **B**, **C**, proximal right scapula SAM P48923 (formerly AMNH 11438) (lateral and medial views); **D**, **E**, left coracoid AMNH 11426 (dorsal and ventral views). a, acromion; am, angulus medialis; ai, apophysis interclavicularis; csc, cotyla scapularis; css, corpus scapulae; fcc, facies art. clavicularis; fcs, facies art. clavicularis; fhc, facies art. humeralis; fhs, facies art. humeralis; fs, facies art. sternalis; ia, impressio lig. acrocoracohumeralis; is, impressio m. sternocoracoidei; mp, medial projection on sternal end of coracoid; pa, processus acrocoracoideus; pp, processus procoracoideus; s, symphysis; sc, scapus claviculae; ss, sulcus m. supracoracoidei; tc, tub. coracoideum. Scale bar equals 10 mm.

Palankarinna, Etadunna Formation, Ditjimanka LF, Zone B.

Measurements of holotype: Length = 123.3 mm, depth of caput humeri = 6.2 mm, distal width = 15.1 mm, distal depth = 8.8 mm.

Paratypes: Humeri (Fig. 3C), Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 11402 pR, AMNH 11403 pR, AMNH 11404 pR and AMNH 11405 pL, each retaining only caput humeri and tuberculum dorsale; AMNH 11406 pR retaining caput humeri and proximal section of crista deltopectoralis; AMNH 11407 pR lacking caput humeri and proximal edges of cristae deltopectoralis and bicipitalis; AMNH 11409 dL lacking fragment of shaft; AMNH 11441 dR retaining about half the shaft; AMNH 11451 L in two parts with the proximal end retaining some shaft and missing the edge of the crista deltopectoralis; AMNH 11452 dL retaining about half the shaft; AMNH 11454 pR with crista deltopectoralis and crista bicipitalis damaged; AMNH 11470 dR in good condition; AMNH 11476 dR lacking shaft with damage to surface of condylus lateralis. Lake Pinpa, Site C, collection code QMAM133, Namba Formation, Pinpa Fauna: AMNH 10836 dR with condyli heavily abraded. Lake Pinpa, Site C, collection code QMAM243, Namba Formation, Pinpa Fauna: AMNH 10859 dL missing condylus ventralis. Lake Pinpa, Site C, Namba Formation, Pinpa Fauna: AMNH 10723 dL quite abraded. Lake Palankarinna, Site 5 (V5765), RHT#455, Etadunna Formation, Ditjimanka LF: UCMP 57005 dL with about 50 % of shaft.

Description: Humeri: Assignment of the humeral fossils to the Burhinidae is based on the following suite of characters. The non-pneumatic fossa pneumotricipitalis is broad, relatively deep, rather rectangular and has its major axis directed about 145° to shaft. The impressio coracobrachialis is wide and shallow, poorly defined ventrally and distally (in cranial view). The processus supracondylaris dorsalis, strongly developed in most charadriiforms, is small and relatively close to the distal end, roughly level with proximal border of the condylus dorsalis.

Wilaru differs from living burhinids in the following features: The caput humeri merges more smoothly with the tuberculum dorsale, rather than being separated by a depression or notch (cranial view). The proximal third of the shaft on both the dorsal and ventral sides slopes sharply away from the margo caudalis. On the ventral side, this results because the fossa pneumotricipitalis is large and deep and extends to the margo caudalis, rather than being separated by a gap c. 30 % of the fossa width as in other burhinids. A crus dorsale fossae does not appear to be present;

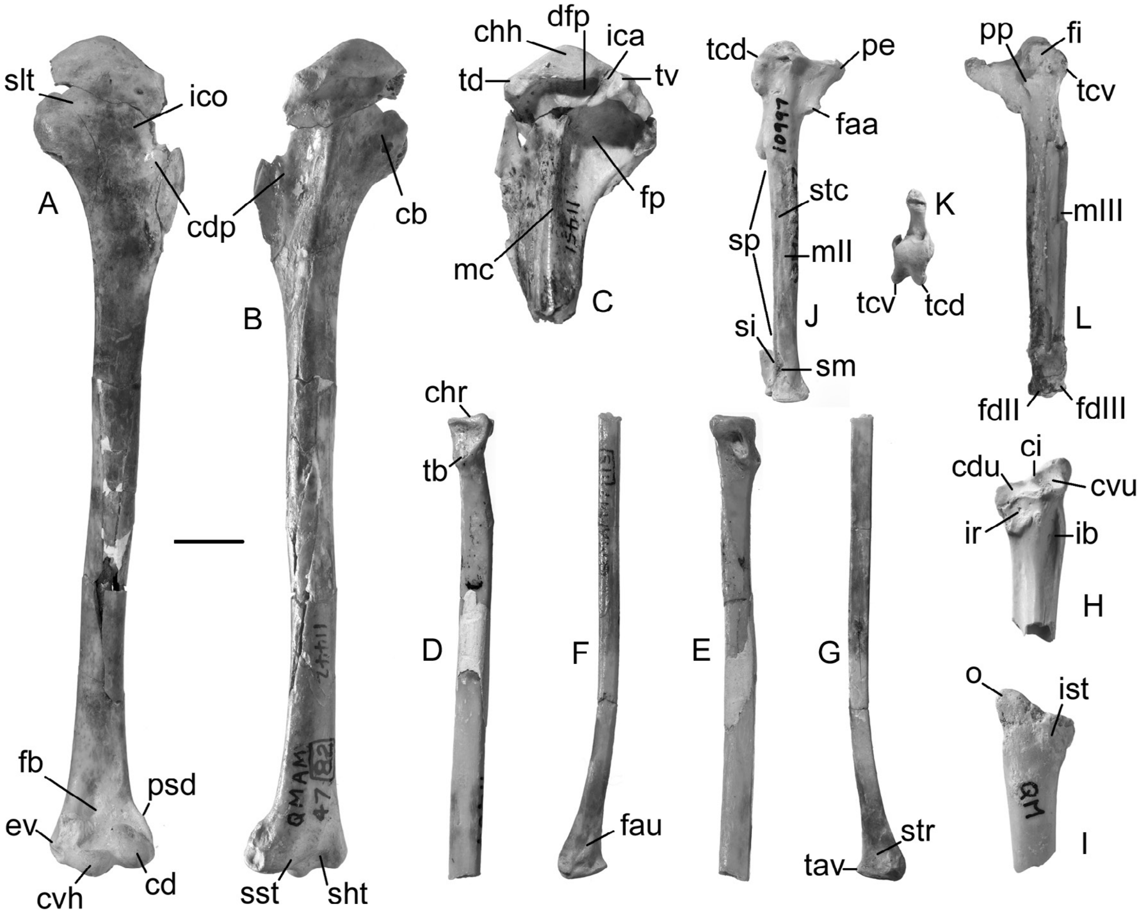

FIGURE 3. Forelimb elements of *Wilaru tedfordi* nov. spec.: **A**, **B**, left humerus SAM P48925 (formerly AMNH 11442; holotype) (cranial and caudal views); **C**, proximal left humerus AMNH 11451 (caudal view); **D**, **E**, proximal left radius AMNH 11464 (ventral and dorsal views); **F**, **G**, distal left radius AMNH 11464 (ventral and dorsal views); **H**, **I**, proximal right ulna unnumbered; **J**, **K**, right carpometacarpus SAM P48928 (formerly AMNH 10997) (dorsal and proximal views); **L**, right carpometacarpus AMNH 11448 (ventral view). cb, crista bicipitalis; cd , condylus dorsalis; cdp, crista deltopectoralis; cdu, cotyla dorsalis; chh, caput humeri; chr, cotyla humeralis; ci, crista intercotylaris; cvh, condylus ventralis; cvu, cotyla ventralis; dfp, dorsal fossa pneumotricipitalis; ev, epicondylus ventralis; faa, facies art. alularis; fau, facies art. ulnaris; fb, fossa m. brachialis; fdII, facies art. digitalis major; fdIII, facies art. digitalis minor; fi, fossa infratrochlearis; fp, fossa pneumotricipitalis; ib, impressio brachialis; ica, incisura capitis; ico, impressio coracobrachialis; ir, incisura radialis; ist, impressio m. scapulotricipitalis; mc, margo caudalis; mII, os metacarpale majus; mIII, os metacarpale minus; o, olecranon; pe, processus extensorius; pp, processus pisiformis; psd, processus supracondylaris dorsalis; sht, sulcus humerotricipitalis; si, sulcus interosseus; sm, symphysis metacarpalis distalis; sp, spatium intermetacarpale; sst, sulcus scapulotricipitalis; slt, sulcus lig. transversus; stc, sulcus tendineus; str, sulcus tendineus; tav, tub. aponeurosis ventralis; tb, tub. bicipitale radii; tcd, dorsal rim of trochlea carpale; tcv, ventral rim of trochlea carpale; td, tub. dorsale; tv, tub. ventrale. Scale bar equals 10 mm.

this absence, whether natural or owing to breakage, might overemphasise the medial extension of fossa deltopectoralis.

The shaft appears to be more or less straight; this may be an artefact of how damage to this area was reconstructed, but specimens retaining smaller sections of shaft are similar in this regard; the distal quarter of the shaft is only slightly curved (ventral view) with less curvature on the ventral margin where it merges with the epicondylus ventralis (cranial view); in other burhinds, the shaft is more sigmoid and has a more ventrally directed curve (cranial view). The fossa m. brachialis is pronounced, extending across the proximal sides of condyli to the dorsal and ventral borders of the cranial face. The proc.

supracondylaris dorsalis is flatter and even less developed than in modern burhinids. The condylus ventralis is more prominent both cranially (distal view) and distally, protruding further, and being spherical rather than oblong (cranial view).

Overall the humerus in *Wilaru* is large and similar in robustness to that of *Esacus* (distal width slightly less than *Esacus* and similar to that of *B. grallarius*) but substantially more so than in other burhinids. The caput humeri is fairly large and hemielliptical. The sulcus lig. transversus is broad but occupies only the ventral side of the caput humeri (cranial view). The proximal end of the fossa pneumotricipitalis undercuts the prominently developed tuberculum ventrale and produces a triangular indentation in the border.

Mayr (2011) scored burhinids as having a single fossa pneumotricipitalis and Strauch (1978) scored *Esacu*s has having a single fossa. T.H. Worthy (pers. comm.), however, noted that, in some specimens of *Esacus* at least, there is a narrow but distinct second fossa located dorsally. The area immediately distal to the caput humeri on the caudal face is excavated in such a manner to create a second fossa in both *Esacus* and *Wilaru*, but not in *Burhinus*.

The tuberculum dorsale is extensive and flat (but clearly elevated off the shaft facies). The crista deltopectoralis is moderately extensive distally, joining the shaft rather smoothly; in no specimen is the crista sufficiently undamaged to provide further description. The crista bicipitalis follows the curve of the fossa pneumotricipitalis. The epicondylus ventralis does not protrude far from the ventral corner of the distal end (cranial view). The sulcus humerotricipitalis is wide and shallow and the ridge between this and the sulcus scapulotricipitalis is low.

Referred specimens: None of the specimens were associated, although several were in close proximity and most were found in the same small area at one site at Lake Pinpa (Site C, QMAM47). It was assumed that, given the number of burhinid remains at the site, these represented most skeletal elements. Ongoing examination indicates that some specimens initially assigned to the Burhinidae more likely represent one or more other taxa. These are omitted here. Likewise, among the remaining putative burhinid specimens, some are too fragmentary or damaged to assign to this family with any confidence and so are not considered further. Of those that are here referred to the new taxon, some are done so more tentatively than others. When diagnostic characters cannot be identified on the material available, assignment is made for those most comparable to modern burhinid morphology. Measurements are given in Table 1 (Appendix).

Furcula (Fig. 2A) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 10983, furcula missing articular ends to both scapus claviculae; SAM P48922 (formerly AMNH 11479), symphysial fragment retaining part of the left scapus clavicula. For the material, there are no readily distinguishable characteristics except for size, which seems more massive than in most other burhinds (but similar in size to that of *Esacus*), with thicker scapus claviculae, especially near the apophysis interclavicularis. The symphysis is longer than the adjacent scapus claviculae and the apophysis interclavicularis projects caudally as a low but prominent ridge.

Scapula (Fig. 2B, C) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 10989 pR retaining a third of shaft; AMNH 10990 pL end missing acromion; AMNH 11434 pL; AMNH 11435 pL; SAM P48923 (formerly AMNH 11438) pR and about half the shaft; AMNH 11463 pR, retaining about half of shaft with tip of acromion missing; AMNH 11477 pR with tip of the acromion damaged.

These specimens are referred to *Wilaru* because of their relative abundance in the site with the other burhinid fossils and the absence of any other potential scapular specimens. This is while recognising that there are some major morphological differences between them and the scapulae of modern burhinids: The acromium is much longer and more pointed overall and the bulbous tuberculum coracoideum is much larger than in any other burhinid.

The facies art. clavicularis is folded laterally, also seen in *Esacus*. The facies art. humeralis is more rounded and less elongate proximodistally than in modern burhinids and it has a distinct indentation running through its proximodistal midline (lateral view). The facies art. humeralis is separated from the tuberculum coracoideum by a low but distinct notch, rather than being confluent with it. The portion of the corpus scapulae that is preserved is straight and rather thin. The extremitas caudalis are missing; preserved lengths are 52.1 mm (SAM P48923) and 43.4 mm (AMNH 11463).

Coracoid (Fig. 2D, E) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: SAM P48924 (formerly AMNH 11412) R missing processus lateralis and tip of angulus medialis; AMNH 11414 oR; AMNH 11426 L missing processus lateralis and tip of angulus medialis; AMNH 11428 R in two non-joining pieces retaining sections of shaft, a proximal fragment with abrasion to processus procoracoideus and a distal end with abraded sternal end and missing tips of processus lateralis and angulus medialis; AMNH 11433 R missing distal border, processus lateralis and angulus medialis; AMNH 11458 L abraded and missing processus lateralis; AMNH 11473 oL with general abrasion to edges; AMNH 11478 oR broken through about midshaft. Lake Palankarinna, Mammalon Hill, Etadunna Formation, Ngama LF: SAM P23625 R without processus lateralis.

These fossils are referred to the Burhinidae because there is a well developed projection on the sternal end of the medial margin, identified by Mayr (2011) as characteristic of the burhinid coracoid. The omal end is large, rather bulbous and more massive than in many families with similarly sized coracoids. The facies art. clavicularis overhangs, and is deeply undercut by the sulcus m. supracoracoidei; the distal border of the facies is more or less straight across most of its length (slight protrusion at midpoint), not sloping sternomedially as in some taxa (*e.g.*, *Haematopus*).

The coracoid is a stout and strong bone. The facies art. clavicularis is expanded dorsoventrally and extends beyond the proximal shaft on the dorsal and ventral sides (lateral view). The processus procoracoideus is rather short and triangular at base. The sulcus m. sternocoracoidei is deep, strongly bordered dorsally and ventrally. The facies art. humeralis is large, slightly longer than the impressio lig. acrocoracohumeralis. The cotyla scapularis is deep and distinct. The impressio m. sternocoracoidei is shallow, very broad mediolaterally and extends omally along shaft. The facies art. sternalis is deep with a prominent ridge separating it from the impressio m. sternocoracoidei (dorsal view). The sternomedial corner is squared off between the project on the medial border and the angulus medialis. The processus lateralis is missing in all specimens.

Wilaru differs from modern burhinids in having the omal half deflected further medially (30–40°) in relation to the main shaft (ventral view), with the medial border of the shaft more curved (ventral view). The sulcus m. supracoracoidei has a flatter dorsal border. The processus acrocoracoideus extends dorsally and ventrally beyond the fossa art. humeralis, rather than being slightly narrower than, or subequal to the width of the fossa (lateral view). The cranially-directed strap-like projection on the end of the processus procoracoideus, seen in modern taxa, is not present. The projection on the sternal end of the medial margin is placed more distally than in modern burhinids.

Radius (Fig. 3D, E, F, G) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 11410 pR with abrasion to edges of cotyla humeralis; AMNH 11411 dL damaged on distal end, particularly tub. aponeurosis ventralis and ventral face; AMNH 11453 R most of the shaft missing the proximal and distal ends; AMNH 11464 L in two pieces comprising both ends and almost complete shaft; AMNH 11468 dR slightly abraded particularly on distocaudal corner; AMNH 11469 dL retaining about third of shaft; AMNH 11471 dR; and SAM P48927 (formerly AMNH 11431) pR including distal half of shaft with slight abrasion to cotyla humeralis. Lake Pinpa, Site C, collection code QMAM125, Namba Formation, Pinpa Fauna: AMNH 10800 dL abraded on surface of dorsal face. Lake Pinpa, Site C, collection code QMAM151, Namba Formation, Pinpa Fauna: AMNH 10943 dL abraded on distal surface. Lake Pinpa, Site C, collection code QMAM243, Namba Formation, Pinpa Fauna: AMNH 10744 pL with abrasion on edges of cotyla humeralis and tub. bicipitale radialis; and AMNH 10813 dR with detailed features lost to abrasion. Billeroo Creek, Site 3, collection code QMAM 199, Namba Formation, Pinpa Fauna: AMNH 10777 dL with abraded end; AMNH 11060 pR with abraded edges to cotyla humeralis. Lake Palankarinna, White Sands Basin, Etadunna Formation, Zone B, Ditjiminka LF: MV P.199593 dL.

The fossil fragments of the radius referred to this family agree with the morphology of modern burhinids in overall shape. The radius of *Wilaru* is slightly less robust than that of *Esacus*, comparable in size with that of *B. grallarius*, and larger than that of other extant species.

Wilaru has a more prominent facies art. ulnaris produced as a ridge running proximodistally on the ventral surface of the distal end. The cotyla humeralis is rather rectangular (deeper than wide) in (proximal view), agreeing with the modern configuration, although abrasion to the edges of this structure in most specimens adds some uncertainty to ascertaining the shape. The tuberculum bicipitale radii is a pronounced ridge. The shaft is smooth and slender; the degree of curvature cannot be assessed owing to breakage and repair of the specimen. The distal end is relatively flat and compressed (cranial view), with the distomedial corner rounded. The sulcus tendineus is shallow. The tuberculum aponeurosis ventralis is short and triangular, protruding cranially**.**

Ulna (Fig. 3H, I) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 10992 pL with abraded edges and missing olecranon; AMNH 10994 pL retaining about a quarter of shaft; SAM P48926 (formerly AMNH 11422) pL retaining about a quarter of shaft; AMNH 11456 pL includes an associated section of mid-shaft although pieces do not match neatly; AMNH 11457 pR retaining about a quarter of shaft; unnumbered pR in good condition.

There are no complete specimens of this element, all of which are proximal fragments. The specimens provide a good match in structure with modern burhinid species, having the incisura radialis prominently developed and moderately deep and the tuberculum lig. collateralis ventralis obsolete. The ulnae are slightly smaller than in *Esacus*, comparable in size with *B. grallarius* and larger than in other burhinids, and are tentatively referred to *Wilaru*.

The olecranon is prominent with a bluntly rounded point. The incisura radialis bounded distally by a well developed and rugose ridge. The impressio m. scapulotricipitalis is a very shallow circular depression, separated from the shaft surface by low ridge, although like other burhinids, features of the dorsal face of the distal end are not strongly expressed. The crista intercotylaris is low (dorsal view). The cotyla ventralis is circular with moderately high borders. The impressio m. brachialis is long and narrow with parallel sides (ventral view). The shaft, where represented on the proximal fragment, is cylindrical, smooth and straight.

Carpometacarpus (Fig. 3J, K, L) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: SAM P48928 (formerly AMNH 10997) R missing os metacarpale minus; AMNH 10998 pL proximal end with a third of os metacarpale minus; AMNH 11401 pL lacking os metacarpale majus and minus with facies artic. digitalis major damaged; AMNH 11432 R missing os metacarpale minus; AMNH 11448 R near complete but os metacarpale minus broken and embedded in plasticine and distal end damaged; AMNH 11460 L complete but os metacarpale minus broken and embedded in plasticinem; AMNH 11462 pL missing distal third of os metacarpale major and all of os metacarpale minus; AMNH 11467 R complete but os metacarpale minus repaired and reattached in approximate position; AMNH 11474 dL symphysis metacarpalis distalis and distal half of os metacarpale majus. Lake Pinpa, Site C, collection code QMAM 243, Namba Formation, Pinpa Fauna: AMNH 10962 pR missing distal third of os metacarpale majus and all of os metacarpale minus.

The carpometacarpi are referred to the Burhinidae because the processus extensorius is elongated (proximal view), the dorsal surface of the os metacarpale majus is angular at mid length (but rectangular in cross section) and the facies art. digitalis minus projects distally about same extent as the facies art. digitalis majus, rather than further.

This element in *Wilaru* differs from that of modern burhinids in several aspects. The dorsal rim of the trochlea carpalis is roughly circular with its proximodistal length roughly equal to its

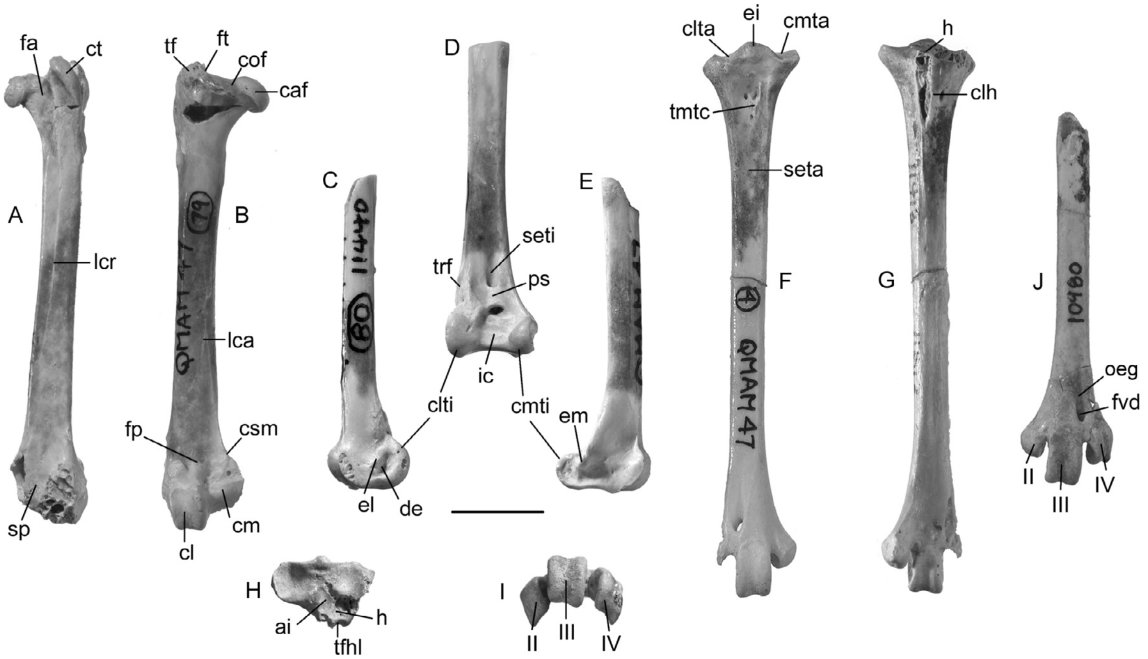

FIGURE 4. Hindlimb elements of *Wilaru tedfordi* nov. spec.: **A**, **B**, left femur SAM P48929 (formerly AMNH 11439) (cranial and caudal views); **C**, **D**, **E**, distal right tibiotarsus SAM P48930 (formerly AMNH 11440) (lateral, cranial and medial views); **F**, **G**, **H**, **I**, right tarsometatarsus AMNH 11413 (dorsal, plantar, proximal and distal views); **J**, distal left tarsometatarsus SAM P48931 (formerly AMNH 10980) (dorsal view). ai, area intercotylaris; caf, caput femoris; cof, collum femoris; cl, condylus lateralis; clh, crista lateralis hypotarsi; clta, cotyla lateralis; clti, condylus lateralis; cm, condylus medialis; cmta, cotyla medialis; cmti, condylus medialis; csm, crista supracondylaris medialis; ct, crista trochanteris; de, depressio epicondylaris lateralis; ei, eminentia intercotylaris; el, epicondylus lateralis; em, epicondylus medialis; fa, facies art. antitrochanterica; fp, fossa poplitea; ft, fossa trochanteris; fvd, foramen vasculare distale; h, hypotarsus; ic, incisura intercondylaris; II, trochlea metatarsi II; III, trochlea metatarsi III; IV, trochlea metatarsi IV; lca, linea intermuscularis caudalis; lcr, linea intermuscularis cranialis; oeg, outer extensor groove; ps, pons supratendeus; sp, sulcus patellaris; seta, sulcus extensorius; seti, sulcus extensorius; tf, trochanter femoris; tfhl, tendon for m. flexor hallucis longus; tmtc, tuberculum m. tibialis cranials; trf, tub. retinaculi m. fibularis. Scale bar equals 10 mm.

craniocaudal width (in other burhinids it is more oblong and longer than wide) and extends further caudally, to roughly the same extent or slightly further as the caudal edge of the os metacarpale minus (dorsal view). The ventral rim of the trochlea carpalis extends to about the same extent. In *Esacus* and *Burhinus*, the dorsal rim only slightly exceeds caudally the caudal face of os metacarpale majus, while the ventral rim has a markedly greater extent compared to the dorsal rim and to the ventral rim in *Wilaru*. The sulcus tendineus, on the distal half of the dorsal face adjacent to the spatium intermetacarpale, is deeper (shallow to obsolete in extant burhinids).

The processus extensorius is bluntly pointed (proximal view). The borders of the facies art. alularis are well defined. The fossa infratrochlearis is entirely proximocaudal of the processus pisiformis (the cranial and distal borders are level with the processus extensorius); it is more proximocranially-distocaudally oblong than the round shape in *Burhinus*, agreeing more closely with the condition in *Esacus*. The processus pisiformis is pronounced, with little excavation around its base. The os metacarpale majus and os metacarpale minus are straight and roughly parallel. The symphysis metacarpalis distalis is long, about 22–24 % of the length of the spatium intermetacarpale. The sulcus interosseus spans the length of the symphysis metacarpalis distalis from the distal end of the spatium intermetacarpale (dorsal view).

Femur (Fig. 4A, B) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: SAM P48929 (formerly AMNH 11439) L with damage to caput femoris, both condyli and parts of proximal shaft; AMNH 11444 dR, fragment with damage to condyli**.**

The specimens are referred to the Burhinidae because of their overall similarity in size and morphology, and because of the suite of characters identified by Howard (1973): the trochanter femoris bends medially, the caput femoris projects abruptly, the shaft is straight and stocky, the sulcus intercondylaris is wide, the fossa popliteal is deep and the crista supracondylaris medialis is high and sharp.

Compared to living burhinids, the collum femoris in *Wilaru* is more constricted (proximal view) and the facies art. antitrochanterica has a more prominent lip protruding caudally over the shaft with the area immediately distal to this more excavated.

This is a sturdy, robust element, larger than in most burhinids, but noticeably smaller than in *Esacus*. The caput femoris is round and bulbous with a shallow but extensive fovea lig. capitis. The trochanter femoris is distinctly rounded on its cranial border (medial view), curving over the facies art. antitrochanterica (proximal view) and projecting proximally beyond the caput femoris (by about same distance as dorsoventral diameter of caput). The crista trochanteris recurves slightly over the facies art. antitrochanterica, with the mediocranially directed apex forming the fossa trochanteris. The ridge extending distally from the base of the trochanter femoris on the cranial face is sharply delineated, creating a deep and distinct depression between the caput and trochanter. The fossa on the pretrochanteric facies is moderately excavated between the strong linea intermuscularis cranialis and the cranial border of facies art. antitrochanterica. The shaft is straight in lateral, cranial and caudal views, lacking any pronounced curvature, is parallel-sided, and subcylindrical in cross-section. The fossa poplitea is extensive and bounded medially by the crista supracondylaris medialis, which links to the linea intermuscularis caudalis running proximally along the shaft's midline (caudal view). The sulcus patellaris is deep and broad. The condyli lateralis and medialis merge smoothly, almost confluently, with the shaft on the cranial side (lateral and medial views).

Tibiotarsus (Fig. 4C, D, E) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 11417 dR with caudal side of condylus medialis missing; AMNH 11423 dL with damage to caudal surface; AMNH 11424 dR damaged on cranial side of condylus medialis; AMNH 11427 dL retaining section of shaft; AMNH 11430 dL with repaired damage to condyli and shaft; SAM P48930 (formerly AMNH 11440) dR; AMNH 11445 dR missing caudal face with shaft crushed and repaired; AMNH 11455 dL with condyli abraded. Billeroo Creek, Site 3, collection code QMAM199, Namba Formation, Pinpa Fauna: AMNH 10885 dR with heavy abrasion to condyli lateralis and medialis and damage to attached shaft. Lake Palankarinna, Tedford Locality Site 3, (V5762), RHT#465, Etadunna Formation, Ditjiminka LF, collected R. H.Tedford 1957: UCMP 57152 dL with condylus lateralis damaged on caudal surface and missing distal edge. Lake Palankarinna, SAM North, Etadunna Formation, Zone B, Ditjimanka LF: MV P.199595 dR with a portion of the adjoining shaft.

The distal fragments are referred to Burhinidae on the basis of agreement in size and morphology. They are intermediate in size between *Esacus* and *B. grallarius*. The sulcus extensorius is shallow and situated between the midline and medial border (cranial view). The degree of curvature of the shaft to meet the condylus medialis (cranial view) shows some variability among individuals from rather minimal (condylus more or less in line with shaft's medial border) to more pronounced (condylus medial to shaft border). The tuberculum retinaculi m. fibularis is large and flat, extending proximally well beyond the pons supratendineus. The condyli are of roughly equal widths (cranial view) and are parallel to each other and to the midline of the shaft. Both have raised borders and meet the shaft abruptly on their caudally and cranially sides. The condylus lateralis is a rounded oval in profile, the epicondylus lateralis is a low peak and the depressio epicondylaris lateralis is moderately deep. The condylus medialis is a more elongate oval and has a notch in the midpoint of its distal border (medial view). The caudal half of the condylus medialis slopes sharply medially from the epicondylus medialis (expressed as a strong ridge) and has a strongly raised border. The incisura intercondylaris is wide, much more so than width of either condyli.

A single proximal fragment (AMNH 10986) lacks the end (cotylae and cristae), but the remaining sections agree in overall size and in the configuration of the crista fibularis. Despite these few similarities, it is too damaged to be referred to this taxon.

Tarsometatarsus (Fig. 4F, G, H, I, J) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: SAM P48931 (formerly AMNH 10980) dL with damage to trochlea metatarsi IV (this is accompanied in its box by an unnumbered pL fragment that has been repaired and is missing the hypotarsus; the two pieces do not fit comfortably together); AMNH 10981 dR; AMNH 11413 R with hypotarsus damaged and trochlea metatarsi IV missing.

The fossils agree with that of Burhinidae by being long, straight and slender and having both cotylae lateralis and medialis rounded (not oval) and deep. The trochlea metatarsi II is not recessed far plantarly relative to trochlea metatarsi III; its dorsal border is level with the midline of the trochlea metatarsi III, while its distal border is only slightly more proximal than that for trochlea metatarsi IV (Strauch 1978); it is not recurved dorsally. The angle formed between the trochleae metatarsi II and IV about 40° (distal view). Although only a dorsal fragment of the hypotarsus is preserved, the remaining section shows that it was rather deep on the lateral side, caudal to the cotyla lateralis, and retains a groove for the tendon of m. flexor hallucis longus. *Esacus* is also deeper in this section of the hypotarsus; *Burhinus* is less so, as are some other charadriiform groups, such as *Haematopus*, in which this lateral side of the hypotarsus is shallower. Unfortunately, the relative positions of the canalis for the tendon of m. flexor digitorum longus and the sulcus for the tendon of musculi perforans et perforatus digiti 2, identified by Mayr (2011) as important feature characterising some charadriiform groups, cannot be ascertained. He also reported that in burhinids the tendon of musculus flexor digitorum longus is enclosed in a bony canal (this is not so in some specimens of *B. grallarius*).

The area intercotylaris is round, smaller, more excavated than in *Haematopus*. The plantar rim of the cotyla lateralis is lower than in taxa such as *Haematopus* and is not visible in dorsal view. The tuberculum m. tibialis cranialis is broad and low, not projecting as far as in many charadriiform groups.

Wilaru differs from living burhinids in several features of the tarsometatarsus. In the fossil taxon, the proximal and distal ends are proportionally wider, both roughly 16–17 % of the element length (compared to roughly 7.5–8 % in other burhinids). The apex of the eminentia intercotylaris is broader and more rounded (dorsal view). The crista lateralis hypotarsi (as preserved) is longer and thinner than the short, broad condition in other burhinids (plantar view). The sulcus extensorius is much shallower distally from about midpoint of shaft. The foramen vasculare distale is larger and more obvious and the outer extensor groove (Howard 1929) leading into the foramen longer, wider and more excavated into shaft surface (dorsal view). The trochlea metatarsi II has greater medial inflection, particularly on the dorsal side (dorsal view), and its plantar extent is greater than 50 % of that of the trochlea metatarsi III (< 50 % in other burhinids) (medial view).

The eminentia intercotylaris protrudes noticeably proximally. The sulcus extensorius is elongate and deep dorsally. The cotyla medialis is slightly larger than the cotyla lateralis. The lateral and medial borders of the shaft are straight and parallel until they converge slightly distally towards the trochleae, with the cross-section of the distal half roughly rectangular (wider than deep). The trochlea metatarsi II is not grooved. The widths of trochleae metatarsi II and IV are subequal. The rims of trochlea metatarsi III are parallel (plantar view). The trochleae metatarsi III and IV have a marked groove along the midline of the dorsal surface.

Discussion

Most *Burhinus* species have more or less similar proportions (tarsus length:wing length 0.30–0.42). *Burhinus grallarius* is similar except for its markedly elongated tarsometatarsus (tarsus length:wing length 0.49). *Esacus magnirostris* has proportionally shorter legs (tarsus

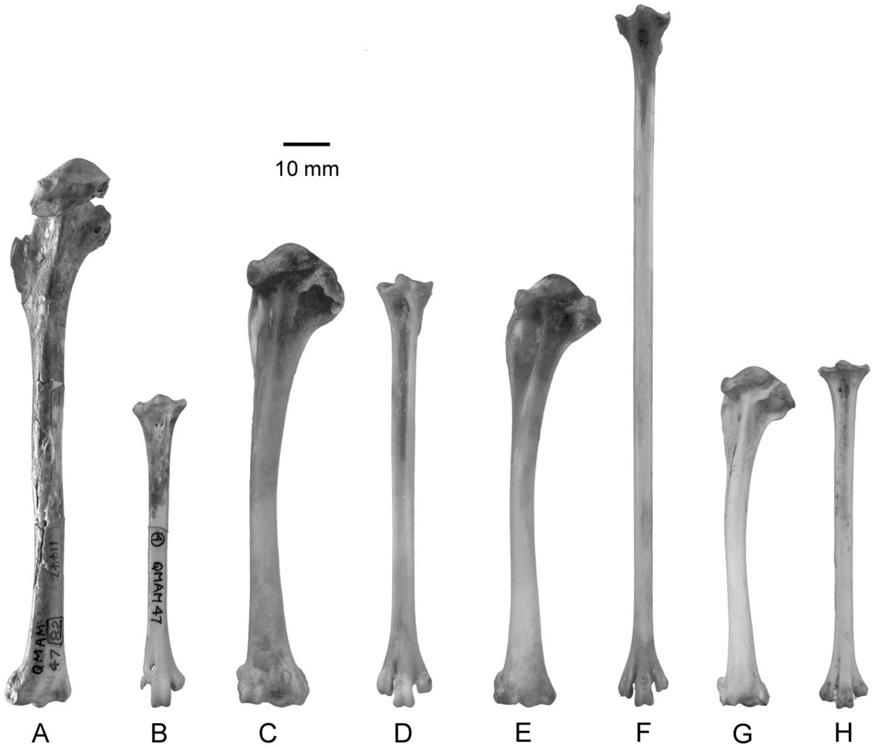

FIGURE 5. Size comparisons of humeri (caudal view) and tarsometatarsi (dorsal view) of fossil and extant burhinids: **A**, *Wilaru tedfordi* nov. spec. SAM P48925 (formerly AMNH 11442). **B**, *Wilaru tedfordi* nov. spec. (AMNH 11413), **C**, **D**, *Esacus magnirostris*, **E**, **F**, *Burhinus grallarius* and **G**, **H**, *B*. *oedicnemus*.

length:wing length 0.30), comparable to the lower end of the *Burhinus* range. This difference between the fore and hind limbs is expressed in most skeletal elements of *Esacus*. Its humerus and carpometacarpus are larger, but its tarsometatarsus is actually and proportionally shorter, than those of *B. grallarius* and several of the smaller species of *Burhinus* (Fig. 5, Appendix: Tab. 2). *Esacus* is also more robust in most of its skeletal elements than is *B*. *grallarius*.

The evidence suggests that *Wilaru* had a forearm length markedly greater than that of the hindlimb (Fig. 5). Demonstrating this is confounded by the fact that the available elements likely come from several individuals, which might have shown the same intraspecific size variation as seen in living taxa. Among living species of *Burhinus*, the ratio of humeral length to tarsometatarsal length varies from 0.72 to 0.86. Except for *B*. *grallarius*, however, the comparative samples are too small to give an indication of intraspecific variation. In this species, the range of hum:tmt ratios is 0.77–0.83. Comparing the longest humerus in the sample with the shortest tarsometatarsus gives a value of 0.86. The reverse (shortest humerus versus longest tarsometatarsus) yields a ratio of 0.69. A comparative figure for the single humerus and tarsometatarsus of *Wilaru*, regardless of being from different individuals of possible different sizes, is 1.89. A similar finding comes from comparing the carpometacarpus and tarsometatarsus: in modern taxa, the ratio is 0.37–0.39, whereas in *Wilaru* (again with the same caveats) it is 0.80. For *Esacus magnirostris*, values for hum:tmt and cmc:tmt are 0.57 and 1.13, respectively, again outside the range of *Wilaru*. The values for *Wilaru* are well outside the range of modern taxa and thus likely valid indications that the fossil taxa had a much longer forelimb relative to the hindlimb than occurs in modern burhinid species.

Do these limb proportions suggest that *Wilaru* may have been less cursorially adapted than extant burhinids? The relatively short-legged *Esacus magnirostris* is not obviously less cursorial than the much longer-legged *B*. *grallarius*. The longer wings of *Wilaru* might be indicative of a greater reliance on flight than modern forms, but there is no obvious evidence to support this. Alternatively, the limb proportions of *Wilaru* may reflect the ancestral condition in this lineage. Recent molecular studies (*e.g.*, Ericson *et al.* 2003) have placed the Burhinidae in a clade with the sheathbills (Chionidae) and the Magellanic Plover *Pluvianellus socialis* Gray, 1846. Both are southern groups, suggesting that they and burhinds may have had southern origins. Morphological comparisons by Mayr (2011) identified cranial synapomorphies in the Burhinidae and Egyptian Plover *Pluvianus aegyptius* (Linneaus, 1758), a taxon not included in the molecular analyses. All these putatively related taxa have comparatively short tarsi compared to wing length. In living burhinids, the ratio of tarsal length to wing length is 0.30–0.49. *Pluvianus aegyptius*, with a tarsus:wing ratio of 0.25, may be most similar to the proportions and appearance of *Wilaru*.

When *W. tedfordi* lived in northern South Australia, fluvio-lacustrine conditions with inland seas existed where today open desert occurs (Alley 1998; Martin 2006). The marine regression that occurred during the Miocene and the northward drift of Australia into drier latitudes saw the development of more open landscape by the end of the Miocene (Alley 1998; Martin 2006), likely opening new niches and making flight less important in more open grassland conditions. As such, more cursorial burhinids took advantage of new ecospace.

Feduccia (1980) considered that "species of *Burhinus* are . . . good indicators of tropical, dry savannah". Bickart (1981), citing habitat preferences across the living species of burhinids, disagreed, noting that "such inferences . . . cannot be safely based merely being a burhinid". It is suggested here that that *Wilaru* likely occupied shorelines of water bodies, much like species of *Esacus* do today.

Attempts to reconstruct the evolution and biogeography of the burhinids are hampered by the sparse fossil record and limited systematic attention to the family. The presence of *Burhinus lucorum* in North America in the early Miocene demonstrates that burhinids were widespread by this time, and the living genus *Burhinus* was contemporaneous with *Wilaru*. The latter was thus unlikely to be directly ancestral to extant taxa. Meinertzhagen (1924) published a revision of the family, recognising only a single genus, *Burhinus*. The traditional practice of most classifications has been to accept *Burhinus* and *Esacus*. Livezey (2010), however, segregated *B. grallarius* from *Burhinus* and created two subfamilies, placing *grallarius* with *Esacus* in one and the remaining species of *Burhinus* in the other. Many of the diagnostic characters that Livezey (2010) used were from the skull, not available in the material of *Wilaru*. Thus, the fossil taxon cannot be incorporated within Livezey's classification.

In terms of limb proportions, *Wilaru* most closely resembles *Esacus*. These taxa also share several character states to the exclusion of *Burhinus*, including a small second dorsal fossa pneumotripicitalis, laterally folded facies art. clavicularis, more oblong fossa infratrochlearis and laterally deeper hypotarsus. Whether these similarities are phylogenetically important is uncertain. Determination of this and the placement of *Wilaru* in the classification of Burhinidae await further clarification of modern intrarelationships in the family (including molecular studies) and analysis using a greater coverage of the skeletal elements and incorporating *Wilaru*.

Acknowledgments

We thank the staff of Museum Victoria, American Museum of Natural History, United States National Museum, Los Angeles County Museum of Natural History, Kansas University Natural History Museum, University of California Museum of Paleontology, South Australian Museum and Australian National Wildlife Collection who provided fossil and Recent specimens and images for this study. Trevor Worthy (Flinders University, Adelaide) and an anonymous referee made valuable criticisms and suggestions. Carl Bento, Australian Museum Photography Section, took the photographs.

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Appendix.

TABLE 1. Measurements of specimens of *Wilaru tedfordi* nov. spec. (mm). Scapula: *acro.-fac. art. hum.* measured from tip of the acromion to the distal edge of the facies art. humeralis. Coracoid: *proc. acro.-cot. scap.* measured from tip of the proc. acrocoracoideus to the sternal edge of the cotyla scapularis. Ulna: *olecranon-cot. dorsalis* measured from the tip of the olecranon to the cranial edge of the cotyla dorsalis. Tibiotarsus: *cond. lat.*, condylus lateralis; *cond. med.*, condylus medialis.

FURCULA	length, symphysis	depth, symphysis	breadth, widest point
AMNH 10983	7.7	6.0	33.0
SAM P48922 (= AMNH 11479)	6.4	5.1	

SCAPULA	proximal width	depth. fac. art. hum.	acro.-fac. art. hum.
AMNH 10989	10.1	3.3	12.5
AMNH 10990		3.5	
AMNH 11434	8.3	4.1	12.5
AMNH 1143	9.7	4.3	11.6
AMNH 11463		4.3	
AMNH 11477		4.2	12.0
SAM P48923 (= AMNH 11438)	8.4	4.0	13.6

CORACOID	length	proximal width	width. fac. art. hum.	proc. acro.-cot. scap.
AMNH 11414		4.1	5.1	15.5
AMNH 11426		4.9	6.0	17.4
AMNH 11428		5.4	5.7	15.9
AMNH 11433		4.4	5.3	15.9
AMNH 11458	36.9	4.9	6.1	17.0
AMNH 11473		*c.* 4.5	5.7	15.8
AMNH 11478			6.0	18.1
SAM P23625	38.9		6.9	19.6
SAM P48924 (= AMNH 11412)	35.9	4.7	6.1	17.0

HUMERUS	length	prox. width	prox. depth	depth caput humeri	distal width	distal depth
AMNH 10836					*c.* 13.9	
AMNH 10723					14.7	
AMNH 10859					15.9	
AMNH 11402				6.4		
AMNH 11403				5.8		
AMNH 11404				5.9		
AMNH 11405				5.9		
AMNH 11406				6.1		
AMNH 11409					13.3	
AMNH 11441					14.6	8.3
AMNH 11451		22.8	8.9	5.9	15.1	8.3
AMNH 11452					15.2	9.3
AMNH 11454		23.2		6.7		
AMNH 11470					14.0	7.9
AMNH 11476					15.1	
SAM P48925 (= AMNH 11442)	123.3			6.2	15.1	8.8
UCMP 57005					14.9	8.8

RADIUS	length	prox. width	prox. depth	distal width
AMNH 10744		4.5	4.7	
AMNH 10777				6.7
AMNH 10800				7.4
AMNH 10813				*c.* 6.8
AMNH 10943				6.9
AMNH 11060		*c.* 4.2	*c.* 5.3	
AMNH 11410		4.6	4.8	
AMNH 11411				7.9
AMNH 11464	*c.* 113.5	4.5	4.8	6.7
AMNH 11468				6.9
AMNH 11469				6.6
AMNH 11471				7.3
MV P.199593				7.3
SAM P48927 (= AMNH 11431)		4.4	4.7	

ULNA	prox. width	olecranon-cot. dorsalis
AMNH 10992	9.4	
AMNH 10994	10.8	8.8
SAM P48926 (= AMNH 11422)	11.3	8.6
AMNH 11456	11.0	7.6
AMNH 11457	9.6	7.7
unnumbered	9.2	7.8

CARPOMETACARPUS	length	prox. width	prox. depth	distal depth
AMNH 10962		13.6	4.6	
AMNH 10998		12.9	4.7	
AMNH 11401		12.0	4.7	
AMNH 11448	54.8	15.2	5.2	5.6
AMNH 11460	52.2	12.2	4.9	5.6
AMNH 11462		13.6	4.9	
AMNH 11467	53.5	13.3	5.6	4.6
AMNH 11474				5.0
SAM P48928 (= AMNH 10997)	50.7	13.3	4.7	6.0

FEMUR	length as preserved	prox. width	prox. depth	distal width	distal depth. medial side
AMNH 11444				10.6	8.1
SAM P48929 (= AMNH 11439)	52.8	10.5	10.3	17.4	

TIBIOTARSUS	distal width	distal depth. cond. lat.	distal depth. cond. med.
AMNH 10885	9.9	7.7	9.8
AMNH 11417	10.6	8.8	
AMNH 11423	10.6	8.2	
AMNH 11424	9.6	7.2	
AMNH 11427	10	7.6	9.2
AMNH 11430	9.8	7.6	9.2
AMNH 11445	10.2	9.1	10
AMNH 11455	10.2	7.5	9.6
MV P.199595	9.8	7.9	9.3
SAM P48930 (= AMNH 11440)	10.1	7.6	9.6

TARSOMETA-TARSUS	**length**	**prox. width**	**distal width**	**distal depth**
AMNH 10981			10.6	8.0
AMNH 11413	66.0	11.5		7.7
SAM P48931 (= AMNH 10980)			11.5	8.1
unnumbered		10.6		

TABLE 2. Comparative measurements (mm) of the humerus, carpometacarpus and tarsometatarsus of *Wilaru tedfordi* nov. spec. and extant species of *Burhinus* and *Esacus*.

	Burhinus oedicnemus	***Burhinus capensis***	***Burhinus bistriatus***	***Burhinus grallarius***	***Esacus magnirostris***
Humerus	76.7	79.0–80.6	84.7	87.2–101.3	102.5–103.7
Carpometacarpus	39.2	41.4–41.6	40.5	46.0–50.9	51.1–52.4
Femur	47.2	47.5–50.9	51.9	53.1–61.2	62.2–65.9
Tarsometatarsus	73.4	97.4	98.1	118.3–147.5	91.0–91.1

Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

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Miocene fossils show that kiwi (*Apteryx*, Apterygidae) are probably not phyletic dwarves

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Abstract — Until now, kiwi (*Apteryx*, Apterygidae) have had no pre-Quaternary fossil record to inform on the timing of their arrival in New Zealand or on their inter-ratite relationships. Here we describe two fossils in a new genus of apterygid from Early Miocene sediments at St Bathans, Central Otago, minimally dated to 19–16 Ma. The new fossils indicate a markedly smaller and possibly volant bird, supporting a possible overwater dispersal origin to New Zealand of kiwi independent of moa. If the common ancestor of this early Miocene apterygid species and extant kiwi was similarly small and volant, then the phyletic dwarfing hypothesis to explain relatively small body size of kiwi compared with other ratites is incorrect. *Apteryx* includes five extant species distributed on North, South, Stewart and the nearshore islands of New Zealand. They are nocturnal, flightless and comparatively large birds, 1–3 kg, with morphological attributes that reveal an affinity with ratites, but others, such as their long bill, that differ markedly from all extant members of that clade. Although kiwi were long considered most closely related to sympatric moa (Dinornithiformes), all recent analyses of molecular data support a closer affinity to Australian ratites (Casuariidae). Usually assumed to have a vicariant origin in New Zealand (*ca* 80–60 Ma), a casuariid sister group relationship for kiwi, wherein the common ancestor was volant, would more easily allow a more recent arrival via overwater dispersal.

Key words: Apterygidae, fossil record, evolution, new species, flightlessness

Introduction

Kiwi (*Apteryx*, Apterygidae) are the most iconic of New Zealand birds. Smallest of the extant ratites, the five species of *Apteryx* now recognised (Gill *et al.* 2010) are all chicken-sized, flightless, nocturnal birds that are superficially convergent on mammals with their fur-like plumage, burrow-breeding behaviour, and dependence on olfactory and tactile rather than optical senses (Calder 1978). One of the most extraordinary peculiarities of kiwi (kiwi and moa may be both singular and plural because in Māori there is no ‘s’ to denote the plural) is the huge egg that they produce – more than four times the size of that predicted from their body weight – which allows the production of an extremely precocial chick (Calder 1978). This characteristic led to the hypothesis that kiwi are phyletic dwarfs, as first espoused by Calder (1978, 1984) and championed by Gould (1986, 1991). This hypothesis suggested that extant kiwi were the outcome of an evolutionary trajectory of a reduction in body size based on a perceived sister-group relationship with the giant moa

(Dinornithiformes) and a lack of any Cenozoic fossil record.

Ratites (ostrich, rhea, cassowary, emu, elephant bird, moa and kiwi) are flightless palaeognaths with greatly reduced wings, or, in the case of moa, completely lost. In the absence of an informative fossil record, interpretation of ratite origins has been limited to inference from the highly modified extant representatives. In recent decades, ratites have come to be regarded as one of the best vertebrate exemplars of a group with vicariant origins *e.g.*, ROFF (1994), following initial promotion of the idea by CRACRAFT (1974). However, analyses of molecular data, *e.g.*, COOPER *et al.* (2001) and HADDRATH & BAKER (2001), cast doubt on the vicariant origin of various ratite clades with unanimous support for kiwi having a closer relationship to Australian ratites (Casuariidae) than to moa. Thus the first premise underpinning the phyletic dwarfing hypothesis of kiwi origins – a sister-group relationship with moa – is now doubtful. With the divergence of kiwi from casuariids then calculated to have occurred at about 60 Ma, it has been suggested that the occurrence of kiwi in New Zealand required dispersal over a significant oceanic barrier following Zealandia's separation from East Gondwana approximately 80 Ma (MCNAB 1994; COOPER *et al.* 2001). However, it is now recognised that the unzipping of Zealandia (inclusive of New Zealand) from East Gondwana took over 27 Ma, commencing 82 Ma and finishing approximately 55 Ma (GAINA *et al.* 1998; SCHELLART *et al.* 2006). If this was indeed the case, then a vicariant origin for kiwi remains a possibility (TENNYSON 2010). This is especially so given that the most recent estimates for the divergence of kiwi from casuariids continue to support their ancient origin, *e.g.*, 53.5 (95 % CIs 36.9–72.1) Ma, estimated with both external and internal fossil calibrations (PHILLIPS *et al.* 2010), and 73 (95 % CIs 50–100) Ma as estimated in BEAST by HADDRATH & BAKER (2012). But the question arises, was the common ancestor of kiwi and casuariids large and flightless, or was it small and volant as might be predicted by the multiple loss of flight hypothesis invoked for ratites (HARSHMAN *et al.* 2008; PHILLIPS *et al.* 2010)? More recently, even the vicariant origin of moa has been questioned, as molecular analyses suggest multiple independent origins of ratites involving dispersal by volant ancestors and subsequent convergent evolution towards the ratite form (HARSHMAN *et al.* 2008; PHILLIPS *et al.* 2010), although morphological data (JOHNSTON 2011; WORTHY & SCOFIELD 2012) still supports a vicariant origin. It is therefore possible that both moa and kiwi may have dispersed as volant, and therefore small, birds to New Zealand after its separation from East Gondwana.

Resolution of these contrasting hypotheses will be helped by a fossil record that establishes limits such as lineage presence and actual morphological form at crucial times. The fossil history of moa prior to the Quaternary remains elusive, but eggshell and tantalising fragments from the St Bathans Fauna, South Island (WORTHY *et al.* 2007; TENNYSON *et al.* 2010) show that moa ancestors were present and were large birds in the Early Miocene.

The St Bathans Fauna has produced a diverse assemblage of terrestrial vertebrates including leiopelmatid frogs, reptiles including skinks, geckos, turtles and crocodilians, and mammals (JONES *et al.* 2009; LEE *et al.* 2009; WORTHY *et al.* 2006, 2011a, 2011b). The terrestrial vertebrate fauna (non-fish) is however dominated in diversity and abundance by about 40 species of birds, principally of waterfowl (Anatidae), with a minimum of eight taxa in five genera. It includes moa (Dinornithiformes), a tubenose (Procellariiformes), birds of prey (Accipitriformes), several gruiforms (Rallidae), a gull (?Laridae) and other charadriiforms, herons (Ardeidae), a palaelodid (Phoenicopteriformes), pigeons (Columbidae), parrots (Psittaciformes), a swiftlet (Apodidae), an owlet-nightjar (Aegothelidae), and passerines (Passeriformes) (SCOFIELD *et al.* 2010; TENNYSON *et al.* 2010; WORTHY *et al.* 2007, 2009, 2010a, 2010b, 2011c, 2011d). The fauna includes representatives of all the quintessential endemic New Zealand terrestrial vertebrates such as leiopelmatids (WORTHY *et al.* 2011b), sphenodontids (JONES *et al.* 2009), moa (TENNYSON *et al.* 2010), the basal gruiform *Aptornis* (WORTHY *et al.* 2011c), and acanthisittid wrens (WORTHY *et al.* 2010a). It has, however, not revealed any evidence of that most iconic of all New Zealand taxa, the kiwi. This absence is now informed by the discovery of two fossils referrable to Apterygidae. They allow assessment of the phyletic dwarfing hypothesis and have bearing on when kiwi joined the New Zealand biota.

Material and methods

Nomenclature: We follow Gill *et al.* (2010) for nomenclature of kiwi and use names from specimen labels interpreted via Davies (2002) for tinamous. We use the anatomical nomenclature given in Baumel *et al.* (1993) and Elzanowski & Stidham (2010) and abbreviate common terms as follows: artic., articularis; cond., condyle; m., musculus; proc., processus; tuber., tuberculum.

Abbreviations: AM, Australian Museum, Sydney, New South Wales, Australia; CM, Canterbury Museum, Christchurch, New Zealand; MV, Museum Victoria, Melbourne, Victoria, Australia; NMB, Naturhistorisches Museum, Basel, Switzerland; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; NMW, Naturhistorisches Museum, Vienna, Austria; SAM, South Australian Museum, Adelaide, South Australia, Australia; SMF, Forschungsinstitut Senckenberg, Sektion Ornithologie, Frankfurt am Main, Germany. Ma, million years ago.

Comparative material examined: Comparisons were made widely among birds using the skeletal collections of the Australian Museum and South Australian Museum. Following determination of the apterygid affinity of the fossils, detailed observations were made of the following kiwi and tinamou specimens.

Apteryx owenii: SAM B.5051, MV B56009, AMS535, AM A.1980, AM A.1992, AM A.4570; NMNZ OR.22815a; NMNZ OR.23044; NMNZ OR.23717a; NMNZ OR.24415; NMNZ OR.24416; *A. haastii*: MV B40905, CM Av31538; NMNZ OR.19773a; NMNZ OR.23022a; NMNZ OR.23038; NMNZ OR.23045; NMNZ OR.23648a; NMNZ OR.27983; NMNZ OR.28010a; *A. australis*: CM Av14447, CM Av32404, CM Av36637, CM Av36638, CM Av39065, AM O. unregistered; *A. a. australis*: NMNZ OR.22089a; NMNZ OR.27761a; NMNZ OR.27965; *A. a. lawryi*: NMNZ OR.23591; NMNZ OR.23756; *A. mantelli*: CM Av5492; NMNZ DM.909-S; NMNZ OR.13588; NMNZ OR.14964; NMNZ OR.17206; NMNZ OR.17207; NMNZ OR.17208; NMNZ OR.17209; NMNZ OR.17210; NMNZ OR.17211; NMNZ OR.17212; NMNZ OR.17213; NMNZ OR.24640; NMNZ OR.24984; *A. rowi*: CM Av16691, CM Av16717, CM Av16718.

Crypturellus obsoletus, SMF 2148; *C. noctivagus noctivagus*, SMF 11394; *C. tataupa*, SMF 11392; *C. parvirostris*, SMF 2164, SMF 9357, SMF 8184; *C. cinnamomeus*, SMF 2537; *C. undulatus vermiculatus*, SMF 2149; *Eudromia elegans*, NMW 3.071, SMF 9306, SMF 9260, SMF 6111, SMF 5415, SMF 6416, SMF 6298; *Nothoprocta perdicaria*, NMNZ OR.22983, NMW 4.068; *Nothura maculosa*, NMW 1061; *Tinamus major robusta*, SAM B.31339; *T. major major*, NMNZ OR.1433; *T. major*, NMW 4.559; *T.* (*Trachpilmus* Cab.) *robustus*, NMB C.2004; *T. solitarius*, SMF 2150; SMF 2146; *Rhynchotus fasciatus =rufescens*, NMW 161, NMW 160; *R. rufescens*, SMF 2147, NMB 5537.

We describe two fossil bones from the Early Miocene St Bathans Fauna, from Central Otago, New Zealand. The locality details and general stratigraphy of the sites producing this fauna have been described already (Worthy *et al.* 2007; Schwarzhans *et al.* 2012).

We estimated mass for the fossil kiwi based on its femoral circumference using six different algorithms, including four from the literature based on all kinds of birds (Anderson *et al.* 1985; Campbell & Marcus 1992) and ratites (Dickinson 2007), as well as two newly derived ones based on kiwi and tinamous. Circumference was determined by wrapping a narrow and thin piece of cellotape (or string for extant kiwi specimens in NMNZ) around the mid-shaft and marking the point where it overlapped itself, then measuring the length with callipers. Given apterygids are rather atypical palaeognaths, we also computed algorithms for mass from data for tinamous and for apterygids separately, and used these to estimate the mass of the fossil kiwi. We reasoned that if the fossil taxon was volant the value based on tinamou may be more pertinent but if it were flightless then that based on kiwi would be relevant. Measurements were taken with dial callipers or a graticule in a binocular microscope and rounded to the nearest 0.1 mm.

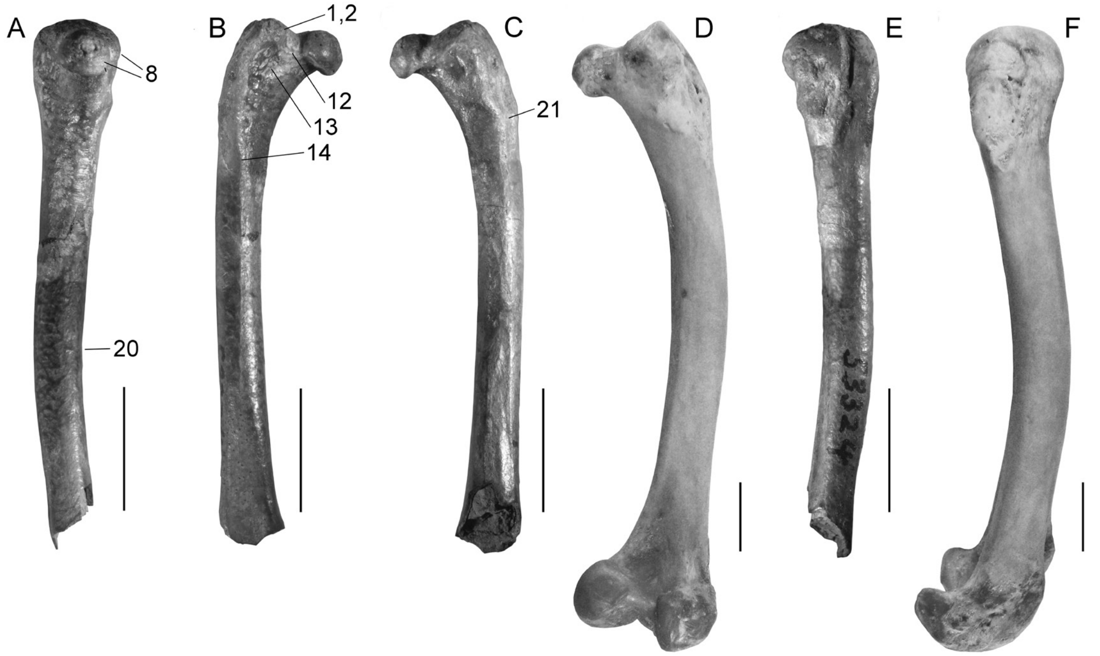

FIGURE 1. Apterygid right femora. *Proapteryx micromeros* (NMNZ S.53324, A-C, E) and *Apteryx owenii* (MV 56009, D, F), in medial (A), cranial (B), caudal (C, D), and lateral (E, F) views. Scale bars are 10 mm. Numbers refer to family attribution characters.

Systematic Palaeontology

Order Casuariiformes: Cassowaries, Emus and Kiwi

Family Apterygidae G.R. Gray, 1840: Kiwi

The fossil is identified as an apterygid by the following combination of femoral characters (Figs 1, 2): the facies artic. antitrochanterica is convex in cranial-caudal section (1) and lateromedially about same width as the caput femoris (2); in caudal view, the proximal profile has a marked notch between the caput femoris and the facies artic. antitrochanterica (3); the collum femoris is constricted proximodistally and craniocaudally (4); the caudal facies distal to the facies artic. antitrochanterica is flat (5), forming a near right angle with the lateral facies (6), not a curved transition, as in *e.g.* galliforms; the insertion area for the major part of m. obturatorius medialis is on a distinct bulge traversing the caudal facies distolaterally, ending laterally level with the insertion area for m. ischiofemoralis (7); the depth of the crista trochanteris is about twice the depth of the caput femoris (8); the crista trochanteris not extending proximad of the facies artic. antitrochanterica, no fossa trochanteris (9), rounded cranially (10), merges gradually to the corpus femoris distally (11), and lateromedially broad adjacent to the collum femoris such that a narrow groove, less than the diameter of the caput, connects the pretrochanteric surface to the facies artic. antitrochanterica (12); the pretrochanteric surface is shallowly concave cranially, lacking pneumatic foramina (13); the linea intermuscularis cranialis extends to the distal end of the crista trochanteris (14); the area for the insertion of the m. obturatorius lateralis on an elevated bulge, not marked by any scar (15); large sulcus centred on the lateral facies proximally for insertion areas of the m. iliotrochantericus caudalis cranially and the m. iliofemoralis externus caudally (McGowan 1979), is elongate, extending about half the length of the crista trochanteris (16); insertion areas for the mm. iliotrochanterici medius et cranialis form a narrow elongate groove, slightly separated from the insertion area for the m. iliofemoralis externus, extending distally to point level with end of the crista trochanteris (17); insertion area of the m. ischiofemoralis forms a short, broad sulcus, caudal of and overlapping, in the proximodistal plane, the distal end of the insertion area for the m. iliofemoralis externus and the proximal end of the insertion area for the m. iliotrochantericus medius (18); the corpus femoris is elongate relative to its proximal width (19), arched dorsally at mid-length (20), and bent medially at the distal end of the crista trochanteris, such that the lateral facies beside the trochanter is markedly inclined medially relative to more distal parts (21).

The insertion area for the m. iliotrochantericus caudalis being centred craniocaudally on the lateral facies, not more cranially, may be a synapomorphy of Casuariiformes. Characters 15 and 16 are considered apterygid autapomorphies. Femora of all other birds are further distinguished from those of apterygids by numerous features (see Appendix 1).

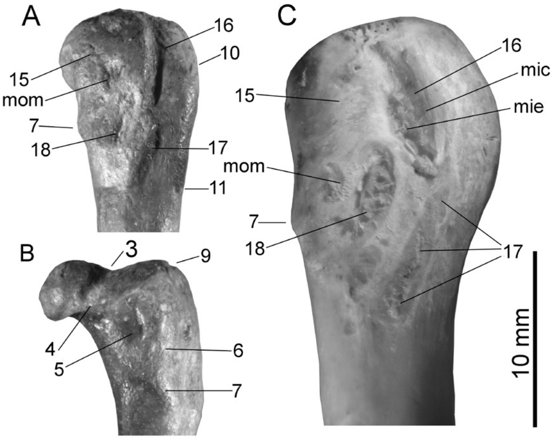

FIGURE 2. Apterygid right femora. *Proapteryx micromeros* (NMNZ S.53324, A, B) and *Apteryx owenii* (a small example, SAM B.5095, C), in lateral (A, C), and caudal (B), views. Numbers refer to family attribution characters. Abbreviations: mic, insertion area of m. iliotrochantericus caudalis; mie, insertion area of m. iliofemoralis externus; mom, insertion area of m. obturatorius medialis pars minor.

Proapteryx gen. nov.

Types species: *Proapteryx micromeros* spec. nov.

Diagnosis: An apterygid distinguished from *Apteryx* by the facies artic. antitrochanterica of the femur having a well-formed lobe overhanging the caudal facies; insertion area for the minor part of the m. obturatorius medialis a marked scar about a third the length of and located proximocaudal to the insertion area of the m. ischiofemoralis, not immediately caudal to it; and by its markedly smaller size with a femoral shaft diameter about half that of *A. owenii*, the smallest *Apteryx* species.

Etymology: Addition of the Latinised Classical Greek prefix προ- (pro-), meaning before, to the scientific name of kiwi (*Apteryx*). *Apteryx* is Latinised Classical Greek and derives from the Greek “α”, a prefix indicating to be without or absent, and “πτέρυγας”=wings; neuter noun. Denoting that this taxon precedes *Apteryx* in the geological record.

Proapteryx micromeros spec. nov.
(Figs 1–3)

Holotype: NMNZ S.53324 (Figs 1, 2), right femur missing distal condyles; collected 20 April 2012.

Diagnosis: As for genus.

Etymology: Latinised Classical Greek μικρός (mikros) for small or little and μηρία (meros) for thigh; neuter noun. For the markedly smaller femur than in extant apterygids.

Type locality: In a clay layer enveloping stromatolites, Site FF1 (Lindqvist 1994), a fossil stromatolite bed at 44.90359°S, 169.85840°E, Manuherikia River, Otago, New Zealand. Fossil Record Number (FRN) in the archival Fossil Record File of the Geological Society of New Zealand is H41/f0058 (stromatolites) and H41/f0059 (clay draping stromatolites).

Stratigraphy/Age/Fauna:Bannockburn Formation, Manuherikia Group, Early Miocene (Altonian); 19–16 Ma; St Bathans Fauna. The stratigraphic relationship of site FF1 to other Bannockburn Formation exposures is presently unknown but the associated faunas are similar.

Measurements of holotype: Preserved (incomplete) length 42.2 mm, proximal width 8.4 mm, maximum proximal depth 7.6 mm ; shaft width at former mid length 3.6 mm, shaft depth at former mid length 4.0 mm.

Comparison and description: In addition to the listed diagnostic characters, there are few differences between *Proapteryx* and *Apteryx*. The nutrient foramen caudally on the shaft is distinctly proximal to mid-length in *Apteryx*, but near original mid-length in *Proapteryx*. The linea intermuscularis caudalis extends proximally towards the lateral facies laterad of an elongate prominence for the insertion of m. puboischiofemoralis pars medialis (as in Casuariidae). This

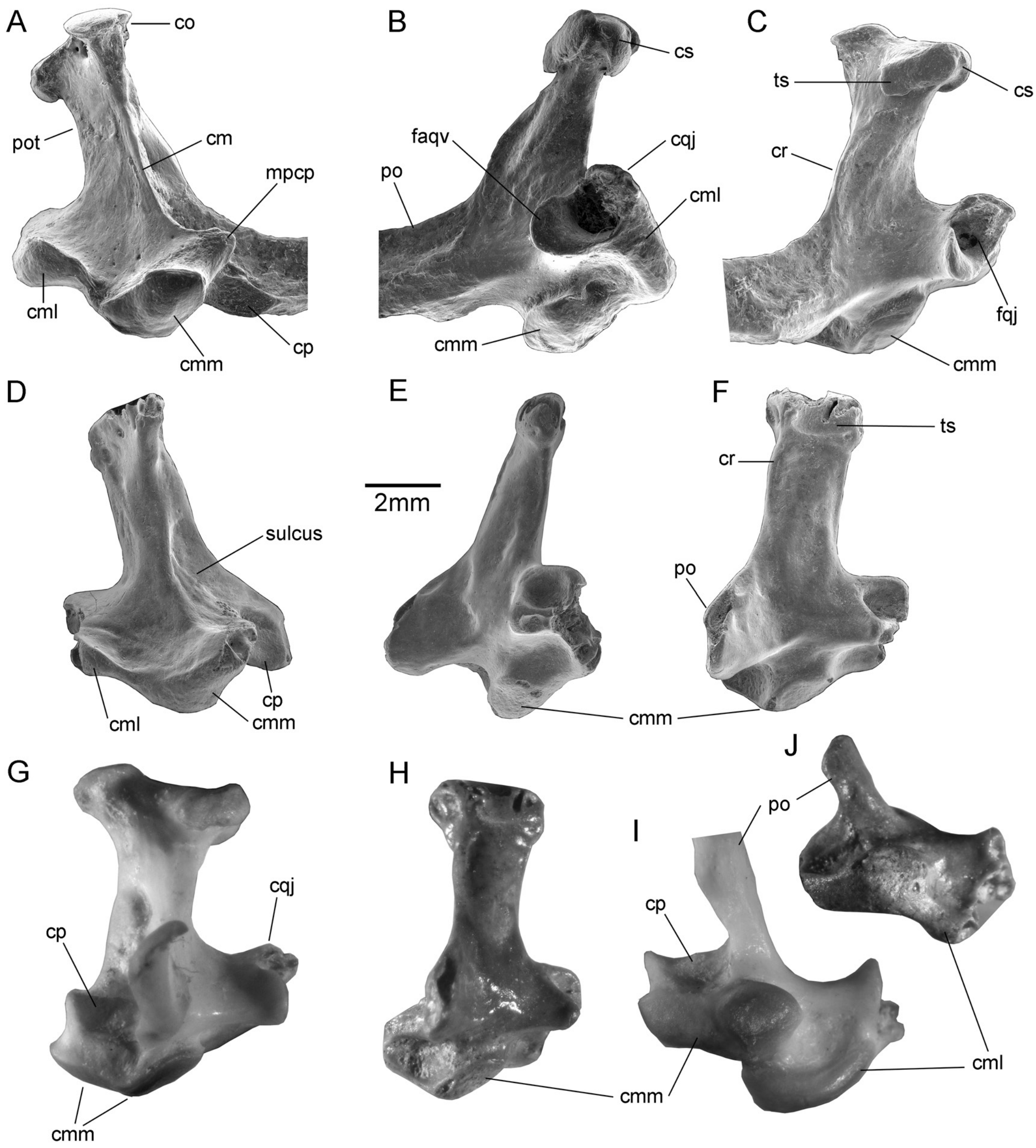

FIGURE 3. Apterygid left quadrates. *Apteryx owenii* (SAM 5051 A-C, G, I) and *Proapteryx micromeros* (NMNZ S.53209, D-F, H, J) in medial (A, D), lateral (B, E), anterolateral (C, F), anterior (G, H) and ventral (I, J) views. Abbreviations: cm, crista medialis; cml, cond. mandibularis lateralis; cmm, cond. mandibularis medialis; co, capitulum oticum; cp, cond. pterygoideus; cqj, cotyla quadrateojugalis; cr, crista; cs, capitulum squamosum; faqv, facies artic. quadrateojugalis ventralis; fqj, fovea quadrateojugalis; mcpc, medial process cond. pterygoideus; po, proc. orbitalis; pot, proc. oticus; ts, tuber. subcapitulare.

prominence in *Proapteryx* is relatively more proximally located, ending level with the caudal bulge that is the insertion area for the major part of m. obturatorius medialis, rather than distal to the crista trochanteris.

Referred specimen: NMNZ S.53209, a left quadrate (Fig. 3).

Locality of referred specimen: Bed HH1b, 10–15 cm thick sand and cobble layer 9.5–9.58 m above the base of the Bannockburn Formation, Trench Excavation, at 44.90780° S 169.85844° E, Manuherikia River section; FRN is H41/f0103.

Stratigraphy/Age/Fauna: As for holotype.

Measurements of referred specimen: Total height from proc. oticum to cond. medialis 9.2 mm; height above cotyla quadratojugalis 4.9 mm.

Comparison and description: The fossil is worn and damaged with the proc. orbitalis lost anterior to the cond. pterygoideus, loss of much of the cond. mandibularis lateralis including the caudoventral rim of the fovea quadratojugalis, and the anteriomedial tip of the cond. mandibularis medialis is worn.

NMNZ S.53209 differs markedly from quadrates of all birds except those of *Apteryx* with which it shares the following combination of features (Fig. 3) and so it is referred to Apterygidae: 1, the head of the proc. oticus is expanded laterally and medially into a broad ‘dumbell’ shape, about three times wider than long, aligned at right angles to the proc. orbitalis; 2, caudally, there are pneumatic foramina at the base of the capitulum oticum; 3, the capituli oticum et squamosum are linked by a craniocaudally narrow articular surface lacking an incisura intercapitalis; 4, the capitulum squamosum widens laterally and its articular surface extends caudoventrally as a small oval lobe protuberant over the caudal facies; 5, the tuber. subcapitulare on the anterior side of the capitulum squamosum is prominent, robust, and about twice as wide as high; 6, the proc. oticus has a flat caudal facies, straight in lateral aspect, centred above the cond. mandibularis medialis, and forming an angle of approximately 100 degrees with the proc. orbitalis; 7, the crista medialis is acute, extending from the medial prominence of the cond. pterygoideus towards the capitulum oticum, forming the caudal boundary to a deep triangular sulcus without a foramen pneumaticum rostromediale; 8, the corpus lacks pneumatic foramina both caudally and laterally; 9, the cotyla quadratojugalis is very prominent laterally, the fovea quadratojugalis is deep, and the facies artic. quadratojugalis ventralis is proportionately large; 10, the proc. orbitalis is lateromedially thin with a shallow sulcus medially; 11, the cond. pterygoideus is rectilinear, separated by a sulcus from and lies dorsal to the medial half of the cond. mandibularis medialis, broader than high, dorsally convex in section, lateromedially concave, and extends continuously from a prominence medially onto the ventromedial part of the proc. orbitalis; 12, in ventral view, the condyli mandibularis medialis et lateralis are aligned roughly at right angles to the proc. orbitalis; 13, the articular surface of the cond. mandibularis lateralis is laterocaudal of, narrower than, subparallel to, and overlaps the cond. mandibularis medialis; 14, the cond. mandibularis medialis has two distinct parts: a ventrally convex medial part, and an anterocaudally broader lateral part that extends dorsally onto the lateral facies on the anterior side of the cotyla quadratojugalis.

In addition, NMNZ S.53209 reveals the following features. The preserved dorsal surface of the capitilum squamosum is level with the eroded surface of the capitulum oticum, indicating that the latter was originally slightly more prominent dorsally. Medially, the tuber. subcapitulare abuts a crest linking the capituli to the proc. orbitalis. A deep partially pneumatic sulcus at the base of the capitulum oticum lies medial to this crest. The proc. oticus is robust, extending dorsad of the cotyla quadratojugalis by slightly over half (53 %) of total quadrate height, anterior and caudal borders are subparallel in anterolateral view, being formed respectively from crests extending from the proc. orbitalis to the capituli anteriorly and from the cotyla quadratojugalis to the capitulum squamosum posteriorly. The anterior margin of the proc. oticus meets the dorsal margin of the proc. orbitalis in a broad (approximately 140º) angle level with the dorsal side of the cotyla quadratojugalis. Anterior to the cond. mandibularis lateralis and lateral to the cond. medialis a shallow sulcus undercuts the cotyla quadratojugalis ventrally.

Quadrates of *Apteryx* species differ from NMNZ S.53209 as follows. (1) They are relatively more robust, although the smallest extant species, *A. owenii*, has a similar height (Table 1; Appendix 2). (2) They lack a pneumatic fossa anteriorly under the capitulum oticum. (3) The proc. oticus is relatively shorter with its height above the cotyla quadratojugalis slightly less than half of the maximum dorsoventral height. (4) The laterocaudal margin of the proc. oticus above the cotyla quadratojugalis is more rounded (in NMNZ S.53209, the corpus is notably craniocaudally compressed forming a ridge extending from under the capitulum squamosum down nearly to the cotyla quadratojugalis). (5) The cond. mandibularis medialis is proportionally larger but relatively less protuberant ventrally, and less offset ventrally from the ventral margin of the base of the proc. orbitalis, creating a deeper sulcus under the cond. pterygoideus. (6) In lateral view, the proc. orbitalis meets the proc. oticus below the dorsal margin of the cotyla quadratojugalis, a result of the more robust ventral half of the quadrate compared to NMNZ S.53209. (7) The tuber. subcapitulare is sometimes (*A. owenii*) not bound medially by a ridge extending from the proc. orbitalis, but in other species, *e.g.*, *A. haastii* and *A. australis*, a ridge is present, as in NMNZ S.53209.

While the fossil quadrate was only similar to those of apterygids among a large range of compared taxa, we present detailed comparisons with three other palaeognath groups, the dinornithiforms because they were previously considered the sister group of kiwi (Cracraft 1974) and the tinamids and extinct lithornithids, because their volant nature makes them or taxa in their lineages potential candidates for the ancestral kiwi in New Zealand via dispersal across oceans (Houde 1988; Phillips *et al.* 2010).

Dinornithiformes. Apart from being considerably larger, moa quadrates differ markedly from those of the fossil and *Apteryx* as follows: proc. orbitalis short, relatively about half the length in kiwi, robust, dorsally convex (not laminar in nature, elongate and concave dorsally); they have a large foramen pneumaticum rostromediale (lacking in *Apteryx*); the capitulum oticum is relatively smaller, more poorly differentiated from the capitulum squamosum, not pneumatic caudally; in ventral view, the articular surfaces of the condyles differ markedly such that the articular facies of the cond. mandibularis medialis has very little medial prominence, and so rather than being lateromedially broad and sub-parallel to the cond. mandibularis lateralis as in kiwi, is craniocaudally elongate and aligned at near right angles to the cond. mandibularis lateralis. The fossil therefore has little similarity with dinornithiform quadrates.

Lithornithidae. Lithornithids are volant palaeognaths found in the Northern Hemisphere in the Early Tertiary (Houde 1988) and could conceivably have been ancestral to Casuariiformes, which are not known to be older than Late Oligocene *ca*. 24 Ma (Boles 2001). If so, a closer relationship and hence greater osteological similarity with *Apteryx* than to most other ratites might be predicted. We compared images of quadrates of *Lithornis celetius* Houde, 1988 (USNM 290601) with *Apteryx* quadrates. Similarities include: the proc. oticus is dorsally expanded with poorly separated capituli aligned at right angles to the proc. orbitalis, the cond. mandibularis medialis is medially prominent below the saddle-like cond. pterygoideus whose articular facet curves around onto the ventral part of the proc. orbitalis; the proc. orbitalis is relatively low (dorsoventrally) with a sulcus medially. However, the *Lithornis* quadrate differed from *Apteryx* quadrates and the fossil as follows: the proc. oticus is dorsally convex across the capituli, rather than the capituli being separated by a slight hollow; the capitulum oticum is markedly convex dorsally, does not overhang the corpus either posteriorly or anteriorly (not comparable in fossil); the capitulum squamosum is less protuberant laterally; the tuber. subcapitulare is lacking or poorly developed; the cotyla quadratojugalis is located relatively more ventrally, its ventral margin aligned with the ventral margin of the proc. orbitalis, has subequal ventral extent with the cond. mandibularis medialis; the cotyla quadratojugalis is not as protuberant laterally, has a crest extending from the dorsal margin to the corpus at slightly above mid height; the rostromediale facies of the corpus lacks a distinct sulcus at mid-height (present in *Apteryx*) where the foramen

TABLE 1. Summary statistics for *Apteryx* species of % TH above cotyla quadrateojugalis from Appendix 2.

	A. mantelli	*A. rowi*	*A. australis*	*A. lawyri*	*A. owenii*	*A. haastii*
Mean	48.6	45.8	47.1	45.0	48.2	45.4
Standard Error	1.08	1.14	1.47	1.34	1.04	1.13
Standard Deviation	3.42	1.98	3.90	3.00	3.28	2.53
Minimum	44.4	43.6	40.9	41.7	42.6	42.5
Maximum	53.5	47.5	50.8	49.4	54.8	49.1
Count	10	3	7	5	10	5

pneumaticum is present in dinornithiforms; and the cond. pterygoideus is not so prominent above the medial side of the cond. mandibularis medialis. Thus, *Lithornis* quadrates differ substantially and in the same way from both *Apteryx* quadrates and the fossil quadrate referred to *Proapteryx*.

Tinamidae. The South American small volant palaeognaths in Tinamidae potentially could be related to the bird represented by this fossil as tinamous render ratites paraphyletic in recent analyses (Harshman et al. 2008; Phillips et al. 2010) and potentially are the sister taxon to moa (Phillips *et al.* 2010). Moreover, the oldest tinamou fossils, clearly recognisable as similar to modern tinamous, are of similar Early Miocene age to the St Bathans Fauna (Bertelli & Chiappe 2005). However, tinamou quadrates differ markedly from those of the fossil and *Apteryx* in having the cotyla quadratojugalis and condyli mandibularis medialis et lateralis displaced caudally relative to the proc. oticus, and the cotyla quadratojugalis more separated vertically from the cond. mandibularis medialis, being located above the base of the proc. orbitalis (see Silveira & Höfling 2007: figs 40, 41). Tinamous or their recent ancestors can thus be ruled out as being closely related to the fossil or as ancestral to apterygids.

Assignment to *Proapteryx*

In summary, NMNZ S.53209 is more similar to *Apteryx* than to any other palaeognath group, which supports its referral to the *Apteryx* lineage. While NMNZ S.53209 is most similar to kiwi quadrates among known birds, the above features 2–5 are notable departures from the quadrate form of all extant *Apteryx* species and support the generic distinction based on femoral differences. We tentatively refer NMNZ S.53209 to *Proapteryx micromeros* because it represents a kiwi of similar size to that estimated for the holotype (see below) and it is presently most parsimonious to consider that only one such species is represented in the St Bathans Fauna. With several thousand bird bones having been collected from various sites sourcing this fauna, it seems unlikely that the two apterygid elements collected thus far would belong to separate taxa. The collection of additional material will hopefully confirm this idea.

Mass estimate for *Proapteryx*

The measured femoral circumference of the holotype femur of *Proapteryx* is 12.4 mm. We assessed body mass with several techniques.

Assessment of mass using algorithms based on a range of birds

1. Body mass (W) in g was estimated using the power function $W=0.16C^{2.73}$ (Anderson *et al.* 1985; Murray & Vickers-Rich 2004). This equation suggests that a bird with a femoral circumference of 12.4 mm would weigh 154.6 g.

2. We also used equations from Campbell & Marcus (1992) based on Group AL (all 795 species from diverse families), using Ordinary Least Squares regression (OLS), the intercept is −0.065 and the slope is 2.411: thus $log10W=2.411log10C+0.065$ or $W=1.1645C^{2.411}$, and the estimated weight is 502 g.

3. Using the equation based on heavy-bodied (HB) birds using Reduced Major Axis regression (RMA) from Campbell & Marcus (1992), where the intercept is 0.11 and the slope is 2.268: thus $log10W=2.268log10C-0.11$ or $W=0.775427C^{2.268}$, the estimated weight is 234.1 g (95% CIs 166–337.3 g.

Assessment of mass using only palaeognaths: Because kiwi are palaeognaths and not typical birds and because the above values varied widely, we assessed mass using formulae based only on palaeognaths. Assessing the mass of flightless ratites and the estimating the mass of extinct forms has a sizable literature (see review in Dickison 2007), however most studies found mass estimates of Apterygidae are not well predicted by algorithms based on other ratites, probably because kiwi measurements lie well outside of the data generating those equations.

4. Ratite-specific algorithms. First we used Dickison's (2007) formula from OSL regression of known ratite body mass on bone measurements: $W=0.114815C^{2.83}$. This gives a predicted mass of 142.69 g. This estimate suffers from being based on a data range that does not encompass that for the fossil and further which is biased towards large size of extant ratites and is considerably smaller than other estimates.

5. Palaeognaths – tinamous. It is possible *Proapteryx* was volant, so for this reason

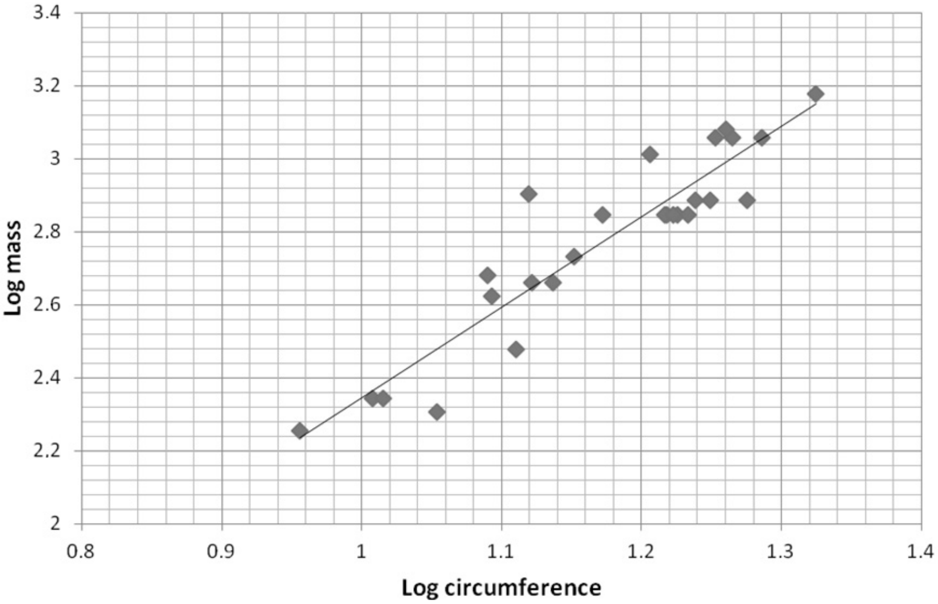

FIGURE 4. The least-squares regression of the raw data between the log circumference and log body mass in a sample of 28 tinamous of 14 species from Appendix 3. The coefficient of determination (R^2) was 0.8613.

we compared femoral diameter with mass in the volant and similar-sized palaeognaths, the tinamous (Tinamidae). Using the data in Appendix 3, and Fig. 4, we computed a RMA regression of log10W = 2.4639log10C − 0.1173 thus W = 0.763308 × C^2.4639. This equation suggests the fossil femur with circumference of 12.4 mm was from a bird weighing 377 g (95% CIs 307.2–463.6 g). This predicted mass is greater than the result from the heavy-birds algorithm of Campbell & Marcus (1992), which is consistent with the observation that Tinamidae include some of the more bulky birds among those listed as heavy birds by Campbell & Marcus (1992). We note, however, that this estimate would only be valid if *Proapteryx* was volant and of similar proportions to tinamous.

6. Palaeognaths – apterygids. If *Proapteryx* had body proportions similar to *Apteryx* then an algorithm based on kiwi would be the most accurate way of estimating its mass. We took measurements of femora from 30 individuals of kiwi of known weight in the collection of the National Museum of New Zealand Te Papa Tongarewa (Appendix 5) and generated a kiwi-specific algorithm. The calculated RMA regression equation for kiwi was log10W = 2.654307log10C − 0.56 108 thus W = 0.274739C^2.1496. This equation suggests that a bird with a femoral circumference of 12.4 mm would weigh 281.9 g (95% CIs 141.2–339.5 g).

These various calculations suggest that the predicted mass of *Proapteryx* probably lay within the range of 234.1 g (95% CIs 166–337.3 g), using Campbell & Marcus's (1992) equation based on heavy-bodied birds, and 377 g (95% CIs 307.2–463.6 g), assuming it was volant and based on tinamou. We note that the equation based on extant kiwi gave an intermediate value of 281.9 g (95% CIs 141.2–339.5 g). It seems the algorithm based on all birds from Campbell & Marcus (1992) probably over-estimated the weight of *Proapteryx* at 502 g. Therefore, *Proapteryx* was markedly smaller than all extant *Apteryx* species (Appendix 4) and similar in mass to the banded rail *Gallirallus philippensis* (Linnaeus).

Discussion

The fossils we describe as *Proapteryx micromeros* reveal, minimally, that a small apterygid species was present in New Zealand, about 19–16 Ma. The holotype femur derives from site FF1, an isolated outlier of the Bannockburn Formation (Lindqvist 1994) whose stratigraphic relationships to bed HH1b 9.5–9.58 m above the base of the Bannockburn Formation in the extensive

Manuherikia River section (Schwarzhans *et al.* 2012) which lies 300 m south, are presently undeterminable, so the two fossils may represent two species. However, we favour conspecificity of these fossils because they indicate a similar-sized bird (see below) and the associated fossils from FF1 are of species found in bed HH1b indicating the same source fauna. The addition of *Proapteryx* to the St Bathans Fauna reveals the assembly of all extant iconic terrestrial vertebrates of New Zealand, *e.g.*, leiopelmatid frogs, *Sphenodon*, moa, *Aptornis*, and acanthisittid wrens (see above), was complete by the Early Miocene: not one has arrived in the subsequent 16 Ma.

The holotype femur reveals that, at an estimated 234.1 g (95% CIs 166.0–337.3 g) – 377 g (95% CIs 307.2–463.6 g), *Proapteryx* was only 0.27–0.43 times the mass of the smallest individual (880 g) of the smallest extant kiwi species (*A. owenii*), or 0.2–0.3 times the mass of the approximate modal size (1200 g) of *A. owenii* (Appendix 5). In contrast, the quadrate is about the size of that in a small individual of *A. owenii*, and assuming it reflects skull size, might indicate that *Proapteryx* and *A. owenii* had similar sized skulls. However, *Proapteryx* has a more gracile proc. oticus, which may indicate a shorter bill than in *Apteryx*. The proportion of femur size to quadrate size seen in *Proapteryx* lies intermediate between those observed in similar-sized but distantly related birds such as Banded Rail, *Gallirallus philippensis*, *e.g.*, SAM B36299, and the Australian Little Bittern, *Ixobrychus dubius* (a species that has a relatively large head), *e.g.*, SAM B48804, (height quadrate 7.1 mm and 7.5 mm, respectively, versus 9.2 mm; femur proximal width 8.6 mm and 5.9 mm, respectively, versus 8.4 mm; femur mid shaft width 3.5 mm and 2.3 mm, respectively, vs 3.6 mm). Thus assuming the two bones belong to the same species, *Proapteryx* had a quadrate to femur proportion not greatly different from the Banded Rail. The two fossils, if conspecific, point to a bird with a head only slightly smaller than *A. owenii*, but with proportionally much smaller, more gracile legs, more like those of an average terrestrial bird, rather than with the relatively large legs modern kiwi have.

The presence of *Proapteryx* in the Early Miocene of New Zealand places the apterygid lineage in New Zealand at this time. If, as we prefer to interpret the fossils, only a single taxon is represented, then this taxon was of very small size compared to extant kiwi, being only about 0.195–0.314 times the mass of *A. owenii*, the smallest extant kiwi. We do not know whether *Proapteryx* was the only apterygid present in Zealandia during the Early Miocene, but the large sample size of birds from the St Bathans Fauna, some 5000 specimens, makes the undiscovered presence of another larger apterygid in this local fauna unlikely. However, our samples for this period derive from a single local fauna from one lacustrine environment in a rather large and diverse landscape, so there is a reasonable possibility that other forms existed elsewhere in Zealandia at that time. Despite this, given *Proapteryx* is an undoubted apterygid, it seems reasonable to assume that if its morphology was similar to that of a shared (hypothetical) common ancestor with extant apterygids, then small size was plesiomorphic for the clade. If so, it then follows that since the early Miocene, kiwi have evolved into larger birds with proportionately larger legs. Most terrestrial flightless birds have smaller volant relatives with proportionately smaller legs (Roff 1994; McNab 1994). The small size and slenderness of the femur makes it distinctly possible that *Proapteryx* was volant, supporting an overwater dispersal origin to New Zealand of kiwi that was independent of moa (Roff 1994; Cooper *et al.* 2001; Phillips *et al.* 2010). Further fossils will be required to confirm this suggestion. The divergence of kiwi from casuariids, for which estimates range from 53.5 Ma (Phillips *et al.* 2010) to 73 Ma (Haddrath & Baker 2012) long preceded *Proapteryx* leaving a large gap in the lineage history. This is significant because if *Proapteryx* was volant then the common ancestor of kiwi and Australian casuariids was also likely to have been volant, as is predicted by the multiple loss of flight hypothesis for ratites (Phillips *et al.* 2010). Given that the oldest Australian casuariid fossil presently known, *Emuarius gidju* a species similar to a small emu, is about 25 Ma (Boles 1992), then a ghost lineage in Australia of between 25 and 50 Ma, is inferred, providing more than enough time for the lineage to produce flightless and large species. If *Proapteryx* was flightless, a flightless lineage minimally spanning 16 Ma has to be invoked. The crown radiation of kiwi has a recent basal divergence most recently estimated at 6.3 Ma (2.3–1.4 Ma, 95% CIs) in BEAST by Haddrath & Baker (2012). Therefore, if *Proapteryx* was similar to the shared common ancestor with the crown radiation of kiwi and if it were volant, there was minimally a 10 Ma period during which the flightless condition could have been attained and body size of taxa increased. Even more rapid loss of flight and attainment of similar large body size is advocated for such divergent taxa as *Porphyrio* rails in New Zealand over only 1 Ma (Trewick 1997) and for ancestral ducks becoming moa-nalos in Hawaii in just the last 3.6 Ma (Sorenson *et al.* 1999).The phyletic dwarfing hypothesis advocated by Calder (1978, 1984) and Gould (1986, 1991) explains the large size of kiwi eggs as the result of an emu-sized ancestor evolving smaller body size while retaining the large size of the ancestor's egg. Regardless of its position on the volant–flightless continuum, *Proapteryx* reveals that ancestral kiwi were probably small in the Early Miocene. There remains no evidence in the fossil record to support the idea that geologically older kiwi were large like the emu and the cassowary, which are the sister taxa of Apterygidae. If this was so, then whether the ancestor of kiwi arrived in New Zealand vicariantly or by overwater dispersal is irrelevant; it was already small and probably volant – it cannot have been large and flightless like modern casuariids. This reasoning further suggests that the *Apteryx* lineage evolved larger size over the last 19–16 Ma. Thus the super-large egg of kiwi is probably not an historic holdover, but rather is more likely to be the result of adaptive advantage. It results in a highly precocial chick, which on emerging from the egg is independent of adults. We contend that this feature and the nocturnal habits of kiwi are perhaps best interpreted as adaptations to avoid avian predators, including terrestrial *Aptornis* and aerial raptors, both present in the Early Miocene and subsequently (Worthy *et al.* 2007; Worthy *et al.* 2011b), to which the evolution of flightlessness made them more vulnerable. The discovery of *Proapteryx* provides strong evidence to suggest that the origin of *Apteryx* by phyletic dwarfing is probably incorrect and that the opposite is instead more likely, that kiwi are the result of an evolutionary trajectory towards increased body mass during the Neogene and that their large eggs are an evolutionary novelty resulting from development towards extreme precociality.

Acknowledgements

We acknowledge generous support from the landowners A. and E. Johnstone (Home Hills Station, St Bathans) from whose land the fossils were excavated. We thank Walter Boles (Australian Museum), Wayne Longmore (Museum Victoria), Philippa Horton (South Australia Museum), Gerald Mayr (Forschungsinstitut Senckenberg, Frankfurt am Main, Germany), Vanesa De Pietri and Loic Costeur (Naturhistorisches Museum, Basel, Switzerland), and Anita Gamauf (Naturhistorisches Museum, Vienna, Austria) for access to comparative material. We thank Helen James (Smithsonian Institution) for images of *Lithornis*. We acknowledge the comments of Andrei Zinoviev and another anonymous reviewer that helped to improve the text. This research supported by the Australian Research Council (DP120100486) and a UNSW Goldstar award (PS22963). R.P.S. was funded by a grant from The Brian Mason Foundation.

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Appendix 1

Femoral features distinguishing Apterygidae from other birds.

Other modern birds, with an emphasis on those likely to be related for reasons of geographic proximity, have femora that differ from those of apterygids by the following features, which are considered sufficient to distinguish them, but which are not intended to be a comprehensive list of differences.

Dinornithiformes. All species of moa are vastly larger; facies artic. antitrochantica concave; pattern of ligament insertions proximolaterally differ greatly as follows (terminology after McGowan (1979) with preferred synonyms from Vanden Berge (1982) and Vanden Berge & Sweers (1993) in brackets, although we note McGowan's caveat that size and the presence of few muscles in *Apteryx* can be correlated with impressions on bones): large elongate sulcus for insertions for m. iliotrochantericus posterior (m. iliotrochantericus caudalis), m. gluteus medius et minimus (m. iliofemoralis externus), and m. iliotrochantericus medius et anterior (mm. iliotrochanterici medius et cranialis) shallower, located well craniad, nearly adjacent to cranial margin of crista trochanteris; insertion area for m. ischiofemoralis broad, well separated from the latter, just caudad of centre; impression for m. obturator internus (m. obturatorius medialis) closer to caudal margin, small, just caudad of the insertion area for m. ischiofemoralis; impression for M. obturator externus (m. obturatorius lateralis), shallow, broad.

Casuariidae. Similarities include lack of fossa trochanteris, notably convex facies artic. antitrochantica separated from caput by marked notch and ligamental insertion for m. iliotrochantericus caudalis largest and at mid craniocaudal depth. Differences include markedly larger size and a distinct pattern of sulci for ligamental insertions proximolaterally, interpreted by Patak & Baldwin (1998) as follows: a large oval sulcus at mid-craniocaudal depth for m. iliofemoralis externus, but the bipartite appearance of this sulcus suggests it also houses the insertion for m. iliotrochantericus caudalis; distal to this sulcus lies a circular and deep impression for m. ischiofemoralis; impression for m. obturator externus (=m. obturatorius lateralis), shallow, relatively small, stronger-marked in *Casuarius*.

Tinamidae, Galliformes. Proportions similar, but differ with a well-marked fossa trochanteris; facies artic. antitrochantica concave; impressio m. iliotrochantericus caudalis shallower and more cranially located; insertion area of m. obturatorius lateralis well marked; proximally, caudal and lateral facies meet in even curve; facies artic. antitrochanterica connected via broad groove to cranial surface.

All the following taxa lack a marked notch proximally separating the caput from facies artic. antitrochanterica, have a well-marked impression for m. obturatorius lateralis, and are further distinguished as follows:

Gruiformes (Gruiidae, Otididae, *Rhynochetos jubatus*, and Rallidae). Proportions similar, but have a fossa trochanteris; and lateral facies is markedly convex adjacent to the crista trochanteris.

Ardeidae. Proportions similar, but the shaft lacks dorsal curvature; crista trochanteris craniocaudal depth is much shallower and proximally is lateromedially narrow, so a broad flat groove connects the cranial surface to the facies artic. antitrochanterica.

Anseriforms. Femoral shaft relatively much shorter; caput on shorter neck.

Podicipedidae, Spheniscidae, Procellariiformes, Anhingidae, Phalacrocoracidae, Sulidae, Phaethontidae. Femoral shaft much shorter; craniocaudal depth crista trochanteris subequal or only slightly deeper than caput depth; neck with little or no constriction.

Pelecanidae. Femoral shaft relatively shorter, thin-walled, no dorsal curvature, crista trochanteris shorter, arrangement of insertion areas laterally differs.

Threskiornithidae. Femoral shaft relatively shorter, no dorsal curvature, crista trochanteris relatively short (proximodistally) with little cranial elevation.

Ciconiidae, Phoenicopteridae, Accipitriformes, Cathartidae and Falconidae. Femora as for Theskiornithids, but with pneumatic foramina in cranial pretrochanteric area and linea intermuscularis cranialis extends mesad of crista trochanteris.

Charadriiformes. Shaft lacks dorsal curvature; fossa trochanteris present. In addition, in Haematopodidae, Recurvirostridae, Charadriidae, Laridae, and Glareolidae, linea intermuscularis cranialis extends mesad of and parallel to crista trochanteris.

Columbidae, Psittaciformes, Caprimulgiformes, Cuculidae, Strigiformes, Coraciiformes and Passeriformes. Crista trochanteris cranially low, often with craniocaudal depth subequal to caput depth. Columbidae further differ with a fossa trochanteris and Caprimulgiformes and Strigiformes have crista trochanteris proximodistally shorter, and passed medially by well-marked crista intermuscularis cranialis.

Appendix 2

Measurements (mm) of quadrates of *Apteryx* species. TH is total height. Catalogue numbers starting with OR, DM, and S are all prefixed by NMNZ.

Catalogue number	Taxon	TH (capitulum squamosum – base of cond. medialis)	TH above cotyla quadratojugalis	% TH above cotyla quadratojugalis
DM.492-S	*australis*	11.1	5.6	50.5
OR.4738	*australis*	11.0	4.5	40.9
OR.21035	*australis*	10.5	5.3	50.5
OR.22114	*australis*	11.6	5.5	47.4
OR.22115	*australis*	11.9	5.5	46.2
OR.27965	*australis*	12.0	6.1	50.8
CM Av 39065	*australis*	11.5	5.0	43.2
OR.21415	*haastii*	11.3	5.1	45.1
OR.23045	*haastii*	11.4	5.6	49.1
OR.27983	*haastii*	12.3	5.7	46.3
MV B40905	*haastii*	12.1	5.3	43.8
CM Av31538	*haastii*	12.4	5.3	42.5
OR.21832	*lawryi*	12.1	5.3	43.8
CM Av 14447	*lawryi*	11.7	4.9	41.7
CM Av 32404	*lawryi*	13.5	6.7	49.4
CM Av 36637	*lawryi*	13.0	5.7	43.6
CM Av 36638	*lawryi*	12.0	5.6	46.4
DM.909-S	*mantelli*	11.1	5.9	53.2
OR.23048	*mantelli*	11.1	5.4	48.6
OR.24640	*mantelli*	10.1	5.4	53.5
OR.24984	*mantelli*	11.3	5.8	51.3
OR.27604	*mantelli*	11.3	5.2	46.0
OR.28614	*mantelli*	11.3	5.1	45.1
OR.28615	*mantelli*	11.7	5.2	44.4
OR.28616	*mantelli*	10.8	5.5	50.9
OR.29374	*mantelli*	11.3	5.1	45.1
CM Av 5492	*mantelli*	10.8	5.2	48.1
OR.20990	*owenii*	9.6	4.6	47.9
OR.22369	*owenii*	9.3	4.8	51.6
OR.23214	*owenii*	9.3	5.1	54.8
OR.24414	*owenii*	8.4	4.0	47.6
OR.24415	*owenii*	8.9	4.4	49.4
OR.24416	*owenii*	9.0	4.3	47.8
OR.25100	*owenii*	10.0	4.8	48.0
OR.25794	*owenii*	9.4	4.0	42.6
MV B56009	*owenii*	10.1	4.7	46.2
SAM B5051	*owenii*	9.3	4.3	46.5
CM Av 16691	*rowi*	12.2	5.3	43.6
CM Av 16717	*rowi*	11.0	5.2	47.5
CM Av 16718	*rowi*	12.3	5.7	46.2
USNM 290601	*Lithornis celetius*	10.8	7.6	70.7
S.53209	*Proapteryx*	9.2	4.9	53.3

Appendix 3

Relationship of Tinamidae estimated femoral circumference (using the formula circumference = PI* SQRT(2*((POWER((1/2*SD),2)) + (POWER((1/2*SW),2)))) to average weight. SW is width at mid shaft, SD is shaft depth at mid shaft, C is circumference, measurements in mm. Weights were taken from Davies (2002) except for SMF 2147, which was from Queiroz & Cooper (2011).

Reg. No.	Taxa	SW	SD	C	Weight	log C	log mass
SAM B.31339	*Tinamus major robusta*	5.6	5.8	17.9	1140	1.253092	3.056905
NMNZ OR.1433	*Tinamus major major*	4.7	5.5	16.1	1028.5	1.206052	3.012204
NMNZ OR.22983	*Nothoprocta perdicaria*	3.9	4.5	13.2	458	1.121504	2.660865
NMW 4.559	*Tinamus major*	6.1	6.2	19.3	1140	1.286039	3.056905
NMW 1061	*Nothura maculosa*	4.2	4.0	12.9	300	1.110063	2.477121
NMW 3.071	*Eudromia elegans*	5.5	5.0	16.5	703.5	1.217801	2.847264
NMW 160	*Rhynchotus fasciatus* = *rufescens*	5.6	5.7	17.8	770	1.249215	2.886491
NMW 161	*Rhynchotus fasciatus* = *rufescens*	6.1	5.9	18.9	770	1.275361	2.886491
NMW 4.068	*Nothoprocta perdicaria*	4.6	4.1	13.7	458	1.136355	2.660865
NMB 5537	*Rhynchotus rufescens*	5.8	5.3	17.3	770	1.238748	2.886491
NMB C.2004	*Tinamus* (*Trachypilmus* Cab.) *robustus*	5.9	5.8	18.4	1140	1.26507	3.056905
SMF 2148	*Crypturellus obsoletus*	4.1	3.7	12.3	480	1.089952	2.681241
SMF 11394	*Crypturellus noctivagus noctivagus*	4.2	4.2	13.2	800	1.119375	2.90309
SMF 11392	*Crypturellus tataupa*	3.4	3.8	11.3	202	1.053995	2.305351
SMF 2164	*Crypturellus parvirostris*	3.0	2.8	9.0	180	0.955935	2.255273
SMF 8184	*Crypturellus parvirostris*	3.5	3.1	10.4	220	1.015069	2.342423
SMF 9357	*Crypturellus parvirostris*	3.4	3.1	10.2	220	1.0081	2.342423
SMF 2537	*Crypturellus cinnamomeus*	3.9	4.0	12.4	419	1.092696	2.622214
SMF 2149	*Crypturellus undulatus vermiculatus*	4.4	4.6	14.2	540	1.151456	2.732394
SMF 2146	*Tinamus solitarius*	5.7	5.9	18.2	1200	1.260642	3.079181
SMF 2150	*Tinamus solitarius*	6.5	6.9	21.1	1500	1.324752	3.176091
SMF 5415	*Eudromia elegans*	5.5	4.9	16.5	703.5	1.216318	2.847264
SMF 6111	*Eudromia elegans*	5.8	5.1	17.1	703.5	1.233381	2.847264
SMF 6416	*Eudromia elegans*	5.6	5.0	16.7	703.5	1.222983	2.847264
SMF 9260	*Eudromia elegans*	5.6	5.1	16.8	703.5	1.225977	2.847264
SMF 9306	*Eudromia elegans*	5.0	4.5	14.9	703.5	1.172044	2.847264
SMF 6298	*Eudromia elegans*	5.4	5.4	16.9	703.5	1.227935	2.847264
SMF 2147	*Rhynchotus rufescens*	5.2	5.2	16.3	747	1.213153	2.873321

Appendix 4

The range in mass values (grams) by sex for *Apteryx* species from Marchant & Higgins (1990) and for *A. rowi* from Tennyson *et al.* (2003).

Species	Males	Females
Apteryx owenii	880–1356	1000–1400
Apteryx mantelli	1820–2590	2090–3270
Apteryx rowi	1575–2250	1950–3570
Apteryx australis lawryi	2300–3060	2700–3600
Apteryx haastii	1215–2320	1530–2718

Appendix 5

Relationship of *Apteryx* femoral circumference to weight of individual recorded at death. (SW is width at mid shaft, SD is shaft depth at mid shaft, circumference is estimated using the formulae PI*SQRT (2*((POWER((1/2*SD),2))+(POWER((1/2*SW),2)))). All specimens are from the Museum of New Zealand Te Papa Tongarewa.

Taxon	Reg no.	SD	SW	Circumference	weight (g)
A. mantelli	DM.909-S	9.6	8.5	25.1607	785
A. mantelli	OR.13588	11	11	29.6656	2428
A. mantelli	OR.14964	10	9	27.0852	1988
A. mantelli	OR.17206	10	9.6	27.0332	1366
A. mantelli	OR.17207	11	10	28.4908	2563
A. mantelli	OR.17208	9.8	9.2	26.13	1729
A. mantelli	OR.17209	11	10	28.1212	2336
A. mantelli	OR.17210	12	11	30.7656	2919
A. mantelli	OR.17211	12	12	32.0138	2495
A. mantelli	OR.17212	11	11	29.9376	2526
A. mantelli	OR.17213	10	8.9	26.4356	930
A. mantelli	OR.24640	9.1	8.6	24.3134	815
A. mantelli	OR.24984	9	9.5	24.948	1055
A. a. australis	OR.22089a	14	12	36.9381	2488
A. a. australis	OR.27761a	13	12	33.6873	3400
A. a. australis	OR.27965	11	10	28.842	2200
A. a. lawryi	OR.23591	11	11	28.8394	2800
A. a. lawryi	OR.23756	12	11	31.1584	4335
A. owenii	OR.22815a	8.4	8	22.497	910
A. owenii	OR.23044	7.8	7.4	20.865	885
A. owenii	OR.23717a	7.7	7.4	20.6809	1285
A. owenii	OR.24415	6.8	6.9	18.5919	670
A. owenii	OR.24416	7.8	7.8	21.2215	875
A. haastii	OR.19773a	9.6	8.5	25.1607	1215
A. haastii	OR.23022a	12	12	32.6507	2232
A. haastii	OR.23038	9.5	9.5	25.8466	1890
A. haastii	OR.23045	12	10	29.9895	2435
A. haastii	OR.23648a	11	11	29.8414	2015
A. haastii	OR.27983	9.6	9.2	25.7611	2550
A. haastii	OR.28010a	12	11	31.3853	2843

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A new roller (Aves: Coraciiformes s. s.: Coraciidae) from the Early Miocene of the Saint-Gérand-le-Puy area, Allier, France

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Abstract — *Miocoracias chenevali*, nov. gen., nov. spec., a new genus and species of roller (Aves: Coraciiformes s. s.: Coraciidae) is described from the Early Miocene of Saint-Gérand-le-Puy. This family had not yet been reported from the rich fossil avifauna of this area. Although the material is fragmentary it shows morphological characteristics different from those of the extinct family Geranopteridae, and can be attributed to the Recent family Coraciidae. The rodents found in the same locality make it possible to attribute it to the MN2a zone. An appendix gives an updated list of the fossil birds identified in the Saint-Gérand-le-Puy area.

Key words: Fossil birds, Early Miocene, Saint-Gérand-le-Puy, Mont Merle, Coraciidae, rollers

Introduction

The Coraciiformes sensu stricto include three extinct families, the Primobucconidae, the Eocoraciidae, the Geranopteridae, and two Recent families, the Coraciidae and the Brachypteraciidae (MAYR 2009). The Primobucconidae are known from the Early Eocene of Europe and North America and the Eocoraciidae are known from the Middle Eocene of Messel, Germany. In addition a nearly complete skeleton of a new genus and species has been described from the Lower Eocene of the Green River Fm., Wyoming, United States (CLARKE *et al.* 2009). This new form, *Paracoracias occidentalis*, is placed in the suborder Coracii. Incidentally, the name Coracii has been applied to a clade that has been defined as follows: “the stem clade including all taxa more closely related to Coracioidea than to its nearest outgroup” (CLARKE *et al.* 2009: p. 587). This clade definition is equivalent to the content of the Coraciiformes sensu stricto of MAYR (1998).

The Geranopteridae have been described in the Late Eocene or Oligocene of the Phosphorites du Quercy, in France, but in the new excavations they have been found only in Upper Eocene layers (MAYR & MOURER-CHAUVIRÉ 2000; MOURER-CHAUVIRÉ & SIGÉ 2006). They include the species *Geranopterus alatus* MILNE-EDWARDS, 1892, *Geranopterus milneedwardsi* MAYR & MOURER-CHAUVIRÉ, 2000, and some indeterminate Geranopteridae from the locality of Perrière (MOURER-CHAUVIRÉ & SIGÉ 2006). In the old collections from Quercy, the age of which is not accurately known, there is also a Coraciiforme s. s. incertae sedis species A, represented by an almost complete tarsometatarsus (PQ 1216) (MAYR & MOURER-CHAUVIRÉ 2000).

The species *Nupharanassa bohemica* MLIKOVSKÝ, 1999, described from the Lower Miocene locality of Dolnice, Czechia, (MN 4b), initially

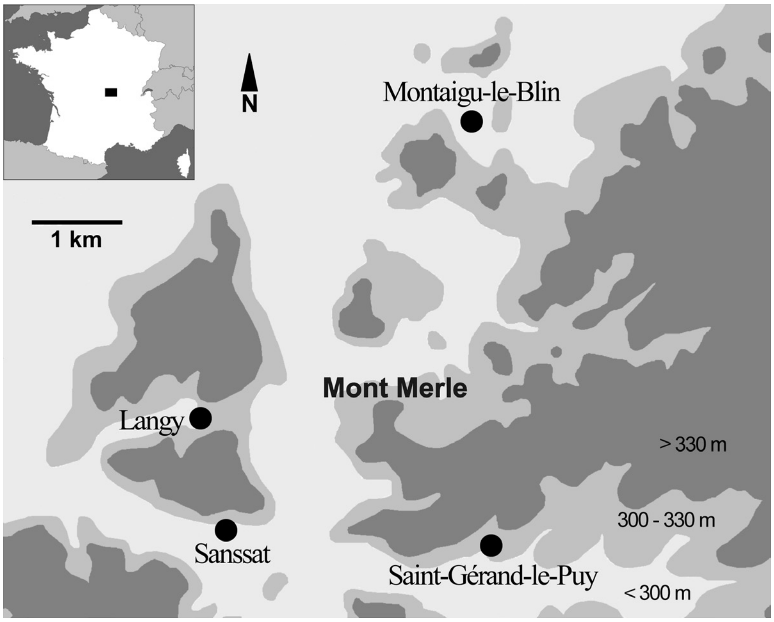

FIGURE 1. Location map of the Mont Merle locality, between the classical localities of Saint-Gérand-le-Puy and Montaigu-le-Blin. The contour lines indicate the height above sea level.

placed in the family Jacanidae, has been transferred to the genus *Geranopterus* and has become *Geranopterus bohemicus* (Mlikovský, 1999) (Mourer-Chauviré 1999).

In Africa Coraciiformes of indeterminate family had been reported from the Early Pliocene of Langebaanweg, South Africa (Rich 1980). These Coraciiformes belong to the family Alcedinidae (Olson 1994) and thus Coraciidae are still unknown at the present time in this avifauna. In Europe, the genus *Eurystomus* is known by an extinct species, *Eurystomus beremendensis* Kessler, 2010, from the Late Pliocene of Beremend 26, Hungary (MN 16) and by *Eurystomus* sp., from the Early Pleistocene of Betfia 2 and Betfia 9, Romania (Kessler 2010). In more recent localities the Coraciidae are represented by the Recent species, *Coracias garrulus* Linnaeus, 1758 (Tyrberg 1998).

The Mont Merle locality (Fig. 1) is situated near the town of Saint-Gérand-le-Puy (Allier, France), an area known for its rich Agenian vertebrate fauna (Viret 1929; Cheneval 1983a; Hugueney 1997). It is a limestone hill constituted by stromatolitic bioconstructions and marly sediments deposited in a lacustrine environment (Wattinne *et al.* 2003). A quarry was opened here, but it is now filled in. Washing and sieving of marl on the top of this hill yielded various fossil remains from fishes (mainly Cyprinidae), amphibians (Salamandridae), lizards (Lacertidae, Anguidae), amphisbaenians, snakes (Scolecophidians, Natricinae, Viperidae), marsupials (Didelphidae), insectivores (Soricidae, Talpidae), small carnivores, ungulates (Cainotheriidae, “Moschidae”), rodents (Sciuridae, Cricetidae, Eomyidae, Gliridae) and a lagomorph. Bird remains are not numerous and include only some crushed fossil bones of Palaelodidae, Laricolidae and a new Coraciidae.

Mont Merle is an unpublished new locality that has not been studied before. Some rodents make it possible to give it a dating. The Eomyid *Rhodanomys schlosseri* Depéret & Douxami, 1902, is represented by upper molars characterized by a continuous longitudinal ridge, and by their size which is included in the variation range observed at Fornant 11 (Engesser 1990) and at Chavroches (Hugueney *et al.* 2006). As the distribution of *R. schlosseri* covers only a short period, these teeth place the Mont Merle locality between the Paulhiac level (MN1) where *R. transiens*, predecessor of *R. schlosseri*, is present, and the upper part of the MN 2a level (top of the quarry of Montaigu-le-Blin and locality of La Chaux in Switzerland) where the species is not reported but is replaced by the Eomyid genus *Ritteneria*.

Material and methods

The anatomical terminology follows BAUMEL & WITMER 1993, and when necessary HOWARD 1929, and BALLMANN 1969a. The fossil specimens are deposited in the collection of the Université Claude Bernard-Lyon1 (acronym FSL for Faculté des Sciences de Lyon) and in the collection of the Muséum d'Histoire Naturelle de Lyon (acronym ML). Other acronyms are: EC (locality of Escamps); EC3 (locality of Escamps 3), EC4 (locality of Escamps 4), MN (Mammal Neogene), PQ (Phosphorites du Quercy), PRR (locality of Perrière), and STG (Saint-Gérand-le-Puy).

Systematic Palaeontology

Order Coraciiformes sensu stricto (see MAYR 1998)
Family Coraciidae BATSCH, 1788 (see DUBOIS & BOUR 2010)

Miocoracias nov. gen.

Type species: *Miocoracias chenevali* nov. spec.

Diagnosis: Distal part of tarsometatarsus showing a foramen vasculare distale situated relatively proximally, proximodistally elongate, and obliquely oriented. Trochlea metatarsi IV slightly shorter than trochlea metatarsi III, and trochlea metatarsi II slightly shorter than trochlea metatarsi IV. On the dorsal face trochlea metatarsi III raised and extended by a longitudinal ridge. Trochlea metatarsi III distally splayed. On the plantar face, opening of foramen vasculare distale elongate and narrow. Canalis interosseus distalis open on the plantar side and forming an elongate and narrow sulcus. Trochlea metatarsi II showing a narrow and projecting wing. Proximal rim of trochlea metatarsi III raised compared to the surface of the fossa supratrochlearis plantaris. In distal view trochleae arranged along a weakly arched line.

Included species: Type species only.

Distribution: Early Miocene, Agenian, MN 2a, Saint-Gérand-le-Puy area, Allier, France.

Etymology: Greek, *Mio*, from the Miocene, and *Coracias*, modern genus of roller.

Miocoracias chenevali nov. sp.

(Fig. 2.1–2.7)

Holotype: FSL 444 229 right tarsometatarsus, distal part.

Paratype: FSL 444 320 right tibiotarsus, distal part, incompletely preserved.

Diagnosis: As for the genus.

Horizon and locality: Locality of Mont Merle, district of Saint-Gérand-le-Puy, Allier, France. Early Miocene, Agenian, Mammal Neogene Zone MN 2a.

Referred material: ML STG 4048 right ulna. This ulna comes from the old collections and it is not possible to know from which locality it has been gathered.

Dimensions (in mm): Right tarsometatarsus, holotype: Length as preserved, 9.0; Distal width, 5.8; Distal depth, 3.1; Width of trochlea metatarsi III, 2.1; Depth of trochlea metatarsi III, 2.4. Right tibiotarsus: Length as preserved, 11.4; Width of shaft at the level of apophysis interna ligamenti obliqui, 2.6; Depth of shaft at the same level, 2.9; Depth of lateral condyle, 4.5. Right ulna: Total length, 53.7; Proximal width, 5.5; Proximal depth, 3.7; Width of shaft in the middle, 2.3; Depth of shaft in the middle, 2.5; Distal width from the cranial border of condylus dorsalis to top of tuberculum carpale, 5.5; Depth of condylus dorsalis, 4.8.

Etymology: This species is named after Jacques CHENEVAL in recognition of his numerous and valuable studies on the avifauna of the Saint-Gérand-le-Puy area.

Description and comparisons with the two Recent genera *Coracias* and *Eurystomus*

Tarsometatarsus (Fig. 2.1–2.3): On the dorsal face, the foramen vasculare distale is situated more proximally in *Miocoracias* and it is more proximodistally elongated than in the Recent genera. In *Coracias* and *Eurystomus*, the opening is dorsoplantarly orientated, while in *Miocoracias* the opening is slit-shaped, obliquely heading from the dorsolateral side to the plantaromedial side of the bone. This foramen is situated at the end of the outer extensor groove (HOWARD 1929).

This extensor groove is deeper in *Eurystomus* than in *Coracias*, and it is also very deep in *Miocoracias*. In *Miocoracias*, as in *Eurystomus* and *Coracias*, trochlea metatarsi IV is slightly shorter than trochlea metatarsi III and trochlea metatarsi II is slightly shorter than trochlea metatarsi IV. In the genus *Eurystomus* trochlea metatarsi III shows two projecting rims, separated by a well-expressed groove. This groove is fainter in the genera *Coracias* and *Miocoracias*. In *Eurystomus* and *Coracias* trochlea metatarsi III is relatively narrow, while it is slightly distally splayed in *Miocoracias*.

On the plantar face, in *Miocoracias*, the opening of the foramen vasculare distale is elongate and narrow, while it is more rounded in *Eurystomus* and *Coracias*. The canalis interosseus distalis, which runs from the foramen vasculare distale to the incisura intertrochlearis lateralis is not covered by a bony blade, and forms a narrow, elongate groove on the plantar side. This character is one of the main characteristics of the Coraciiformes s. s. Trochlea metatarsi II is more clearly separated from trochlea metatarsi III in *Miocoracias* than in *Eurystomus* and *Coracias*, it is narrower than in *Eurystomus* and it shows a wing less projecting plantarly than in *Coracias*. The proximal rim of trochlea metatarsi III is clearly raised compared to the surface of the fossa supratrochlearis plantaris, while in *Eurystomus* and *Coracias* this proximal part is not raised. Trochlea metatarsi IV shows a narrow and projecting wing in *Miocoracias* and *Eurystomus*, while this wing is less developed in *Coracias*. Fossa metatarsi I extends far distally in *Miocoracias* and *Eurystomus*, while it is situated more proximally in *Coracias*.

In distal view the trochleae are arranged on a faintly arched line as in both Recent genera.

Tibiotarsus (Fig. 2.4–2.5): The condylus medialis is not preserved. On the cranial face, the sulcus extensorius and the pons supratendineus are situated on the median axis of the bone, as in the Recent Coraciidae and Brachypteraciidae, while in most of the other Recent birds they are situated on the medial side of the bone. At the proximal part of the condylus lateralis, and on the lateral side of the pons supratendineus, there is a strong, point-shaped tubercle, the apophysis externa ligamenti obliqui (Ballmann 1969a), and on the medial side there is also a thin, elongate, and well projecting apophysis interna ligamenti obliqui.

Compared to the Recent genera *Coracias* and *Eurystomus*, the distal part of the tibiotarsus is less mediolaterally compressed, and the sulcus extensorius is shallower. The apophysis externa ligamenti obliqui is very sharp and projecting while its development is variable in the Recent forms: some specimens have an almost flat apophysis, situated in the continuation of the condylus lateralis, while some others have a sharp apophysis.

On the caudal face, the condylus medialis shows a wing which projects weakly medially, as in the genera *Eurystomus* and *Coracias*, and the condylus lateralis shows a wing less projecting laterally than in *Eurystomus*, but comparable to that of *Coracias*.

On the lateral face, the condylus lateralis is very rounded and the epicondylus lateralis is hardly indicated, as in *Eurystomus* and *Coracias*.

Ulna (Fig. 2.6–2.7): This ulna shows the characteristic shape of the rollers' ulnae. It is elongate and slender, with a slight curvature at its proximal part. The shaft is slightly flattened on its caudal side. Compared to the genus *Coracias*, the olecranon is less projecting proximally and wider at its basis. The cotyla dorsalis is extended distally by a long, narrow lip, clearly separated from the cotyla ventralis. This lip is more rounded in *Coracias*. The distal part of the fossil is not very well preserved, but the condylus ventralis is more projecting distally and the tuberculum carpale is sharper in *Miocoracias* than in *Coracias*. Still in *Miocoracias* there is a small depression on the proximal border of the tuberculum carpale, on its cranial side. This depression is absent in the Recent genera *Coracias* and *Eurystomus*.

The shape of the olecranon looks more similar to that of *Eurystomus*, the olecranon of which is short and wide at its basis. In *Miocoracias* the distal lip of the cotyla dorsalis is incurved and medially directed, while in *Eurystomus* it is dorsally directed. On the ventral side the tuberculum ligamenti collateralis ventralis is more projecting ventrally in *Eurystomus*. At the distal part the condylus ventralis is longer in proximodistal direction in *Eurystomus*.

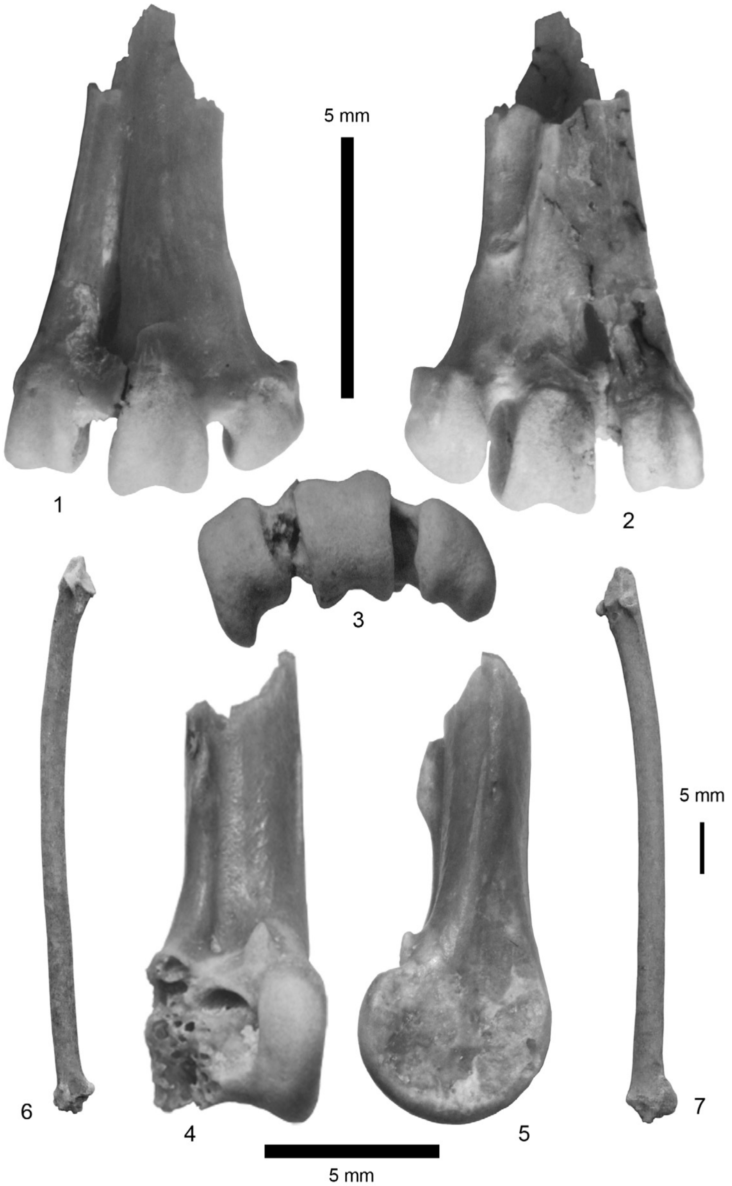

FIGURE 2. *Miocoracias chenevali* nov. gen. et nov. spec. from the Early Miocene of Mont Merle, district of Saint-Gérand-le-Puy, Allier, France. **1–3**, Right tarsometatarsus, distal part, holotype, FSL 444 229 (1: dorsal view, 2: plantar view, 3: distal view); **4–5**, Right tibiotarsus, distal part, paratype, FSL 444 230 (4: cranial view, 5: lateral view); **6–7**, Referred material, right ulna, ML STG 4048 (6: dorsal view, 7: Ventral view).

Comparison with the extinct family Geranopteridae

Tarsometatarsus: The distal part of the tarsometatarsus is known in *Geranopterus alatus* by two specimens from the Late Eocene of Escamps, EC4 n°5 (Mayr & Mourer-Chauviré 2000: fig. 8, Y–Z), and ES n°4. In *Geranopterus* the metatarsal trochleae are shorter and less individualized than in *Miocoracias*. In *Miocoracias* trochlea metatarsi III is more raised on the dorsal face, and it is extended by a longitudinal ridge; the outer extensor groove is deeper. In *Geranopterus* the dorsal surface of the tarsometatarsus is flatter. On the plantar face the proximal rim of trochlea metatarsi III is raised compared to the surface of fossa supratrochlearis plantaris in *Miocoracias* while in *Geranopterus* the two ridges, lateral and medial, of trochlea metatarsi III gradually merge into the surface of this fossa. Trochlea metatarsi III is narrower in *Geranopterus* than in *Miocoracias*. The same characteristics are found on a distal tarsometatarsus of *G. milneedwardsi*, from the Late Eocene of Perrière, n° FSL 330 856, different from *G. alatus* by its smaller size.

In their phylogenetic analysis Clarke *et al.* (2009: p. 607) have used the character 68. Tarsometatarsus, distal interosseal canal: present, canal open on plantar side, forming a deep narrow sulcus between trochleae III and IV (0); absent (1). This open canal is coded as absent (1) in *Geranopterus* while it is coded as present (0) in *Eocoracias* and in the Recent Coraciidae and Brachypteraciidae. It is coded as (?) for the three species of Primobucconidae included in the analysis. This is clearly inaccurate because this character is an important synapomorphy of the clade including the Primobucconidae, Eocoraciidae, Geranopteridae, Coraciidae and Brachypteraciidae (Mayr *et al.* 2004; Mayr 2009). This character is not visible in *Eocoracias* and it is present in the Primobucconidae from the Eocene of France (Mayr *et al.* 2004) as well as in the Geranopteridae (Mayr & Mourer-Chauviré 2000; Mourer-Chauviré & Sigé 2006).

Geranopterus bohemicus looks very similar to *G. alatus* and differs from *Miocoracias* by its shorter trochleae metatarsi with narrow incisurae intertrochlearis, its trochlea metatarsi III which is not raised compared to the dorsal surface of the shaft and not distally splayed. It differs also by the dorsal surface of the shaft, which is flat, and by trochlea metatarsi IV, which is narrower. Finally Mlikovský indicates in the diagnosis of this species “a rather smooth transition between the trochlea metatarsi tertii and fossa supratrochlearis plantaris” (Mlikovský 1999: p. 122). This characteristic corresponds well to the genus *Geranopterus* and differs from the genus *Miocoracias*.

Tibiotarsus: In *Geranopterus alatus* the tibiotarsus is known by two distal extremities from the locality of Escamps, EC3 n°7 and EC4 n°3 (Mayr & Mourer-Chauviré 2000: fig. 8, T–U), and in *G. milneedwardsi* by a distal part from the locality of Perrière, n° PRR 2621. In *G. alatus* the sulcus extensorius and the pons supratendineus are deeper inside the shaft. On the medial side the epicondylus medialis is very projecting. In *Miocoracias* the pons supratendineus is more cranially brought forward, the apophysis externa ligamenti obliqui is more projecting and the epicondylus medialis is hardly visible.

In *G. milneedwardsi* the shaft is very narrow compared to the condyles; the sulcus extensorius is faintly indicated; both condyles, lateral and medial, are narrow, very close together, and strongly projecting cranially. The apophysis externa ligamenti obliqui is projecting. The pons supratendineus is situated between the proximal parts of the condyles. Both epicondyles, lateral and medial, are not well marked.

Ulna: In the genus *Geranopterus* only the distal part of the ulna is known. In this genus, as in *Miocoracias*, the tuberculum carpale is very sharp but the condylus ventralis is flatter and more proximodistally elongate in *Geranopterus* (see Mayr & Mourer-Chauviré 2000: fig. 8, K–L).

Comparison with the small forms from Perrière

Two other, smaller forms, designated as Geranopteridae, genus and species indeterminate, have been reported from the late Eocene locality of Perrière, in the Quercy, level MN 17b (Mourer-Chauviré & Sigé 2006). A distal part of tibiotarsus, n° FSL 367088, corresponds to a bird smaller than *G. milneedwardsi*. It differs from *Miocoracias* by the fact that the sulcus extensorius and the pons supratendineus are deeper between the condyles. A distal part of tarsometatarsus, n° FSL 367073, corresponds to a bird which was still smaller than the preceding one (Mourer-Chauviré & Sigé 2006: pl. 1, i–j). In this form the shaft is very narrow, and triangular in cross section. Trochlea metatarsi IV is not preserved but trochlea metatarsi II is strongly plantarly displaced. This form differs from *Miocoracias* by its very narrow shaft and its trochlea metatarsi II plantarly displaced.

Comparison with a Coraciiformes s. s., incertae sedis, species A (n° PQ 1216)

This form is known by an almost complete tarsometatarsus illustrated in Mayr & Mourer-

Chauviré (2000: fig. 9G–I). *Miocoracias* shares with this form the presence of an elongate and oblique distal vascular foramen, situated at the bottom of a deep outer extensor groove. But it differs from it because in *Miocoracias* trochlea metatarsi II is slightly shorter than trochlea metatarsi III while in PQ 1216 it is distinctly shorter. On the plantar face, unlike *Miocoracias*, trochlea metatarsi III does not have a raised rim, and its two ridges, lateral and medial, merge gradually into the surface of the fossa.

Discussion

The Coraciiformes sensu stricto are represented at the present time by two families, one restricted to Madagascar, and the other mainly distributed in the tropical regions of the Old World (Fry 2001). As it was first indicated by Harrison (1979) small non-passerine birds were much diversified in the early Tertiary of the Northern Hemisphere and occupied the ecological niches which are now occupied by the passerines. Among these small non-passerine birds there are stem group representatives of Coraciiformes s. s., Alcediniformes, Upupiformes, Caprimulgiformes, Apodiformes, Coliiformes, Psittaciformes, etc. Stem group representatives of Coracii are known in the Early Eocene of North America (Clarke *et al.* 2009; Ksepka & Clarke 2010) where rollers are no longer present. These stem group representatives have progressively disappeared and some orders are now only represented by a few relict families.

The stem group family Geranopteridae is still present in the locality of Dolnice, in Czechia, the age of which is MN 4b (Mlikovský 2002) and thus clearly younger than the age of the type locality of *Miocoracias*.

The presence of the genus *Miocoracias* fills a gap between the Eocene and the Recent forms. The small quantity of material found in the Saint-Gérand-le-Puy area can be explained by the fact that this fossil avifauna is mainly composed of waterbirds and only includes a small proportion of terrestrial birds.

The Saint-Gérand avifauna includes a large quantity of forms belonging to families, or subfamilies, the recent distribution of which is mainly tropical. Cheneval (1989) already indicated this abundance in the aquatic avifauna, but the same observation can be made for the terrestrial avifauna. The taxa corresponding to a tropical climate are: Anatidae (genus *Mionetta*), Palaelodidae, Phoenicopteridae, Ciconiidae (tribe Leptoptilini), Threskiornithidae, Pelecanidae, Sagittariidae, Pteroclididae, Psittacidae, Coliidae, Trogonidae and Phoeniculidae. The presence of Coraciidae is in line with this presence of tropical taxa, whether exclusively (taxa with only tropical species, not migrating to temperate zones), or not. In the Recent Coraciidae, most of the species are migratory but they breed and winter inside the intertropical zone, or very close to it (Fry 2001). Two species only are long distance intercontinental migrants, the European Roller (*Coracias garrulus*) and the Dollarbird (*Eurystomus orientalis*). These tropical taxa retreated from the high and middle latitudes during the second half of the Miocene and the Pliocene, leaving in some cases emergent long-distance migrants (Louchart 2008).

Acknowledgements

We thank M. Malhuret who allowed us access to the Mont Merle, Marion Petit who helps us to collect fossil remains, Didier Berthet for the loan of the material from the Muséum de Lyon, and Christine Lefèvre, from the Muséum national d'Histoire naturelle de Paris, for the loan of comparative material. We thank Antoine Louchart and Marco Pavia for their careful comments which have improved the manuscript.

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Appendix

Updated list of the avian species reported in the whole of the localities known as "Saint-Gérand-le-Puy". The material from the old collections comes from different quarries and its age is not accurately known; this age can be MN 1, MN 1/2, or MN 2a (Hugueney 1997). However the largest part of the quarries has yielded fossil material corresponding to the MN 2a zone. This list is founded upon the following works: Ballmann 1969b; Cheneval 1983b, 1984; Cheneval & Escuillié 1992; Mourer-Chauviré 1995; Bocheński 1997; Mlikovský 1998; Mourer-Chauviré 2000; Mlikovský & Göhlich 2000; Mlikovský 2002; Hugueney *et al.* 2003; Göhlich & Mourer-Chauviré 2005; De Pietri *et al.* 2011a, 2011b, 2012; Mayr & Smith 2012; De Pietri & Mayr 2012; De Pietri 2013. The systematic order follows the list of the International Ornithologists' Union (Gill & Donsker 2012). Some modifications brought by Mlikovský (2002) have not been integrated because they do not seem well-founded.

O. Galliformes
F. Quercymegapodiidae Mourer-Chauviré, 1992
  Genus *Ameripodius* Alvarenga, 1995
    Ameripodius alexis Mourer-Chauviré, 2000
F. Phasianidae Horsfield, 1821
  Genus *Palaeortyx* Milne-Edwards, 1869
    Palaeortyx gallica Milne-Edwards, 1869
    Palaeortyx brevipes Milne-Edwards, 1869
    Palaeortyx prisca (Milne-Edwards, 1869)
    syn. *Palaeortyx intermedia* Ballmann, 1966
    Palaeortyx phasianoides Milne-Edwards, 1869
    Palaeortyx media Milne-Edwards, 1869 (nomen nudum)

O. Anseriformes
F. Anatidae Leach, 1820
  Genus *Mionetta* Livezey & Martin, 1988
    Mionetta blanchardi (Milne-Edwards, 1863)
    Mionetta consobrina (Milne-Edwards, 1867)
    Mionetta natator (Milne-Edwards, 1867)
  Genus *Cygnopterus* Lambrecht, 1931
    Cygnopterus alphonsi Cheneval, 1984
O. Gaviiformes
F. Gaviidae Coues, 1903
  Genus *Colymboides* Milne-Edwards, 1867
    Colymboides minutus Milne-Edwards, 1867

O. Procellariiformes
F. Procellariidae Leach, 1820
  Indeterminate genus
    Indeterminate genus *arvernensis* (Milne-Edwards, 1871), syn. *Puffinus arvernensis* Milne-Edwards, 1871, and *Plotornis arvernensis* (Milne-Edwards, 1871) (Cheneval 1984; Mayr & Smith 2012)

O. Phoenicopteriformes
F. Palaelodidae (Stejneger, 1885)
  Genus *Palaelodus* Milne-Edwards, 1863
    Palaelodus ambiguus Milne-Edwards, 1863, syn. *Ibidopodia palustris* Milne-Edwards, 1871, syn. pro parte *Probalearica problematica* (Milne-Edwards, 1868) (Cheneval & Escuillé 1992)
    Palaelodus gracilipes Milne-Edwards, 1863, syn. *Palaelodus minutus* Milne-Edwards, 1868 (Cheneval 1983)
    Palaelodus crassipes Milne-Edwards, 1863
  Genus *Megapaloelodus* Miller, 1944
    Megapaloelodus goliath (Milne-Edwards, 1868)
F. Phoenicopteridae Bonaparte, 1831
  Genus *Phoenicopterus* Linnaeus, 1758
    Phoenicopterus croizeti Gervais, 1852

O. Ciconiiformes
F. Ciconiidae Gray, 1840
  Genus *Grallavis* Cheneval, 1984
    Grallavis edwardsi (Lydekker, 1891b)

O. Pelecaniformes
F. Threskiornithidae Richmond, 1917
  Genus *Gerandibis* De Pietri, 2013
    Gerandibis pagana (Milne-Edwards, 1868) syn. *Milnea gracilis* Lydekker, 1891a (Cheneval 1984)
F. Ardeidae Leach, 1820
  Genus *Proardeola* Harrison, 1979
    Proardeola walkeri Harrison, 1979
F. Pelecanidae Rafinesque, 1815
  Genus *Miopelecanus* Cheneval, 1984
    Miopelecanus gracilis (Milne-Edwards, 1863)

O. Suliformes
F. Sulidae Reichenbach, 1849
  cf. Genus *Empheresula* Harrison, 1975
    cf. *Empheresula arvernensis* (Milne-Edwards, 1867)
F. Phalacrocoracidae Reichenbach, 1850
  Genus *Oligocorax* Lambrecht, 1933
    Oligocorax littoralis (Milne-Edwards, 1863)
  Genus *Nectornis* Cheneval, 1984
    Nectornis miocaenus (Milne-Edwards, 1867)

O. Accipitriformes
F. Sagittariidae Grandori & Grandori, 1935
  Genus *Pelargopappus* Stejneger, 1885
    Pelargopappus magnus (Milne-Edwards, 1868)
F. Accipitridae Vieillot, 1816
  Genus *Aquilavus* Lambrecht, 1933
    Aquilavus depredator (Milne-Edwards, 1871)
    Aquilavus priscus (Milne-Edwards, 1863)
  Genus *Milvus* Lacépède, 1899
    Milvus deperditus Milne-Edwards, 1871
  Genus *Promilio* Wetmore, 1958
    Promilio incertus (Gaillard, 1939)
  Genus *Palaeohierax* Milne-Edwards, 1871
    Palaeohierax gervaisii (Milne-Edwards, 1863)

O. Otidiformes
F. Otididae Rafinesque, 1815 (?)
  Genus *Otis* Linnaeus, 1758 (?)
    Otis agilis Milne-Edwards, 1871 (nomen nudum)

O. Gruiformes
F. Rallidae Vigors, 1825
  Genus *Palaeoaramides* Lambrecht, 1933
    Palaeoaramides christyi (Milne-Edwards, 1869), syn. *Palaeoaramides eximius* (Milne-Edwards, 1869)
  Genus *Paraortygometra* Lambrecht, 1933
    Paraortygometra porzanoides (Milne-Edwards, 1869)
F. Gruidae Vigors, 1825
  Genus *Palaeogrus* Portis, 1884
    Palaeogrus excelsus (Milne-Edwards, 1868)
  Genus *Probalearica* Lambrecht, 1933
    Probalearica problematica (Milne-Edwards, 1868)

O. Charadriiformes
F. Haematopodidae Bonaparte, 1838
  New material to be described (De Pietri *et al.* 2012)
F. Recurvirostridae Bonaparte, 1854
  Genus *Himantopus* Brisson, 1760
    Himantopus brevipes Milne-Edwards, 1871 (nomen nudum)
F. Charadriidae Vigors, 1825
  New material to be described (De Pietri *et al.* 2012)

- Scolopaci sensu Paton *et al.* 2003
- F. incertae sedis
  - Genus *Scolopacimilis* De Pietri & Mayr, 2012
    - *Scolopacimilis lartetianus* (Milne-Edwards, 1863)
    - *Scolopacimilis* sp.
  - Genus *Becassius* De Pietri & Mayr, 2012
    - *Becassius charadriioides* De Pietri & Mayr, 2012
- F. Scolopacidae Rafinesque, 1815
  - Genus *Elorius* Milne-Edwards, 1868
    - *Elorius paludicola* Milne-Edwards, 1868
  - Genus ? *Elorius* Milne-Edwards, 1868
    - ? *Elorius limosoides* De Pietri & Mayr, 2012
  - Genus *Parvelorius* De Pietri & Mayr, 2012
    - *Parvelorius gracilis* (Milne-Edwards, 1868)
  - Genus ? *Parvelorius* De Pietri & Mayr, 2012
    - ? *Parvelorius calidris* De Pietri & Mayr, 2012
    - Genus and species indeterminate

- Suborder Laromorphae De Pietri *et al.*, 2011a
- F. Laricolidae De Pietri *et al.*, 2011a
  - Genus *Laricola* Mlikovský, 2002
    - *Laricola desnoyersii* (Milne-Edwards, 1863)
    - *Laricola elegans* (Milne-Edwards, 1868)
    - *Laricola totanoides* (Milne-Edwards, 1868)
    - *Laricola intermedia* De Pietri *et al.*, 2011a
    - *Laricola robusta* De Pietri *et al.*, 2011a
- Family incertae sedis
  - Genus *Sternalara* De Pietri *et al.*, 2011a
    - *Sternalara minuta* De Pietri *et al.*, 2011a
    - *Sternalara milneedwardsi* De Pietri *et al.*, 2011a

- O. Pteroclidiformes
- F. Pteroclididae Bonaparte, 1831
  - Genus *Leptoganga* Mourer-Chauviré, 1993
    - *Leptoganga sepultus* (Milne-Edwards, 1869)
  - Genus *Gerandia* Lambrecht, 1933
    - *Gerandia calcaria* (Milne-Edwards, 1869)

- O. Psittaciformes
- F. Psittacidae Illiger, 1811
  - Genus *Archaeopsittacus* Lambrecht, 1933
    - *Archaeopsittacus verreauxi* (Milne-Edwards, 1871)

- O. Strigiformes
- F. Tytonidae Ridgway, 1914
  - Genus *Necrobyas* Milne-Edwards, 1892
    - *Necrobyas arvernensis* (Milne-Edwards, 1863)
  - Genus *Prosybris* Brodkorb, 1970
    - *Prosybris antiqua* (Milne-Edwards, 1863)
- F. Strigidae Vigors, 1825
  - Genus *Mioglaux* Mlikovský, 1998
    - *Mioglaux poirrieri* (Milne-Edwards, 1863)

- O. Apodiformes
- F. Apodidae Hartert, 1897
  - Genus *Procypseloides* Harrison, 1984
    - *Procypseloides ignotus* (Milne-Edwards, 1871)

- O. Coliiformes
- F. Coliidae Swainson, 1837
  - Genus *Limnatornis* Milne-Edwards, 1871
    - *Limnatornis paludicola* Milne-Edwards, 1871
    - *Limnatornis archiaci* (Milne-Edwards, 1871)

- O. Trogoniformes
- F. Trogonidae Lesson, 1828
  - Genus *Paratrogon* Lambrecht, 1933
    - *Paratrogon gallicus* (Milne-Edwards, 1871)

- O. Coraciiformes
- F. Coraciidae Batsch, 1788
  - Genus *Miocoracias* nov. gen.
    - *Miocoracias chenevali* nov. spec. (this paper)

- O. Bucerotiformes
- F. Phoeniculidae Bonaparte, 1831
  - Genus *Phirriculus* Mlikovský & Göhlich, 2000
    - *Phirriculus pinicola* Mlikovský & Göhlich, 2000

- O. Piciformes
- F. Picidae Vigors, 1825
  - Genus *Piculoides* De Pietri *et al.*, 2011b
    - *Piculoides saulcetensis* De Pietri *et al.*, 2011b

- O. Passeriformes
- F. Laniidae Rafinesque, 1815
  - Genus *Lanius* Linnaeus, 1758
    - *Lanius miocaenus* Milne-Edwards, 1871
- F. Ploceidae Sundevall, 1836
  - Genus *Passer* Brisson, 1760
    - *Passer* sp.
- F. Motacillidae Horsfield, 1821
  - Genus *Motacilla* Linnaeus, 1758
    - *Motacilla humata* Milne-Edwards, 1871
    - *Motacilla major* Milne-Edwards, 1871
- F. Fringillidae Vigors, 1825
  - Genus *Loxia* Linnaeus, 1758
    - *Loxia* sp. 1
    - *Loxia* sp. 2

Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

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A *Haematopus*-like skull and other remains of Charadrii (Aves, Charadriiformes) from the Early Miocene of Saint-Gérand-le-Puy (Allier, France)

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Abstract — Among Charadriiformes (shorebirds and allies), Charadrii (plovers and allies) have the poorest fossil record. The lacustrine, early Miocene deposits of Saint-Gérand-le-Puy in France have yielded several charadriiform birds, but so far no members of the Charadrii. We identified a *Haematopus* (oystercatcher)-like skull from the early Miocene locality of Montaigu-le-Blin, in the Saint-Gérand-le-Puy area. Affinities to extant Haematopodidae are, apart from an overall similarity, supported by two features of the occipital region not present in any other of the examined charadriiforms. The fossil nevertheless differs from recent oystercatchers in some osteological features, including much shallower temporal fossae. Additionally, we report two fossil remains of plover-like Charadrii, a humerus and a tarsometatarsus, which also represent the first record of this charadriiform clade in Saint-Gérand-le-Puy. The specimens resemble the corresponding bones of Charadriidae but a definitive assignment to that taxon is not possible.

Key words: Fossil birds, shorebirds, plovers, oystercatcher, Charadriidae

Introduction

Most knowledge of early Miocene (Aquitanian, MN 1–2, 23–20.5 Ma) fossil avifaunas from Europe has been gleaned from few fossil rich localities, predominantly in France and Germany (Mlíkovský 1992, 1996). Amongst these, the localities that make up Saint-Gérand-le-Puy are perhaps the best known and, being of lacustrine origin, it is not surprising that most fossil remains recovered from these localities can be referred to aquatic or semi-aquatic taxa. Despite relative abundant remains of Scolopaci and Lari (*e.g.*, De Pietri *et al.* 2011; De Pietri & Mayr 2012), as yet no representatives of Charadrii (plovers, oystercatchers, thick-knees, and allies) have been described or mentioned.

The clade Charadrii encompasses the following families: Chionidae (sheathbills), Pluvianellidae (Magellanic Plover), Pluvianidae (Egyptian Plover) Charadriidae (plovers and allies), Haematopodidae (oystercatchers), Recurvirostridae (stilts and avocets), Ibidorhynchidae (Ibisbill), and Burhinidae (thick-knees). Although phylogenies based on molecular data (Baker *et al.* 2007; Fain & Houde 2007) have recovered a paraphyletic Charadriidae, with *Pluvialis* (golden plovers and the Grey Plover) in a clade together with Recurvirostridae, Haematopodidae, and Ibidorhynchidae, more recent phylogenies (Baker *et al.* 2012) support a monophyletic Charadriidae, with *Pluvialis* occupying a basal position within the family.

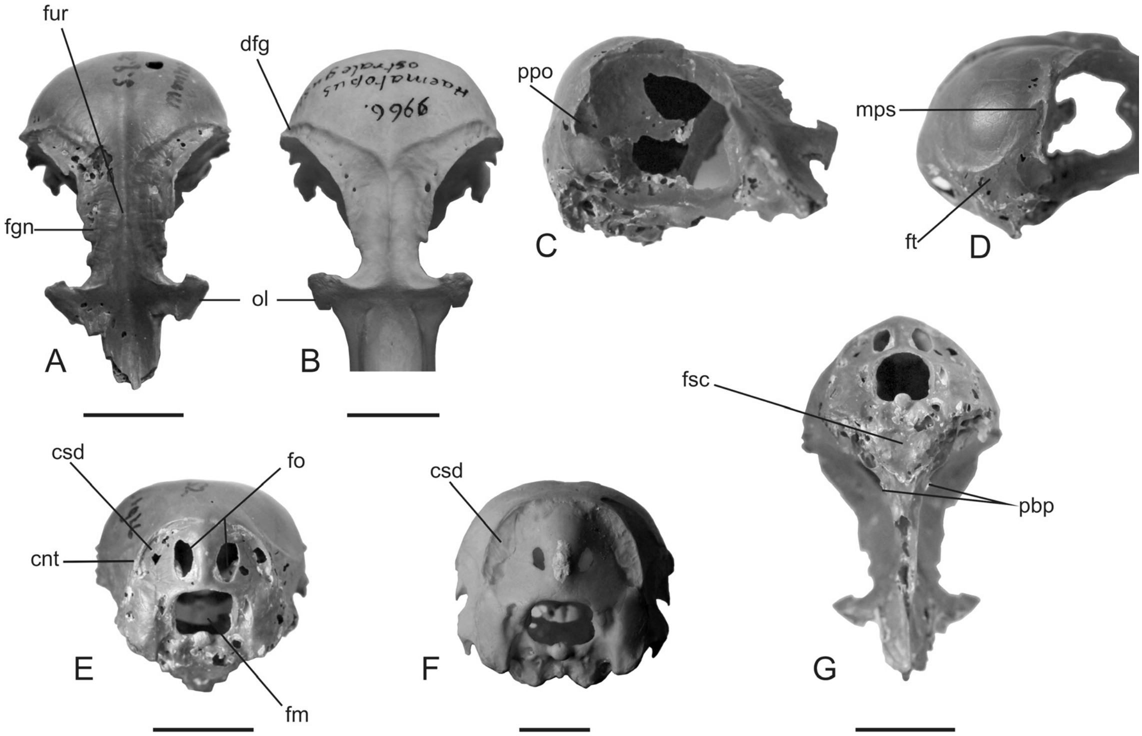

FIGURE 1. The fossil skull NMB S.G.20252 (**A, C–E, G**) from the early Miocene of Saint-Gérand-le-Puy in comparison to the extant Eurasian Oystercatcher, *Haematopus ostralegus* (**B, F**). **A**, **B**, dorsal views; **C**, **D**, right lateral views; **E**, **F**, occipital views, and **G**, ventral view. C and D not to scale. Abbreviations: csd, crescent-shaped deep depression dorsal to the crista nuchalis transversa; cnt, crista nuchalis transversa; dfg, caudal portion of fossa glandulae nasalis; fgn, fossae glandularum nasales; fm, foramen magnum; fo, fonticuli occipitales; fsc, fossa subcondylaris; ft, fossa temporalis; fur, furrow at interorbital surface of the frontal bone; mps, scar marking the attachment for musculus pseudotemporalis superficialis; ol, os lacrimale; pbp, articulation facets for processus basipterygoidei; ppo, processus postorbitales. Scale bars equal 10 mm.

The fossil record of the Charadrii is very poor in comparison to that of other shorebirds (*i.e.*, Scolopaci and Lari), and the scarcity of Paleogene examples is particularly remarkable. Several specimens have been misassigned to this clade (Olson 1985; Mlíkovský 2002; Mayr 2009), whereas better supported records are mostly of dubious affinities. Paleogene remains of the Charadrii include an almost complete skeleton of uncertain affinities from the early Oligocene of France (Bessonat & Michaut 1973) and *Jiliniornis huadianensis* Hou & Ericson, 2002, from the middle Eocene of China, tentatively placed in the Charadriidae by the authors. A putative record of the Recurvirostridae, *Recurvirostra sanctaeneboulae* Mourer-Chauviré, 1978, from the early Eocene of France, was based on the proximal end of an ulna, but genus level assignment of this specimen certainly needs to be corroborated by further material (see Olson 1985). A yet undescribed burhinid from Late Oligocene deposits in Australia was mentioned by Boles (2001).

Miocene Charadrii are somewhat better represented than their Paleogene counterparts. The existence of Charadriidae from the Middle Miocene of France was briefly acknowledged by Ballmann (1972), and further material was reported from the Early Miocene of the Czech Republic (MN 4b; Mlíkovský 2002), although unfortunately it was neither described nor figured. A species of *Charadrius* from the Late Miocene-Early Pliocene of Arizona was noted by Bickart (1990), and from the same locality, this author also described members of the Recurvirostridae, notably the species *Himantopus olsoni*, as well as a species of *Recurvirostra*. A distal ulna from the Middle Miocene of California was assigned to the extant genus *Recurvirostra* by Miller (1961), but because of the uninformative nature of the remains this assignation remains uncertain (see Olson 1985). The only known Miocene representative of the Burhinidae is *Burhinus lucorum*, from the Early Miocene of Nebraska (Bickart 1982), which was described on the basis of a humerus. Determining a well-resolved phylogenetic placement for most of these Miocene specimens is nevertheless likely to remain an elusive task, owing to the fragmentary nature of the material.

In this study we describe a skull of a putative oystercatcher collected from the locality of Montaigu, Allier, France, in the 1920s, which is housed in the Natural History Museum Basel, Switzerland. In addition, we describe a humerus of a plover-like bird and a tarsometatarsus, both of uncertain affinities within the Charadrii. Due to the rarity of Charadrii in early Neogene deposits, these remains contribute importantly to closing a vast gap in the fossil record of the group.

Materials and methods

Institutional abbreviations: *MNHN*, Muséum National d'Histoire Naturelle, Paris, France; *NMB*, Natural History Museum Basel, Switzerland; *SMF*, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Anatomical terminology follows Baumel & Witmer (1993); measurements are in millimetres (mm). The following species of extant Charadriiformes were used in comparisons (from NMB and SMF):

Charadrii: Burhinidae: *Burhinus oedicnemus*; "Charadriidae": *Charadrius hiaticula*, *C. morinellus*, *Vanellus chilensis*, *V. coronatus*, *V. vanellus*, *Pluvialis apricaria*, *P. squatarola*; Chionididae: *Chionis minor*; Haematopodidae: *Haematopus moquini, H. ostralegus*; Pluvianidae: *Pluvianus aegyptius*; Recurvirostridae: *Recurvirostra avosetta*. Lari: Dromadidae: *Dromas ardeola*; Glareolidae: *Cursorius temminckii*, *Glareola pratincola*; "Sternidae": *Anous stolidus*, *Chlidonias niger*, *Larosterna inca*, *Sterna paradisaea*, *S. saundersi*, *Thalasseus bergii*; Stercorariidae: *Catharacta skua*, *Stercorarius parasiticus*; Laridae: *Larus argentatus*, *L. canus*, *L. fuscus*, *L. hyperboreus*, *L. marinus*, *L. ridibundus*, *Rissa tridactyla*, *Xema sabini*, *Rhodostethia rosea*. Scolopaci: Scolopacidae: *Actitis hypoleucos*, *Arenaria interpres*, *Calidris alpina*, *Limosa lapponica*, *L. limosa*, *Numenius arquata*, *N. phaeopus*, *Phalaropus fulicarius*, *Philomachus pugnax*, *Scolopax rusticola*, *Tringa erythropus*, *T. totanus*; Rostratulidae: *Rostratula benghalensis*, *R. semicollaris*; Jacanidae: *Actophilornis africanus*, *Hydrophasianus chirurgus*, *Jacana jacana*.

Systematic Palaeontology

Aves Linnaeus, 1758
Charadriiformes Huxley, 1867
Charadrii sensu Paton *et al.* (2003)

Family incertae sedis, cf. Haematopodidae gen. et sp. indet.
(Fig. 1)

Material: NMB S.G.20252 (cranium).

Locality and age: Montaigu, "Saint-Gérand-le-Puy" area, Allier Basin; Early Miocene, MN2 (22.5–20.5 Ma).

Measurements: Maximum width of cranium across the widest part of the braincase (across processus postorbitales): 19.4 mm; maximum length as preserved: 34.5 mm; greatest diagonal diameter of foramen magnum: 5.2 mm; width across lacrimals: 14.4 mm; condylus occipitalis to ossa lacrimalia: 25.2 mm.

Description and comparisons: NMB S.G.20252 can be assigned to the Charadrii, and particularly a close relationship with Charadriidae, Recurvirostridae, and Haematopodidae can be presumed, based on the combination of the following characters: the presence of well developed, caudally extensive, fossae glandularum nasales, a distinct second opening caudal of foramen nervi maxillomandibularis, the presence of functional processus basipterygoidei, and the presence of well-developed fonticuli occipitales (see description and also Mayr 2011).

The specimen (NMB S.G.20252) is approximately the size of the Pied Avocet, *Recurvirostra avosetta*, and is smaller than all species of extant Haematopodidae. There is a close resemblance between NMB S.G.20252 (Fig. 1A) and the skull of *Haematopus ostralegus* (Fig. 1B).). The fossae glandularum nasales are distinct and separated by a midline furrow. As in most charadriiforms, the interorbital surface of the frontal bone displays a marked furrow between the fossae glandularum nasales (Fig. 1A), whereas in *Haematopus* there is a ridge (Fig. 1B), which is also present in members of the Lari, such as Stercorariidae, Alcidae, and Laridae. The presence of this ridge is likely to be related to the depth of the fossae glandularum nasales, which are deeper in *Haematopus* and the above mentioned taxa. Unlike in *Recurvirostra*, this frontal furrow is well marked. The supraorbital rims of the fossae are not as wide or elevated as that of members of the Charadriidae, and most closely resembles the condition found in species of *Haematopus*. Contrary to the condition present in members of the Charadriidae, there is no marked circular incision or foramen formed by the duct of the nasal gland on the frontal (Mayr 2011). The lacrimals (Fig. 1A) are fused to the nasals, and are wide and dorsally projecting, similar to those of *Haematopus ostralegus* (Fig. 1B), but larger. Only a small portion of the descending process is preserved, which appears to have been mediolaterally compressed.

The processus postorbitales are short (Fig. 1C) and, unlike in oystercatchers, the fossae temporales (Fig. 1D) are weakly developed. The attachment for musculus pseudotemporalis superficialis (Fig. 1D) rostral to the processus postorbitales on the dorsocaudal rim of the orbit is very well marked, as in species of *Haematopus* and some charadriids (*e.g.*, *Vanellus*), ending in a marked projection dorsal to the processus postorbitalis at the orbital rim. A processus zygomaticus is present, but whether it is shorter or approximately the same length as the processus suprameaticus (as in most members of the Scolopaci and Charadrii), cannot be established owing to the skull's preservation.

The general shape of the occipital region of NMB S.G.20252 (Fig. 1E) is also very similar to that of *Haematopus ostralegus* (Fig. 1F). Contrary to the condition in all other examined charadriiforms (except some members of the Alcidae), there is a deep crescent-shaped depression dorsal to the crista nuchalis transversa (Fig. 1E). In addition, the foramen magnum, in occipital view, displays a subsquare shape, with a straight dorsal rim (Fig. 1E); among extant charadriiforms these features are only observed in species of *Haematopus* and NMB S.G.20252. The fossa subcondylaris is deep and wide (Fig. 1G). The fonticuli occipitales (Fig. 1E) are much larger than those of most examined Recent Charadriiformes, but similar to those of some charadriids (*e.g.*, *Charadrius hiaticula*, *C. morinellus*). The presence of functional but weakly developed processus basipterygoidei is demonstrated by the marked articulation surface on the base of the skull (Fig. 1G). Basipterygoid processes are present in most members of the Scolopaci and Charadrii (see Strauch 1978).

Family incertae sedis, gen. et sp. indet.
(Fig. 2, Table 1)

Material: MNHN Av. 4102 (left tarsometatarsus).

Locality and age: "Saint-Gérand-le-Puy", possibly Langy or Montaigu; Early Miocene, MN2 (22.5–20.5 Ma).

Measurements: see Table 1.

Remarks: MNHN Av. 4102 (Fig. 2A) is about the size of the Grey Plover, *Pluvialis squatarola,* which is the largest member of the Charadriidae. This bone was found in MNHN among the material attributed to *Laricola desnoyersii* (Milne-Edwards, 1868; see also De Pietri *et al.* 2011), but was neither figured nor mentioned by Milne-Edwards (1867–1868).

Description and comparison: MNHN Av. 4102 can be assigned to the Charadrii based on the shape of the hypotarsus (Fig. 2C), in which the sulcus for the tendon of musculus flexor digitorum longus is centrally positioned (Fig. 2C, D). This configuration is characteristic for representatives of the Charadrii, and differs from most representatives of the Scolopaci in which there is a canal for the tendon of musculus flexor digitorum longus (Mayr 2011).

The proximal end of MNHN Av. 4102, although appreciably worn, displays a very prominent tuberculum m. fibularis brevis (Fig. 2C), which also characterizes most members of the Charadrii. At the distal end, the foramen vasculare distale (Fig. 2E) is proportionally smaller than in *Pluvianus aegypticus* and members of the Charadriidae, but resembles the condition found in representatives of the genus *Pluvialis*. The osseous bridge (Fig. 2B) between the foramen

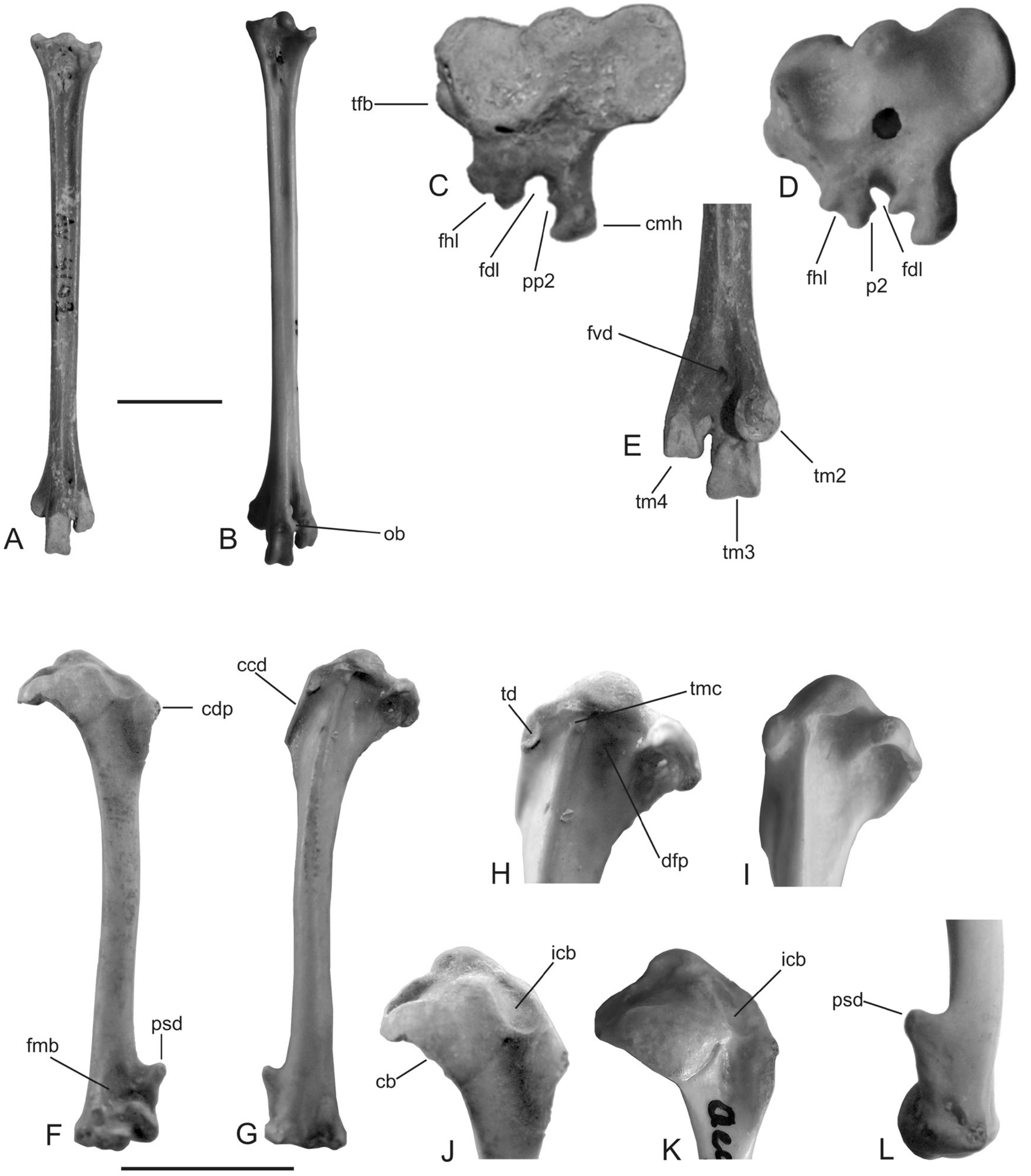

FIGURE 2. Left tarsometatarsus (MNHN Av. 4102) and left humerus (MNHN SG 13754) of plover-like birds from the early Miocene of Saint-Gérand-le-Puy in comparison with extant Charadriidae. **A**, **B**, dorsal view of tarsometatarsus MNHN Av. 4102 (**A**), and of *Vanellus vanellus* (**B**); **C**, **D**, hypotarsi of MNHN Av. 4102 (**C**), and *Pluvialis squatarola* (**D**, mirrored); **E**, plantar view of distal end of MNHN Av. 4102. **F**, **G**, humerus MNHN SG 13754 in cranial (**F**) and caudal (**G**) views; **H**, **I**, caudal views of the proximal end of humeri of MNHN SG 13754 (**H**), and *Vanellus vanellus* (**I**); **J**, **K**, cranial view of proximal end of MNHN SG 13754 (**J**), and *Charadrius hiaticula* (**K**); L, dorsal view of distal humerus MNHN SG 13754. Abbreviations: ob, osseous bridge, cb, crista bicipitalis; ccd, craniodorsal margin of crista deltopectoralis; cdp, crista deltopectoralis; cmh, crista medialis hypotarsi; dfp, dorsal fossa pneumotricipitalis; fdl, canal/sulcus for musculus flexor digitorum longus; fhl, sulcus for musculus flexor hallucis longus; fmb, fossa musculi brachialis; fvd, foramen vasculare distale; icb, impressio coracobrachialis; p2, sulcus for tendon of musculus flexor perforatus digiti II; pp2, sulcus for tendon of musculus flexor perforans et perforatus digiti II; psd, processus supracondylaris dorsalis; sps, scar on processus supracondylaris dorsalis; td, tuberculum dorsale; tfb, tuberculum musculus fibularis brevis; tm2, trochlea metatarsi II; tm3, trochlea metatarsi III; tm4, trochlea metatarsi IV; tmc, tubercle on proximal-most end of margo caudalis. Scale bars equal 10 mm. C–E and H–L not to scale.

vasculare distale and the incisura intertrochlearis lateralis is broader in MNHN Av. 4102 than in members of the Charadriidae, and again, this feature is also found in members of the extant genus *Pluvialis*, but also in *Recurvirostra*.

MNHN Av. 4102 is slightly larger than the tarsometatarsus of most specimens of the fossil laromorph *Laricola desnoyersii* (see De Pietri *et al.* 2011); its distal end clearly differs from that of members of the Lari in the more elongated trochlea metatarsi III (as in the clades Charadrii and Scolopaci). Most importantly, as in all taxa in the Charadrii with the exception of the Chionidae, a fossa metatarsi I is absent.

Overall, MNHN Av. 4102 differs from the tarsometatarsus of *Haematopus ostralegus* in that it is more slender, with a proportionally longer shaft and relatively more narrow articular ends, and from the corresponding bone of *Recurvirostra* (Avocets, Recurvirostridae) in that it is not as long or slender. Thus, MNHN Av. 4102 displays plover-like proportions (Fig. 2A). No other postcranial elements that can be attributed to the Charadrii have been found in the collections housed in NMB and MNHN to match this tarsometatarsus in size, although it would agree with the oystercatcher-like skull described above (see discussion).

Family incertae sedis
cf. Charadriidae gen. et sp. indet.
(Fig. 2, Table 1)

Material: MNHN SG 13754 (left humerus).

Locality and age: "Saint-Gérand-le-Puy", possibly Langy or Montaigu; Early Miocene, MN2 (22.5–20.5 Ma).

Measurements: see Table 1.

TABLE 1. Measurements (in mm) of humerus MNHN SG 13754 and tarsometatarsus MNHN Av. 4102.

	Humerus	Tarsometatarsus
	MNHN SG 13754	MNHN Av. 4102
Greatest length	28.1	49.5
Proximal width	6.9	6.8
Distal width	4.3	6.2
Min. width of shaft	1.9	2.7

Remarks: MNHN SG 13754 (Fig. 2F, G) is very small, approximately the size of humeri of the Common Ringed Plover, *Charadrius hiaticula* (Charadriidae).

Description and comparisons: MNHN SG 13754 can be assigned to the Charadrii based on the combination of the following features: well-developed dorsal fossa pneumotricipitalis, concave crista deltopectoralis (absent in most Scolopaci), absence of transverse ridge across incisura capitis (present in Scolopaci), wide impressio coracobrachialis (narrow in Laromorphae).

On the caudal surface of the proximal end, a well-developed second fossa pneumotricipitalis is present (Fig. 2H), a homoplastic trait within charadriiform birds, but nevertheless present in all representatives of the Charadrii except Burhinidae and absent from most members of the Scolopaci with the exception of taxa in the Thinocoridae (seedsnipes) and some Scolopacidae. This trait is also variable within Lari, and is absent in Turnicidae, Glareolidae, Dromadidae and Stercorariidae (Mayr 2011), *Anous* (noddies), the fossil family Laricolidae (De Pietri *et al.* 2011), and many Pan-Alcidae (Smith 2011). There is a well-marked tubercle on the proximal-most end of the margo caudalis (Fig. 2H), which among some of the examined Charadrii is also developed, albeit not as a tubercle but as an enlarged surface, as in the lapwing *Vanellus vanellus* (Fig. 2I). Contrary to the condition in most members of the Scolopaci, the dorsal surface of the crista deltopectoralis is concave (Fig. 2A, B), and its craniodorsal margin is slender. The tuberculum dorsale is well defined, but it does not protrude as strongly dorsally as in the laromorph genus from the same locality, *Laricola* (see De Pietri *et al.* 2011). The ventral rim of the crista bicipitalis (Fig. 2J) is slightly damaged. The cranial surface of the proximal humerus displays a wide impressio coracobrachialis (Fig. 2J), with a distinctly rounded dorsal margin of the intumescentia humeri, which distinguishes this humerus from that of the Laromorphae (see De Pietri *et al.* 2011). At the distal end, the processus supracondylaris dorsalis does not display the proximodistally elongated scar present in the plover genus *Vanellus* (Fig. 2L).

MNHN SG 13754 differs from *Pluvianus aegyptius* in the better developed, *i.e.*, further dorsally projecting, processus supracondylaris dorsalis, in that the shaft of the bone is not as curved, and in that the proximal and distal ends are not as dorsoventrally compressed as in *Pluvianus*. MNHN SG 13754 can also be differentiated from the corresponding bone of *Haematopus* in that the processus supracondylaris dorsalis projects further dorsally, and in that the fossa m. brachialis is proportionally larger in the fossil. It differs from the plover genus *Pluvialis* in that the second (dorsal) fossa pneumotricipitalis extends entirely under the caput humeri, and in that the impressio coracobrachialis is broader than in *Pluvialis*, thus resembling that of other charadriids in its proportions (Fig. 2K).

Discussion

Most members of the Charadrii are not associated with lacustrine environments, and therefore would not have constituted a significant component of the avifauna of Saint-Gérand-le-Puy. Consequently it is not surprising that the fossil Charadrii here described represent the first record of this group from these Early Miocene localities.

As already mentioned, several features suggest an assignment of NMB S.G.20252 to the Charadrii, and more specifically to a clade including the Charadriidae, Recurvirostridae, and Haematopodidae (a clade including these families and Ibidorhynchidae was recovered by Baker *et al.* (2007), Baker *et al.* (2012), and Mayr (2011)). NMB S.G.20252 shares with species of *Haematopus* two derived features of the occipital region, absent from all other examined charadriiform taxa, namely the well-marked crescent shaped-depressions caudal to the crista nuchalis transversa and the subsquare shape of the foramen magnum. Despite a remarkable resemblance between *Haematopus* and NMB S.G.20252, both can be differentiated on the basis of distinctive features, such as the presence of a furrow at the interorbital region of the frontal of the fossil (as opposed to the presence of a ridge in *Haematopus*); also much shallower fossae temporales and larger fonticuli occipitales are present in the fossil skull. Establishing how NMB S.G.20252 relates to extant species of Haematopodidae and other Charadrii awaits the discovery of additional material.

The earliest unambiguous records of oystercatchers date from the Early and middle Pliocene, and come from North America. Two humeri from the Lower Pliocene of Lee Creek, North Carolina, lacking the proximal end and significantly differing in size, were referred to the extant genus *Haematopus* (Olson & Steadman 1979; Olson & Rasmussen 2001). A further specimen that can be classified within Haematopodidae is *Haematopus sulcatus* (Brodkorb, 1955), from the middle Pliocene of the Bone Valley formation of Florida and known from the distal end of a tibiotarsus. Although originally this specimen was assigned its own genus (*Palostralegus*) within Haematopodidae, it was later referred to the extant genus *Haematopus* by Olson & Steadman (1979). All other fossil remains that have been classified within this family are from Pleistocene and Holocene sites (*e.g.*, Brodkorb 1967; Tyrberg 1998). Given the poor fossil history of oystercatchers, NMB S.G.20252 would not only represent the first Neogene European record of the family, but the earliest record worldwide.

Few species of extant Haematopodidae are present in inland environments; *Haematopus ostralegus* and *H. finschi* are found during the breeding season in inland habitats. The presence of an oystercatcher-like bird in lacustrine deposits therefore indicates that, similarly to *Haematopus ostralegus* and unlike most other oystercatchers, the species from Saint-Gérand-le-Puy was not restricted to coastal environments. The lake system of Saint-Gérand-le-Puy is notable for having functioned as breeding grounds for the very abundant laromorph *Laricola* (De Pietri *et al.* 2011). Whether it was also visited for this purpose by the above-described oystercatcher-like bird can, however, not be said based on the available material.

As already noted in the introduction, Neogene Charadriidae have been recorded as early as the Middle Miocene (MN 4b, Mlíkovský 2002), although in most instances the phylogenetic affinities of these findings have not been formally assessed. The tarsometatarsus (MNHN Av. 4102) and the humerus (MNHN SG 13754) described herein represent the first records of plover-like birds from Saint-Gérand-le-Puy. The tarsometatarsus displays plover-like proportions, and agrees with the tarsometatarsus of species of *Pluvialis* in the relatively smaller foramen vasculare distale, and in the broad osseous bridge between the foramen vasculare distale and incisura intertrochlearis lateralis. A potential close relationship with this genus, however, which in molecular phylogenies was recently recovered as a basal charadriid (Baker *et al.* 2012), is only hypothetical, supported by overall resemblance and size, and the specimen can only be tentatively referred to the Charadriidae. It is also possible, that MNHN Av. 4102 and the oystercatcher-like skull NMB S.G.20252 represent the same taxon, as they do match in size. This would suggest that the morphology of the described tarsometatarsus is plesiomorphic for the Charadriidae/Haematopodidae/Recurvirostridae clade, a claim that can only be substantiated with further fossil finds. Similarly, and in the absence of derived humeral features supporting its referral to the Charadriidae, the small humerus MNHN SG 13754 can only be tentatively referred to as a member of this family, despite its overall resemblance to charadriid plovers. If future evidence supports a more confident placement within Charadriidae, both MNHN Av. 4102 and MNHN SG 13754 would become the earliest records of the family.

Acknowledgements

We thank C. Meyer (NMB) for facilitating the study of the fossil specimens. Ronan Allain (MNHN), Claire Sagne (MNHN), and Vincent Pernègre (MNHN) assisted with the material in MNHN. We thank L. Costeur (NMB) for his help with geological matters, and Adam Smith (University of Texas at Austin) and Trevor Worthy (University of Adelaide) for comments and suggestions that improved our manuscript. A travel grant from Stiftung zur Förderung des Naturhistorischen Museums (Basel, Switzerland) to V.L.D. supported this research.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

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A new barn owl (Aves: Strigiformes: Tytonidae) from the Middle Miocene of the Nördlinger Ries (Germany) with remarks on the history of the owls

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Abstract — We describe a new taxon of barn owl, *Miotyto montispetrosi* nov. gen. et spec. from the Middle Miocene (Astaracium, MN6) localities at Steinberg and Goldberg in the Nördlinger Ries (Southern Germany). A single individual from Steinberg is represented by well-preserved long bones of the limbs, the shoulder girdle and by phalanges of the wing and foot. The description lists almost 60 features used for the determination of the affinities of the fossil. Although *Miotyto montispetrosi* nov. spec. clearly belongs to the Tytonidae, it shows some characters intermediate with Strigidae. Some additional juvenile bones from Goldberg indicate that the species was breeding at the Middle Miocene Ries crater lake.

Key words: Tytonidae, *Miotyto montispetrosi* nov. spec., Steinberg, Goldberg

Introduction

Fossil Strigiformes are by no means rare, Kurochkin & Dyke (2011, Tab.1) list over 40 species representing over 20 genera – most of them extinct – for Europe alone. However, many of those taxa, especially from pre-Pleistocene times, are based on single or a few bones that are often fragmentary. Therefore, relatively complete and well-preserved fossil material, even if it is limited to postcranial elements, deserves special attention, the more so, if it can be attributed to a single individual, as in the present case (Fig. 2).

The current material comes from two localities, Steinberg and Goldberg, in the Nördlinger Ries of Southern Germany (Fig. 1). The Nördlinger Ries is an approximately 15 million years old meteorite impact crater, which forms at present a circular shallow depression, 22–24 km in diameter, that separates the Jurassic limestone plateaus of the Swabian and the Franconian Alb. Subsequent to the impact, the Ries crater was filled by a soda lake without outlet, in which spring mounds of calcareous tufa, the so called “travertine hills”, rose at sources of sub-lacustrine spring water (Pache *et al.* 2001; Arp 2006).

The Steinberg (formerly called Spitzberg) and the Goldberg are two of these spring mounds.

Some of the spring mounds became temporary islands in the ancient lake. During the late freshwater stage of the Ries crater lake, vertebrate fossils accumulated in fissures and pockets on top of some of the hills such as the Goldberg spring mound (Arp 2006). A few specimens of the material presented here come from the locality Goldberg 9 described by Bolten (1977: 68–71). The processes of deposition and accumulation are unclear for the much richer fossil material of

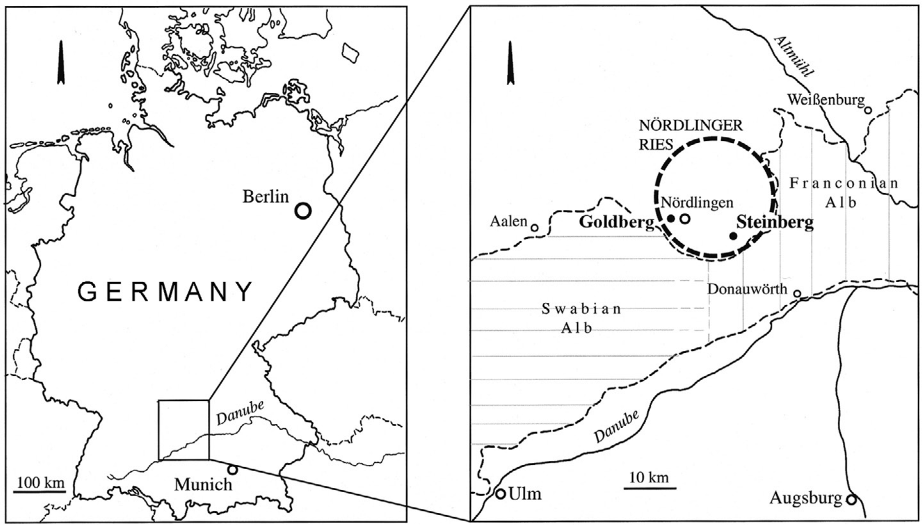

FIGURE 1. Map showing the geographical position of the Steinberg and Goldberg localities within the impact crater of the Nördlinger Ries.

the Steinberg locality. In 1969, a few loose blocks of fossiliferous calcareous tufa were found on the foot of the southwest slope of the Steinberg hill, which is situated on the ring structure in the southeast sector of the crater and whose basis consists predominantly of crystalline basement rocks (Bolten 1977). These loose fossiliferous blocks are also supposed to be the remnants of pocket or fissure, but their exact origin on the top of the Steinberg remains unknown (Heizmann & Fahlbusch 1983: 84). The calcareous tufa from both localities was treated with dilute acetic acid to recover the fossil bones and teeth.

Beside Strigiformes, the following bird taxa are represented by fossils from different localities in the Nördlinger Ries: Pelecanidae, Phalacrocoracidae, Palaelodidae, Anatidae, Rallidae, Charadriidae, Scolopacidae, Glareolidae, Phasianidae, Psittacidae, Coliidae, Apodidae, Capitonidae, and Passeriformes (Ballmann 1979, 1983, 2004; Heizmann & Hesse 1995, Lambrecht, 1933; Mayr & Göhlich 2004). Several of these taxa have not yet been described. The great variety makes the Nördlinger Ries one of the most important sites for Miocene birds in Europe.

On the basis of fossil micro-mammals, the fauna of Steinberg has been determined to be early Astaracium, Mammal Neogene Unit MN6, by Heizmann & Fahlbusch (1983). Besides Soricidae, Gliridae, Cricetidae especially Chiroptera are very rich in the Steinberg fauna; eight species of Chiroptera (Rachl 1983) represent about one third of all mammal species.

Mammals as well as birds from the Steinberg and Goldberg are all small forms, which makes regurgitation pellets by predatory or scavenging birds, especially owls, the most probable origin for these fossil accumulations.

Material and methods

The presented fossil material is kept in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSPG) under the collection numbers BSPG 1970 XVIII 861 to 897 (Steinberg) and BSPG 1966 XXXIV 3276 to 3279 (Goldberg). In the following text only the last digital number is given. The osteological terminology follows Baumel *et al.* 1993, and occasionally Ballmann (1969a, b). Measurements were taken after von den Driesch (1976). Estimated measurements of slightly damaged bones are given in parenthesis. The systematics of extant owls follows König & Weick (2008).

Recent species examined for comparison: Tytonidae. *Tyto alba*, *Phodilus badius*. Strigidae: *Strix aluco*, *S. uralensis*, *S. nebulosa*, *Asio otus*, *A. flammeus, Athene noctua*, *A. cunicularia*, *Aegolius funereus*, *Bubo scandiacus*, *Bubo bubo*, *Otus scops*, *Glaucidium passerinum, Ninox novaeseelandiae*. The specimens are kept at the ornithological department of the Naturhistorisches Museum Wien (NHMW). Some selected limb bones of *Phodilus badius* (specimen USNM 20310) were lent from the National Museum of Natural History (Smithsonian Institution) Washington, Division of birds (NMNH).

For systematic comparisons the following fossil species of Tytonidae were considered: Neogene Tytoninae: *Tyto campiterrae* Jánossy, 1991, *T. gigantea* Ballmann, 1973, *T. robusta* Ballmann, 1973, *T. sanctialbani* (Lydekker, 1893), *Prosybris antiqua* (Milne-Edwards, 1863). Paleogene and Neogene Necrobyinae. *Necrobyas arvernensis* (Milne-Edwards, 1863), *N. edwardsi* Gaillard, 1939, *N. harpax* Milne-Edwards, 1892, *N. rossignoli* Milne-Edwards, 1892, *N. medius* Mourer-Chauviré, 1987.

Following Louchart (2002), the species *Tyto balearica* Mourer-Chauviré, Alcover, Moya & Pons, 1980 can only be confirmed in post-Neogene, thus Pleistocene localities; all previous reports of Neogene findings referred to *Tyto balearica* belong to a different and not yet described tytonid species (Louchart 2002). *Basityto rummeli* Mlíkovský, 1998 from the Early Miocene of Grafenmühle 21 (MN2–3, southern Germany, Coll. Rummel (Weissenburg)) was determined to be a taxon outside Strigiformes by Mourer-Chauviré (2001). Although Mlíkovský (1998) had synonymized *T. campiterrae* with *T. sanctialbani*, we follow Pavia & Mourer-Chauviré (2011), who retain *T. campiterrae* as a separate species. Also *T. robusta* (see Tab. 3), which was taken into synonymy with *T. gigantea* by Mlíkovský (1998), is kept as a discrete species in this article.

The Mammal Neogene-Zones (MN-Zones) are used as defined by Mein (1999), the Neogene and Paleogene stratigraphy follows Hilgen *et al.* (2012) and Vandenberghe *et al.* (2012), respectively.

Osteological abbreviations: tmt: tarsometatarsus, tt: tibiotarsus, dext.: right, sin.: left, prox.: proximal(is), dist.: distal(is), dors.: dorsal(is).

Institutional abbreviations: BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, Munich; NHMW: Naturhistorisches Museum Wien; NHMUK: Natural History Museum, London; USNM: Smithsonian Institution National Museum of Natural History, Washington.

Systematic Paleontology

Order Strigiformes Wagler, 1830

The owls are a well circumscribed order of nocturnal birds of prey and their osteology assigns them to a ‘natural group’ *sensu* Milne-Edwards (1869–71). Up to now, paleontology has been unable to resolve their relationship with other orders but recent DNA studies, place owls in a clade with diurnal raptors (excluding falcons), which is a sister taxon to parrots and song birds (König & Weick 2008).

One of the oldest owls, *Ogygoptynx wetmorei*, was described by Rich & Bohaska (1976) from the Paleocene of Colorado and later placed into a separate family Ogygoptyngidae (Rich & Bohaska 1981). It is known from a fairly complete tarsometatarsus which shows a mosaic of tytonid and strigid features, but is too old to be at the branching point of the two families.

The oldest record of Strigiformes in Europe dates back to the Late Paleocene and belongs to the genus *Berruornis* Mourer-Chauviré, 1994 (Mayr 2009). The Eocene and Oligocene record of strigiforms is quite extensive but restricted to the northern hemisphere and comprises the extinct families Palaeoglaucidae, Sophiornithidae, Protostrigidae and the extant family Tytonidae (Fig. 12). All Neogene to Recent owls belong to two families, the Tytonidae (barn owls) and the Strigidae (typical owls), which together form the crown group Strigiformes (Mayr 2009).

Recent Strigiformes share a unique osteological character in the form of an ossified arch on the radius described by Bock & McEvey (1969). This structure was not found on the radius of *Palaeoglaux artophoron* (Peters, 1992) from the Middle Eocene of Messel.

The fossil record of the Tytonidae dates from a much earlier time than the earliest known Strigidae (Fig. 12) and will be discussed in more detail below.

The oldest Strigidae (typical owls) date back to the Early Miocene: MN2 of Saint-Gérand-le-Puy (France) and MN3 of Wintershof-West (Germany) (Fig. 12). Originally those fossils were placed in geographically widespread recent genera of similar size and shape. This does not look very likely at present and they have con-

FIGURE 2. Schematic figure of a barn owl skeleton indicating the preserved bones (black) from the Steinberg individual. Pedal phalanges and claws of uncertain digital affiliation are shaded in grey. Additional bones from the locality Goldberg, comprising a fragmentary coracoid, a femur, a distal tibiotarsus, and a juvenile tarsometatarsus, are not indicated.

sequently been moved to newly erected extinct genera (Mlíkovský 2002), but for which unfortunately diagnoses are virtually missing. Therefore these genera must be regarded as quite "modern-looking" typical owls with uncertain affinities.

The Strigidae are the most numerous and diverse family among extant owls and account for well over two hundred species in more than twenty genera (König & Weick 2008). They inhabit a wide geographical range and are nearly cosmopolitan except for Antarctica. They are especially speciose in the tropical forests but occupy a variety of habitats from deserts to swamps to sub-polar wooded areas and tundra with severe winter conditions (Burton 1973; Del Hoyo *et al.* 1999). In size the Strigidae range from very small (*Glaucidium*) to very large (*Bubo*) taxa. Their postcranial skeleton appears to be more adapted to the reduction of wing loading and to the seizing of prey than the skeleton of the Tytonidae. Weight reduction is expressed by the degree of pneumatization in the bones of their shoulder girdles (scapula and coracoid) and the great reduction of their furcula. Predatory capability is implied by robust leg bones that are sculpted to accommodate large muscles and tendons, e.g. in the supracondylar fossa of the distal tibiotarsus and in the sulcus extensorius on the proximal tarsometatarsus where only thin lamellae of bone remain between extensor and flexor sides in the Strigidae.

Ford (1967) examined the osteology of over 80 species of Strigiformes belonging to 30 genera including *Tyto* and *Phodilus*. According to him, the taxonomic subdivision of extant owls is mainly based on external morphology that is not always reflected in skeletal characteristics. Furthermore, osteologic features and distinctions between genera, based on postcranial elements of a few species, do not always hold when more species become available for comparison. Consequently, the allocation of a fossil owl in the taxonomic system remains difficult.

The skeletal differences between Strigidae and Tytonidae have been described not only by Ford (1967) but in many publications ranging from Lydekker (1893) to Louchart (2002).

Family Tytonidae Ridgway, 1914

Half of the 17 characters listed by Sibley & Ahlquist (1972) after Ridgway (1914) to differentiate between Strigidae and Tytonidae refer to external morphology and only two of the remainders are applicable to the fossil owl described here: The third toe in Tytonidae is as long as the second and the tarsometatarsus is without an bony loop (arcus extensorius).

The recent Tytonidae comprise two genera, of which *Phodilus* Geoffroy Saint-Hilaire, 1830 is clearly a relict limited to South and Southeast Asia, while the other genus, *Tyto* Billberg, 1828, which comprises 25 species, is widespread in its distribution but mainly within tropical and subtropical regions (König & Weick 2008). The type species, the Common Barn Owl, *Tyto alba* (Scopoli, 1769), comprises 10 subspecies and is the most widespread of all the owls. It is the only barn owl to reach the temperate regions of Europe and North America, where severe winters may decimate its populations (Voous 1962). Its geographical distribution reaches from Europe over Africa and Madagascar to Arabia, Asia Minor,

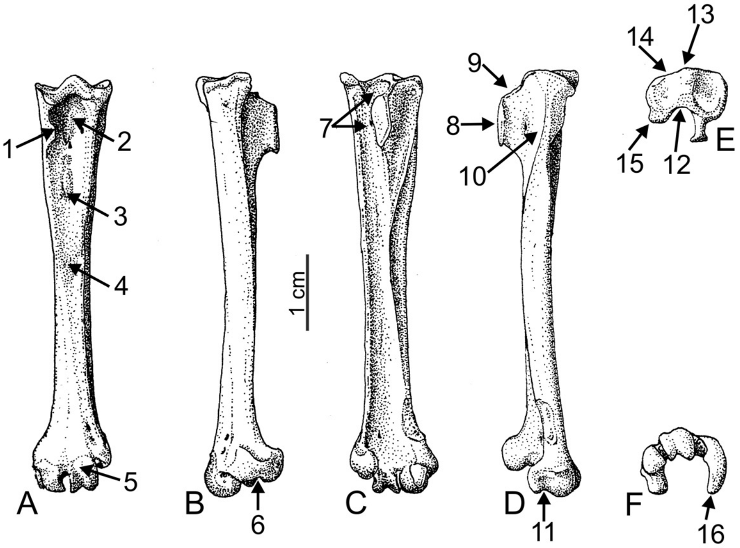

FIGURE 3. Holotype of *M. montispetrosi* nov. spec., tarsometatarsus sin. (1970 XVIII 867) from Steinberg. (numbers refer to the description in the text). **A**) dorsal, **B**) lateral, **C**) plantar, **D**) medial; **E**) proximal, **F**) distal.

India and Malaysia and south into Indonesia. The diet of the European barn owls consists mainly of small nocturnal mammals, like shrews, mice, and voles, but rats and even small rabbits are recorded as well as small birds, bats, frogs, small reptiles and large insects (Burton 1973; del Hoyo *et al.* 1999). The undigested parts including the bones are regurgitated as pellets.

The fossil record for *Tyto alba* goes back to the Early Pleistocene in Europe and to the Late Pliocene in Morocco (Pavia *et al*. 2012).

The origins of the family Tytonidae can be traced back to the Paleogene of France, where the fossil genus *Necrobyas* is documented from the Late Eocene (phosphorites du Quercy) (up to the Early Miocene of Saint-Gérand-le-Puy) (Fig. 12). *Necrobyas* shows similarities to *Tyto* and is usually placed within the Tytonidae (Mourer-Chauviré 1987). From the Oligocene of North America Olson (1985) mentions several undescribed complete skeletons of a small species of owl with a stout 'phodiline' tarsometatarsus without an ossified tendinal loop (arcus extensorius). In Europe the first clearly tytonine species is *Prosybris antiqua* originally described from the early Miocene (MN2) of Saint-Gérand-le-Puy (see Tab. 4), but according to Mlíkovský (1998) also known from early Oligocene of the phosphorites du Quercy. The fossil history of the genus *Tyto* has recently been summarized by Pavia & Mourer-Chauviré (2011).

Miotyto nov. gen.

Type species: *Miotyto montispetrosi* nov. spec.

Included species: The type species only. But see "discussion and conclusion".

Etymology: *Miotyto: Mio*, abbreviated from Miocene, the epoch for which this barn owl is proven; combined to the existing genus name *Tyto* for most extant (and some fossil) barn owls. Feminine in gender.

Diagnosis: Middle-sized member of Tytonidae, about the size of the Recent *Tyto alba guttata*. Tarsometatarsus and coracoid relatively stout. Tarsometatarsus: vestigial arcus extensorius, tuberositas m. tibialis cranialis relatively low on shaft; sulcus extensorius deep, reaching to half the length of the shaft; sulcus of trochlea III extending proximally; crista hypotarsi long; tuberculum m. fibularis brevis directed plantolaterally. Scapula: acromion projecting dorso-laterally. Phalanx proximalis digiti majoris: cranial face flat, not concave. Femur: Cranial linea intermuscularis merges in a curve into crista trochanteris. Tibiotarsus: Lateral condyle slanted proximolaterally. Pedal phalanges: The indices of the lengths of phalanx II 1/phalanx III 1 and phalanx III 1/phalanx III 2 are intermediate between Tytonidae and Strigidae.

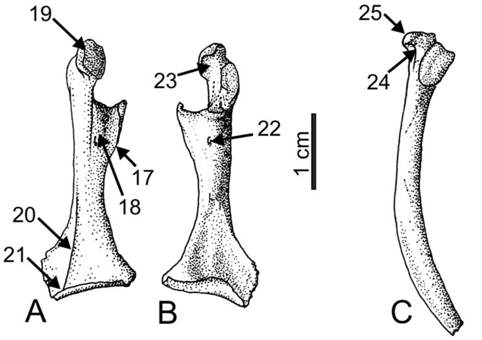

FIGURE 4. Coracoid dext. (1970 XVIII 872) (**A, B**) and scapula dext. (1970 XVIII 873) (**C**) of *M. montispetrosi* nov. spec. from Steinberg. **A**) ventral, **B**) dorsal, **C**) lateral.

Miotyto montispetrosi **nov. spec.**
(Figs 3–11)

Holotype: left tarsometatarsus (BSPG 1970 XVIII 867) (Figs 3, 10H-I, 11C)

Paratypes (Figs 4–9, Fig. 10B, D, O, R, U, W, Fig. 11A, E): coracoid dext. (872), scapula dext. (873), humerus dext., dist. 2/3 (861), humerus dext., prox. end (862), ulna dext., prox. half (863), ulna sin., prox. end (871), ulna dext., dist half (874), os carpi ulnare dext. (876), os carpi ulnare sin. (877), phalanx prox. digiti majoris dext. (875), femur dext., prox. half (865), tt sin. (866), tt dext., dist. half (870), tmt dext. (868), os metatarsale I dext. (878), os metatarsale I sin. (879), phalanx I 1 dext. (880), phalanx I 1 dext. (881), phalanx II 1 dext. (882), phalanx II 1 sin. (883), phalanx II 2 dext. (884), phalanx III 1 dext. (885), phalanx III 1 sin. (886), phalanx III 2 dext. (887), phalanx III 2 sin. (888), phalanx III 3 or IV 4 dext.? (889), phalanx IV 1 dext. (890), phalanx IV 2 dext. (891), phalanx IV 3 dext. (892), phalanx III 3 or IV 4 dext (893), four phalanges terminales (claws) (894–897). Almost all of these bones including the holotype can be attributed to the same adult individual (Fig. 2). The only exceptions are the two specimens of pedal phalanx I 1 dext., one of which must represent a second individual.

Type locality: Steinberg (= Spitzberg, 496 m NN)), about 1 km northeast of the village Appetshofen in the Nördlinger Ries, Southern (Fig. 1). Loose blocks of calcareous tufa found on the SW slope of the Steinberg in the Jungwald forest Germany (N48°49′33″, E10°37′18″), topographic map 7129 Deiningen.

Type horizon: Fissure and pocket fillings in calcareous tufa (“travertine”), Middle Miocene, early Astaracium, MN6 (Heizmann & Fahlbusch 1983).

Differential diagnosis: Tarsometatarsus and coracoid shorter and stouter than in *Tyto* including fossil *T. sanctialbani, T. campiterrae* and *T. balearica* (see Tab. 4). *Miotyto montispetrosi* nov. spec. is distinctly smaller than *T. gigantea* and *T. robusta*, smaller than *T. balearica* and *T. campiterrae*, and distinctly larger than *Prosybris antiqua*. Similar in size to *T. sanctialbani*, but differing by the shorter and stouter tarsometatarsus with vestigial arcus extensorius, sulcus extensorius reaching less distally. Tuberculum m. fibularis brevis directed plantolaterally, whereas oriented plantarly in *Tyto* (*T. alba, T. sanctialbani, T. gigantea,* and *T. robusta*), in *Phodilus*, and in *Prosybris antiqua*. Linea intermuscularis cranialis on femur merging with crista trochanteris clearly below proximal end of femur, whereas linea intermuscularis cranialis reaches up to facies articularis antitrochanterica in *Tyto* (*T. alba, T. sanctialbani,* and *T. robusta*) and in *Phodilus.* Unlike the tibiotarsus of *T. alba* and *T. sanctialbani*, the apophysis of the crista cnemialis cranialis projects distally in *M. montispetrosi* nov. spec.. Index of length of phalanx II 1/phalanx III 1 smaller than in *Tyto*.

Tarsometatarsus relatively longer and more slender than in *Phodilus*. Relative distal width of humerus smaller and intumescentia humeri wider than in *Phodilus*. Unlike *Phodilus*, pedal phalanges IV 1 and IV 2 not fused in *M. montispetrosi* nov. spec..

Etymology: geographic name, *montispetrosi* from Latin mons, montis (= mountain) and petrosus (= stoney) = Steinberg (in German), as possessive noun in genitive case.

Additional referred material (Fig. 8C and D)**:** There are at least two more individuals represented by material from Goldberg (BSPG 1966 XXXIV…): Coracoid sin., fragmentary cranial half (3276), femur dext. (3277), tmt sin. (juvenile) (3278), tt sin., distal half (3279) (subadult).

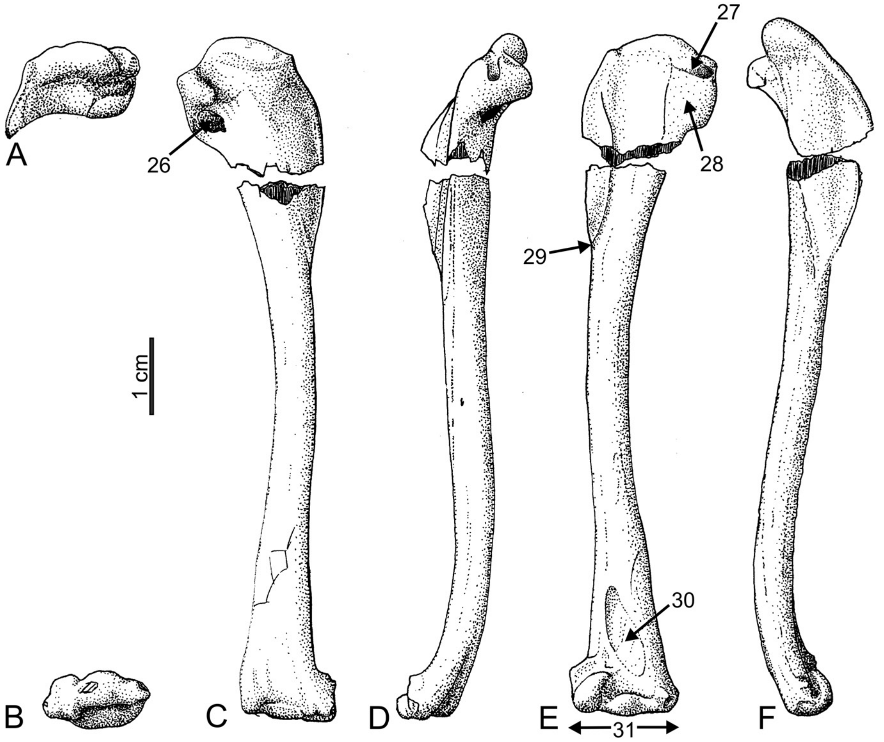

FIGURE 5. Humerus dext. (1970 XVIII 861+862) of *M. montispetrosi* nov. spec. from Steinberg. **A**) proximal, **B**) distal, **C**) caudal, **D**) ventral, **E**) cranial, **F**) dorsal.

Description

Measurements: For measurements of the holotype, paratypes and referred material see Tab. 1.

Holotype tarsometatarsus (Figs 3, 10H-I, 11C)**:** Shape relatively stout and robust. Dorsal view: Arcus extensorius lacking, except vestigial pointed projection on medial side (1); fossa infracotylaris dorsalis equally deep on both sides (2); tuberositas m.tibialis cranialis positioned relatively low on shaft (3); sulcus extensorius deep and reaching to half the length of shaft (4); sulcus of trochlea III extending proximally (5). Lateral view: Distal margin of trochlea IV distinctly indented (6). Plantar view: Proximal part of sulcus flexorius moderately excavated (7). Medial view: Crista hypotarsi relatively long (8) starting proximally somewhat below articular surface and carrying no proximal projection (9); fossa parahypotarsalis medialis (= fossa m. flexoris hallucis brevis) cutting far dorsally into facies subcutanea medialis (10); ligamental fossa on trochlea II at distal margin (11). Proximal view: Sulcus flexorius wide and rounded (12); eminentia intercotylaris protruding slightly dorsally (13); no notch in dorsal margin (14); tuberculum m. fibularis brevis directed plantolaterally (15). Distal view: trochleae arranged in semicircle with trochlea IV projecting furthest in plantar direction (16).

Paratypes and referred material

Coracoid (Figs 4A–B, 10O): The coracoid is almost complete, damaged only at the lateral edge of the processus lateralis. A fragmentary cranial portion of a coracoid is preserved from the Goldberg locality.

Bone short and stout. Ventral view: Processus procoracoideus triangular in shape, with broad basis and slightly convex medial margin (17); sulcus supracoracoideus wide and rounded (18); processus acrocoracoideus rounded, knob-like (19); distinct linea intermuscularis ventralis (20) ends medially of angulus externus (21). Dorsal view: Foramen n. supracoracoidei present (22); acrocoracoid not pneumatized (23).

Scapula (Figs 4C, 10D): The scapula is complete except for the caudal tip.

Lateral view: acromion not pneumatized (24)

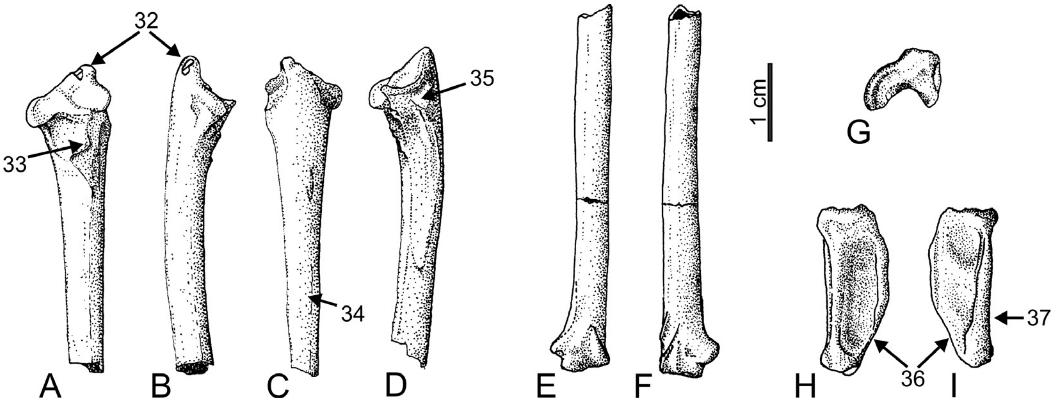

FIGURE 6. Proximal half of ulna dext. (1970 XVIII 863) (**A-D**) and distal half of ulna dext. (1970 XVIII 874+876) (**E, F**), os carpi ulnare dext. (1970 XVIII 876) (**G**), phalanx dig. majoris dext. (1970 XVIII 875) (**H, I**) of *M. montispetrosi* nov. spec. from Steinberg. **A**) cranial, **B**) dorsal, **C**) caudal, **D**) ventral, **E**) ventral, **F**) dorsal, **G**) cranial, **H**) ventral, **I**) dorsal.

and projecting dorso-laterally (25).

Humerus (Figs 5, 10B, 11A): The humerus is almost complete. Shaft sigmoidal in both craniocaudal and dorsoventral direction.

Caudal view: No fossa pneumotricipitalis, opening of foramen pneumaticum level with surface (26).

Cranial view: Ventral end of strongly marked sulcus transversus almost reaching crista bicipitalis (27); intumescentia humeri well-marked and dorsally sharply delimited (28); length of crista deltopectoralis approximately one third of humerus (29); fossa m. brachialis large and well-marked (30); distal end ventrally enlarged (31).

Ulna (Fig. 6A-F): Two proximal and one distal halves of the ulna are preserved.

Cranial view: Olecranon short and blunt (32); tuberculum bicipitale well-marked and elongated (33). Caudal view: Papillae remigales visible but weakly developed (34). Ventral view: Flat, triangular tuberculum lig. collateralis ventralis cutting slightly under cotyla ventralis (35).

Left and right **os carpi ulnare** (Fig. 6G) are perfectly preserved but without conspicuous features.

Phalanx proximalis digiti majoris (Fig. 6H, I): One complete right element is preserved.

Ventral view: Caudal part blade-like, reaching pila cranialis in regular curve without angle or ligamental process (36). Dorsal view: Cranial face of pila cranialis flat (37).

Femur (Figs 7, 10W, 11E): Two right femora are available, one proximal half from the type locality and an almost complete one from Goldberg with slightly damaged distal end.

Shaft almost straight. Caudal view: well developed tuberculum as origin of the intermediate flexor muscles of the toes (38). Cranial view: Trochanter moderately surpassing caput femoris proximally (39); cranial linea intermuscularis simple, not bifurcate distally (40); linea proximally merging with crista trochanteris without reaching up to proximal margin (41).

Tibiotarsus (Fig. 8): Two left tibiotarsi are preserved; a complete one (adult) from the type locality, a distal half of a subadult specimen from the Goldberg locality.

Relatively stout and shaft slightly curved into medial concavity. Cranial view: apophysis interna ligamenti obliqui well-marked (42); spina fibulae fused with shaft (43); fusion well proximal of apophysis interna ligamenti obliqui (44); pons supratendineus lacking (45); groove proximal of area intercondylaris relatively shallow (46); lateral condyle slanted proximo-laterally (47). Medial view: Tiny tooth-like protuberance in proximal end of fossa plantaris (48); apophysis on crista cnemialis cranialis projecting distally (49); impressio ligamenti collateralis medialis well-marked (50); epicondylus medialis strongly protruding plantarly (51). Lateral view: Epicondylus lateralis strongly protruding plantarly (52).

Proximal view: Incisura tibialis deep and U-shaped (53). Distal view: Caudal rim of epicondylus medialis forming sharp edge (54).

Tarsometatarsus: In addition to the left holotype tmt a complete right tmt is preserved from the type locality. An additional juvenile left tmt

TABLE 1. Measurements (mm) of the type material for *Miotyto montispetrosi* nov. spec. from Steinberg and referred material from Goldberg. GL: greatest length, L: length, Wp: proximal width, Dp: proximal depth, Dgp: proximal diagonal (in the scapula cranial diagonal), Dgd: distal diagonal, WF: width of facies articularis basalis in coracoid, Ws: smallest width of shaft, Wd: distal width, Dd: distal depth, Wdg: maximal diagonal width of os carpi ulnare. *length medially, °width basally. Estimated measurements of slightly damaged bones are given in parenthesis.

		GL	L	Wp	Dp	Dgp	Ws	Wd	Dd	
Steinberg	BSPG 1970 XVIII									
coracoid dext.	872	(35)	(33)*					(13)°		WF: (12)
scapula dext.	873	(42)				9.6				
humerus dext., dist. 2/3	861						5.7	14.4		
humerus dext., prox. end	862			17.0						
reconstructed humerus: 861+862		*c*. 90								
ulna dext., prox. half	863			9.7		10.0	4.3			
ulna dext., dist half	874						4.4			Dgd: 7.5
ulna sin., prox. end	871			(9.5)		(10)				
os carpi ulnare dext.	876									Wdg: 8.2
os carpi ulnare sin.	877									Wdg: 8.1
phalanx digiti major. 1 dext.	875	20.1	20.0	7.2				4.4		
femur dext., prox. half	865			10.8	7.3		4.9			
tibiotarsus sin.	866	90.5	89.1			12.1	4.5	10.9	10.0	
tibiotarsus dext., dist half	870						4.9	11.0		
tarsometatarsus sin. (holotype)	867	55.1		10.4			5.5	11.8		
tarsometatarsus dext.	868	55.1		10.5			5.4	11.8		
os metacarpale I dext.	878		6.9					4.4		
os metacarpale I sin.	879		7.1					4.4		
phalanx I 1 dext.	880	12.7		4.6	5.0		3.0	3.5	3.9	
phalanx I 1 dext.	881	12.5		4.5	5.0		3.0	3.4	4.0	
phalanx II 1 dext.	882	13.0		7.0	6.3		3.8	4.5	5.2	
phalanx II 1 sin.	883	13.1		7.0	6.0		3.6	4.3	5.1	
phalanx II 2 dext.	884	17.6		5.0	5.1		4.0	4.2	4.1	
phalanx III 1 dext.	885	7.6		7.4	4.8		4.4	5.1		
phalanx III 1 sin.	886	7.6		7.3	5.1		4.3	5.2		
phalanx III 2 dext.	887	12.9		4.6			3.2	3.9	4.1	
phalanx III 2 sin.	888	12.9		4.6			3.2	3.8	4.2	
phalanx III 3 or IV 4 dext.?	889						3.6	3.7	3.7	
phalanx IV 1 dext.	890	4.8		6.7	5.0					
phalanx IV 2 dext.	891	5.0		5.3	4.1			4.0		
phalanx IV 3 dext.	892	6.8		4.7	4.5			4.0	4.0	
phalanx III 3 or IV 4 dext.?	893	14.4		4.3	4.6		3.5	3.8	3.8	
phalanx terminalis (claw)	894	(13.7)		3.8	5.0					
phalanx terminalis (claw)	895	13.9		3.3	5.1					
phalanx terminalis (claw)	896			3.0	4.9					
phalanx terminalis (claw)	897	13.8		3.8	4.9					
Goldberg	BSPG 1966 XXXIV									
coracoid sin.	3276									
femur dext.	3277	55	53.8*	11.1	(6.3)		4.6	10.5		
tibiotarsus sin. (subadult)	3279						4.7	9.5	9.5	
tarsometatarsus dext. (juvenile)	3278	(50)		(11.3)			4.3	(10.1)		

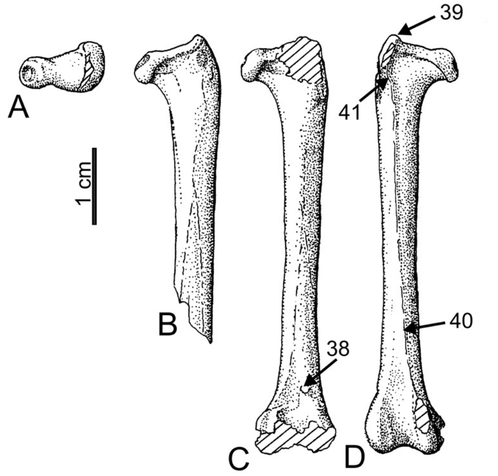

FIGURE 7. Femur dext. of *M. montispetrosi* nov. spec. from Steinberg (BSPG 1970 XVIII 865) (**A, B**) and from Goldberg (BSPG 1966 XXXIV 3277) (**C, D**). **A**) proximal, **B**) caudal, **C**) caudal, **D**) cranial.

comes from the Goldberg locality. For description see holotype.

Pedal phalanges (Figs 9A-J): 18 phalanges, including four claws, are preserved.

The three proximal phalanges of the reversible fourth toe are extremely short. Phalanx I 1 in proximal view notched on the plantar side (55); apophysis extensoris of phalanx II 2 less developed than apophysis flexoris (56); length of phalanx II 1 almost three quarters the length of phalanx II 2 (57); phalanx III 1 slightly more than half the length of phalanx III 2 (58); phalanx II 1 less than double the length of phalanx III 1 (59). (for indices see Tab. 3).

Four claws (Fig. 9J): are preserved, but cannot been assigned with certainty to the corresponding digits.

Taxonomic evaluation of the described characters

The most diagnostic characters of the described skeletal elements are listed in Tab. 2. Together they allow reference of the type material to the Strigiformes, more precisely to the Tytonidae.

A few characters listed in the text are not mentioned on Table 2 as they are purely descriptive and some others have received no numerical value because they describe to the general shape or proportions of a skeletal element. None of the features listed on Tab. 2 is a really unique one, which would, on its own, permit to place the fossil owl in question into a given taxon. But in combination they allow to allocate it accurately. The features listed as strigiform are characteristic of the order but are by no means exhaustive. Nonetheless, the postcranial skeleton of the Tytonidae is fairly well characterized by the features listed.

TABLE 2. Synopsis of diagnostic osteological features for *Miotyto montispetrosi* nov. spec. (numbers correspond to character numbering in description of material). * Ratios for the relative length of tarsometatarsus and coracoid are given on Tabs 4 and 5.

skeletal element	**osteological features**		
	strigiform	agree with Tytonidae	more specific characters
tarsometatarsus	12, 16	1,2,6,9,10,13,14	short and robust* 3,4, 5,7,8,15
coracoid	short and stout, 20, 22	17, 18, 19, 23,	short and stout*
scapula		24	25
humerus	shaft sigmoidal	27, 28, 30	
ulna	32, 33, 34		
phalanx prox. dig maj		36	37
femur	shaft straight, 39	40	41
tibiotarsus	42, 43, 45	46, 48, 50, 51, 52, 53	42, 47, 49
pedal phalanges	basal phalanges extremely short in reversible toe IV	55, 56, 57	59

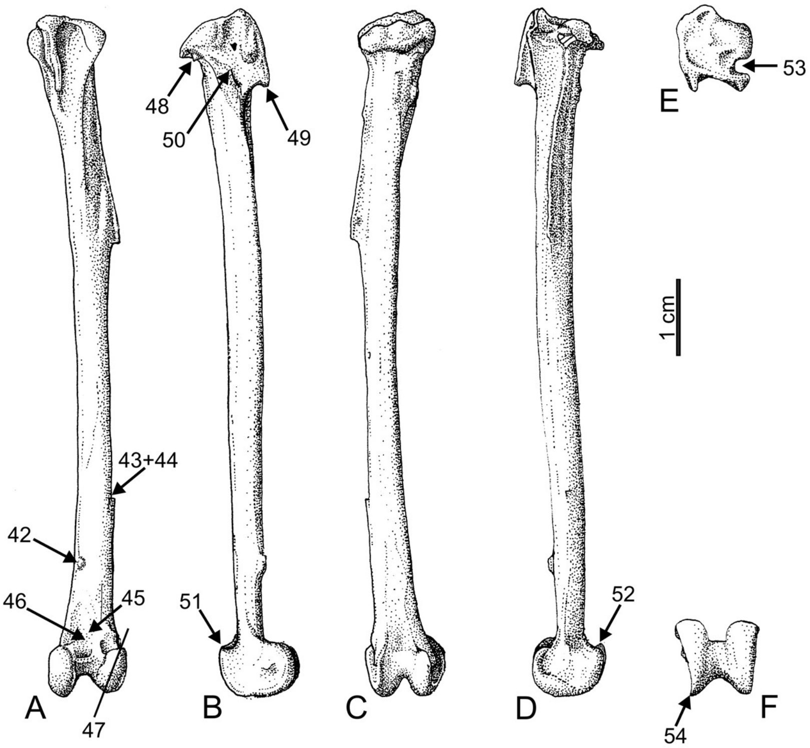

FIGURE 8. Tibiotarsus sin. (1970 XVIII 866) of *M. montispetrosi* nov. spec. from Steinberg. **A**) cranial, **B**) medial, **C**) caudal, **D**) lateral, **E**) proximal, **F**) distal.

Comparisons

Comparison with *Tyto (alba)*

The following features of *Miotyto montispetrosi* nov. spec. are of specific nature within the Tytonidae and some of them appear to have an intermediate character between recent *Tyto alba* and strigid owls. For a separate comparison with *Phodilus* see below and Fig. 11.

The tarsometatarsus of *M. montispetrosi* nov. spec. differs from *Tyto* by being shorter and stouter (see Fig. 10 and Tab. 4), a condition also found in most Strigidae and in Paleogene Tytonidae. The arcus extensorius (1) is not lacking completely as in *Tyto*, but vestigial if compared to Strigidae. The tuberositas m. tibialis cranialis is positioned lower on the shaft than in *Tyto* (3), a feature typical for Strigidae. The sulcus extensorius (4) is longer than in *Tyto*. Also the sulcus of trochlea III (5) is extending further proximally. The proximal part of the sulcus flexorius (7) is more deeply excavated than in *Tyto*, but less so than in Strigidae. The tuberculum m. fibularis brevis (15) is not merely directed plantarly as in *Tyto*, but is not drawn strongly in lateral direction as in strigids. The coracoid is shorter and stouter than in *Tyto*. The cranial face of the phalanx proximalis digiti majoris is flat unlike *Tyto* where it is concave (37). Cranially on the proximal end of the femur, the linea intermuscularis merges in a curve with the crista trochanteris , unlike *Tyto* where it is straight and reaches up to the facies articularis antitrochanterica (41). The lateral condyle of the tibiotarsus is more slanted proximo-laterally than in *Tyto*; the apophysis of the crista cnemialis cranialis projects distally (49) unlike *Tyto*; however this latter feature is potentially age-related and might identify the Steinberg owl as an aged individual.

In his description of the osteology of pedal phalanges of extant owls, Ford (1967) points out that, in *Tyto*, the two basal phalanges of the second toe, i.e. II 1 and II 2, are nearly equal in length, while in Strigidae phalanx II 1 is only about one half the length of phalanx II 2. This finding is supported by the index II 1/ II 2 in Tab. 3 which for *Tyto alba* is 0.8 while in recent Strigidae it is 0.5–0.6. Ford (1967) furthermore points out that, in the third toe of *Tyto* phalanx 1 is one half the length of phalanx 2 while in Strigidae

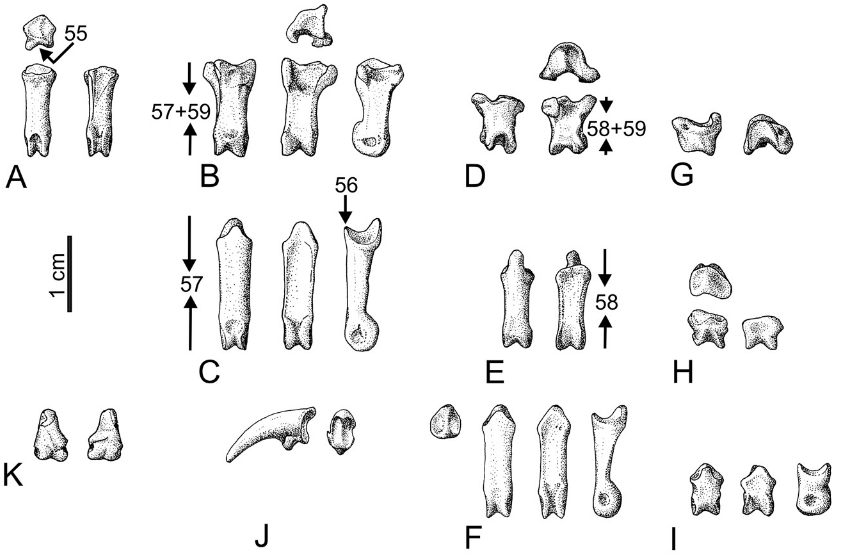

FIGURE 9. Pedal phalanges of the right foot and metatarsal I of the left foot of *M. montispetrosi* nov. spec. from Steinberg (BSPG 1970 XVIII…). **A**) phalanx I 1 dext. (881), **B**) phalanx II 1 dext. (882), **C**) phalanx II 2 dext. (884), **D**) phalanx III 1 dext. (885), **E**) phalanx III 2 dext. (887), **F**) phalanx III 3 or IV 4 dext? (889), **G**) phalanx IV 1 dext. (890), **H**) phalanx IV 2 dext. (891), **I**) phalanx IV 3 dext. (892), **J**) claw of uncertain toe affiliation (897), **K**) os metatarsale I sin. (879). **A**, **D**, and **H** in dorsal, plantar, and proximal view; **B** and **F** in dorsal, plantar, medial and proximal view; **C** and **I** in dorsal, plantar, and medial view; **K** and **E** in dorsal and plantar view; **G** in dorsal and proximal view; **J** in mediolateral and proximal view.

TABLE 3. Length and indices of selected pedal phalanges of extant and fossil Tytonidae and extant Strigidae. Measurements of extant species taken by the authors; measurements of *T. robusta* and *T. gigantea* from Ballmann (1973, 1976).

Length of pedal phalanges	mm **Ph II 1**	mm **Ph II 2**	mm **Ph III 1**	mm **Ph III 2**	Index **II 1 / II 2**	Index **II 1 / III 1**
extant Tytonidae						
Tyto alba (average, n=5)	12.5	15.5 (n=2)	6.3	12.7	0.8	2.0
fossil Tytonidae						
Tyto robusta (different individuals)	20.6 (n=3)	28.0 (n=1)	10.0 (n=1)	21.8 (n=2)	0.7	2.1
Tyto gigantea (different individuals)	26.0 (n=2)	40.0 (n=1)	13.5 (n=2)	28.8 (n=2)	0.7	1.9
M. montispetrosi nov. spec.	13.0	17.5	7.6	12.9	0.7	1.7
extant Strigidae						
Bubo bubo (average, n=2)	15.7	29.5	12.2	17.7	0.5	1.3
Bubo scandiacus (n=1)	12.3	23.3	9.5	14.9	0.5	1.3
Strix aluco (average, n=2)	10.4	17.6	7.3	11.9	0.6	1.4
Asio flammeus (n=1)	9.3	15.3	8.0	10.0	0.6	1.2
Asio otus (average, n=2)	9.1	15.6	6.8	10.0	0.6	1.3
Ninox novaeseelandiae (n=1)	9.0	–	8.0	10.0	–	1.1
Athene noctua (average, n=2)	6.8	10.9	5.2	7.4	0.6	1.3
Athene cunicularia (n=1)	6.2	10.0	5	7.1	0.6	1.2
Otus scops (n=1)	5.4	9.8	3.9	5.7	0.6	1.4
Glaucidium passerinum (n=1)	4.1	7.7	3.6	4.4	0.5	1.1

phalanges III 1 and III 2 are approximately the same length. Again, this is supported by the index III 1/ III 2 in Tab. 3 which is 0.5 for *Tyto* as compared to 0.6 – 0.8 for Strigidae. Consequently for the distinction of *Tyto* from Strigidae the index II 1/ III 1 might usefully be applied. It shows in fact (Tab. 3) a higher index value for *Tyto* (2.0) as compared to strigids (1.1–1.4).

The indices for the fossil species of *Tyto* on Tab. 3 fit well into the general picture if we consider that the measurements do not come from the same individuals.

In the first index (phalanx II 1/ II 2, feature 57) *M. montispetrosi* nov. spec. agrees with the other barn owls. In the other index (phalanx III 1/phalanx III 2, i.e. feature 58) *M. montispetrosi* nov. spec. is intermediate between *Tyto* and the strigids considered.

TABLE 4. Comparison of averaged metrical data and robustness-indices of tarsometatarsus (TMT) of Tertiary European Tytonidae. For comparison the recent European *Tyto alba* has been included. Measurements for *Necrobyas edwardsi, N. harpax, N. rossignoli, N. arvernensis, Sophiornis quercynus,* and *Palaeobyas cracrafti* from Mourer-Chauviré (1987, tab. 5), for *Prosybris antiqua* from Milne-Edwards (1867–1871), for *T. sanctialbani* from La Grive-Saint-Alban from Pavia & Mourer-Chauviré (2011), for *T. campiterrae* from Jánossy (1991) for *T. gigantea* from Ballmann (1973, 1976), and for recent European *Tyto alba* from Langer (1980).

			Tarsometatarsus						
species	**type locality**	**age**	**mean L**	**mean Wp**	**mean Wd**	**mean Ws**	**Wp/L**	**Wd/L**	**Ws/L**
P. cracrafti	Phosphorites du Quercy (F)	Eocene – Oligocene	~53.6 (n=1)	~16.5 (n=1)	~17.9 (n=1)	13.0 (n=1)	0.31	0.33	0.24
N. rossignoli	Phosphorites du Quercy (F)	Late Eocene	33.6 (n=8)	8.4 (n=7)	9.2 (n=8)	4.9 (n=7)	0.25	0.27	0.15
N. harpax	Phosphorites du Quercy (F)	Early Oligocene	37.1 (n=10)	9.1 (n=9)	10 (n=9)	4.9 (n=10)	0.25	0.27	0.13
N. edwardsi	Phosphorites du Quercy (F)	Late Oligocene	41.2 (n=6)	9.8 (n=5)	11 (n=5)	5.4 (n=9)	0.24	0.27	0.13
S. quercynus	Phosphorites du Quercy (F)	Late Oligocene	74.0 (n=1)	19.9 (n=1)	23.7 (n=1)	12.1 (n=1)	0.27	0.32	0.16
N. arvernensis	Staint-Gérand-le-Puy (F)	Early Miocene	43.8 (n=2)	9.8 (n=2)	11.6 (n=1)	4.1 (n=2)	0.22	0.27	0.09
P. antiqua	Saint-Gérand-le-Puy (F)	Early Miocene	34 (n=1)	6 (n=1)	6.5 (n=1)	3.0 (n=1)	0.18	0.19	0.09
M. montispetrosi nov. spec.	Steinberg (D)	Middle Miocene	55.1 (n=2)	10.5 (n=2)	11.8 (n=2)	5.5 (n=2)	0.19	0.21	0.10
T. sanctialbani	La Grive (F)	Middle Miocene	59.1 (n=2)	9.7 (n=6)	11.1 (n=17)	4.7 (n=16)	0.16	0.19	0.08
T. sp* (formerly *T. sanctialbani*)	Gargano, San Giovannino (I)	Late Miocene	77 (n=1)	12 (n=1)	–	–	0.16	–	–
T. campiterrae	Polgárdi (H)	Late Miocene	65.1 (n=2)	10.8 (n=9)	11.3 (n=5)	4.4 (n=3)	0.17	0.17	0.07
T. gigantea	Gargano, San Giovannino (I)	Late Miocene – Early Pliocene	129 (n=1)	21.6 (n=3)	25.6 (n=3)	–	0.17	0.20	–
T. alba, (males)	Europe	Recent	62.3 (n =11)	8.9 (n =11)	10.1 (n =11)	3.7 (n=11)	0.14	0.16	0.06
T. alba, (females)	Europe	Recent	58.7 (n=14)	9.0 (n = 14)	10.1 (n = 14)	3.9 (n=14)	0.15	0.17	0.07

* Formerly described as *T. sanctialbani* from Gargano, Italy (Ballmann 1973, 1976) is synonymized by Mlíkovský (1998, 2002) with *T. balearica,* whereas Louchart (2002: 73) suggests that it probably is a different (new) species (see also Pavia & Mourer-Chauviré 2011). However, it should be considered that the barn owls of Gargano were island inhabiting and show a remarkable increase in size. It is therefore the owl of the lowest stratigraphic level, *i.e.*, Biancone, which must be compared to *T. sanctialbani* from La Grive-Saint-Alban. The age of the Gargano faunas according to Masini *et al.* (2013) span from the Late Miocene to the Early Pliocene.

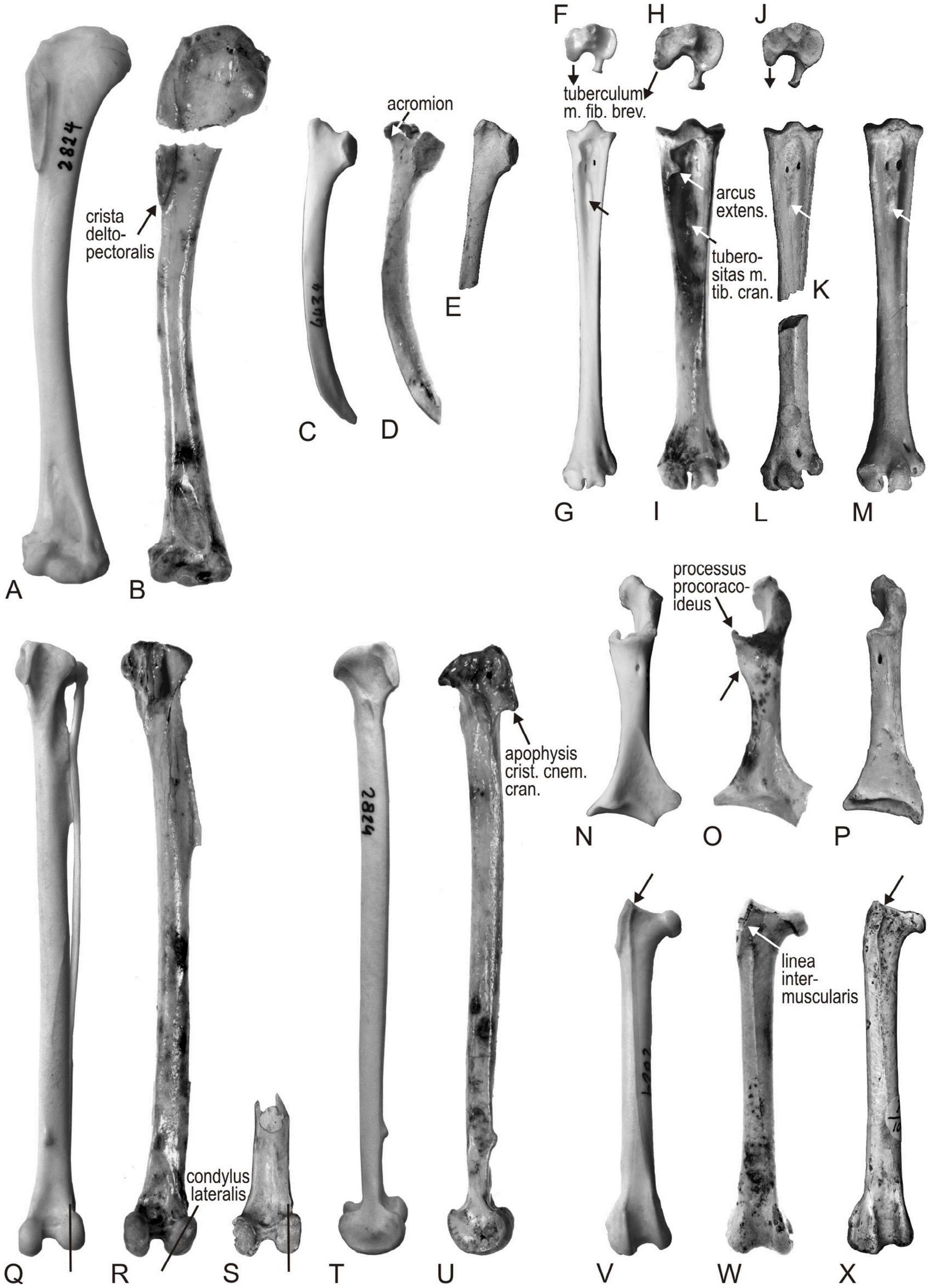

FIGURE 10. Selected distinguishing characters between *M. montispetrosi* nov. spec. (**B**, **D**, **H**, **I**, **O**, **R**, **U**, **W**), the extant *Tyto alba* (**A**, **C**, **F**, **G**, **N**, **Q**, **T**, **V**), and *Tyto sanctialbani* from La Grive-Saint-Alban (**E** invers, **J**, **K**, **L**, **M** invers, **P** invers, **S**, **X**). **A** and **B**) humerus dext. cranial view; **C-E**) scapula dext. lateral view; F-M) tarsometatarsus sin. proximal view (**F**, **H**, **J**), dorsal view (**G**, **I**, **K**, **L**, M); **N–P**) coracoid dext. dors. view; **Q-U**) tibiotarsus sin. cran. view (**Q–S**), medial view (**T**, **U**); **V–X**) femur dext. cran. view. Not to scale. Specimens of *T. alba* (**A**, **Q**, **T**, **V**: NHMW 2824 and **C**, **F**, **G**, **N**: NHMW 4434). Specimens of *T. sanctialbani* (**E**: NHMUK A345, **J**, **K**: NHMUK A305 lectotype, **L**: NHMUK A303 paralectotype, **M**: FSL 91627, **P**: NHMUK A324, **S**: NHMUK A304 paralectotype, **X**: NHMUK A1058; images of *T. sanctialbani* provided by M. Pavia (University Torino).

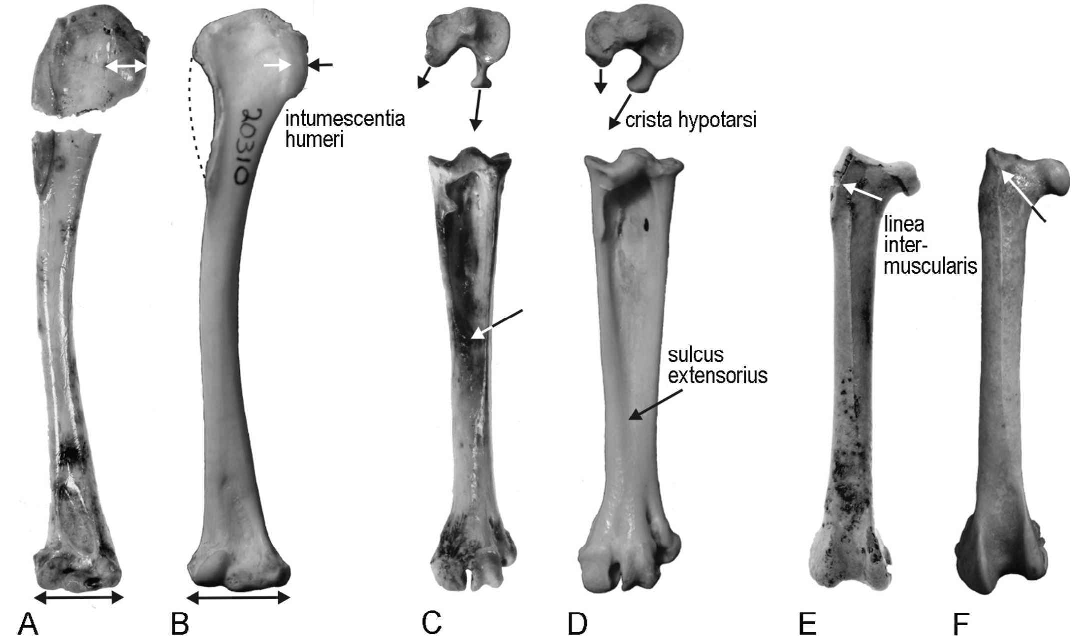

FIGURE 11. Selected distinguishing characters between *M. montispetrosi* nov. spec. (**A**, **C**, **E**) and *Phodilus badius* (USNM 20310) (**B**, **D** invers, **F** invers). **A** and **B**) humerus dext. cranial view, **C** and **D**) tmt sin. in dorsal and proximal view, **E** and **F**) femur dext. cranial view. Not to scale.

Comparison with *Phodilus* (Fig. 11)

The length of the tarsometatarsus of the measured specimen of *Phodilus badius* (USNM 20310) is 40.5 mm, the length of its femur is 46.0 mm. The index of tmt/femur of 0.8 compared to 1 for *M. montispetrosi* nov. spec. (see Tab. 5) shows that the tmt of *Phodilus* is markedly shorter in proportion. Furthermore, in *Phodilus* the sulcus extensorius on the tmt is longer than half the shaft and the crista hypotarsi more deflected in lateral direction (proximal view). On the slightly stouter femur the cranial linea intermuscularis does not merge proximally with the crista trochanteris but reaches up to the facies articularis antitrochanterica. The intumescentia humeri is clearly narrower in *Phodilus* than in *M. montispetrosi* nov. spec. and the distal end of the humerus is more extended to both sides. In *Phodilus* the relative sizes of the phalanges are much the same as in *Tyto* (Ford 1967), whereas *M. montispetrosi* nov. spec. occupies an intermediate position to the strigids in this respect (Tab. 3). Ford (1967) mentions that in *Phodilus* the pedal phalanges IV 1 and IV 2 are fused, which is not the case in *M. montispetrosi* nov. spec.. Unfortunately, pedal phalanges were not available for the investigated specimen USNM 20310.

Comparison with Palaeogene and Neogene Tytonidae

In Tab. 4 the pertaining species are listed including their type localities and measurements of their tmt.

The tmt of Paleogene owls, where it is known (*Sophiornis quercynus, Palaeobyas cracrafti)* is characteristically stout. The distal extremity of the humerus is broad, where documented (*Nocturnavis incerta*). The species of *Necrobyas* are smaller than *Miotyto montispetrosi* nov. spec. and their tmt again is stouter, especially its distal extremity is broader (Tab. 4). Starting with *Prosybris antiqua* in the Early Miocene the proportions of the tmt become more comparable to extant *Tyto*. *Prosybris antiqua* is very similar to *M. montispetrosi* nov. spec. by its tmt proportion, but is distinctly smaller; furthermore, its tuberculum m. fibularis brevis is shorter and directed plantarly. Of the Neogene barn owls of the genus *Tyto, T. campiterrae* is larger. The skeletal elements of *T. balearica* from the type locality Cova de Canet (Mallorca), of which the length is known (humerus: 102mm; coracoid: 45mm; phalanx II 2: 20.7 mm) are longer than the corresponding bones in *M. montispetrosi* nov. spec. Also its tmt, as far as preserved, is more slender than in *M. montispetrosi* nov. spec. The subspecies *T. balearica cyrneichnusae* from Corsica and Sardinia is also clearly of greater size and its tarsometatarsus is more slender.

Nearest in size and shape to *M. montispetrosi* nov. spec. is *T. sanctialbani* from the type locality La Grive-Saint-Alban (France) such as described by Lydekker (1893) and more recently by Pavia & Mourer-Chauviré (2011). There are, however, some morphological differences (see also Fig. 10). The tarsometatarsus of *M. montispetrosi* nov. spec. is shorter and stouter (Tab. 4). The ratio of length of tarsometatarsus and coracoid to the femur, respectively, shows that the proportions of the leg and shoulder girdle of *M. montispetrosi* nov. spec. were different (Tab. 5). On the tarsometatarsus the arcus extensorius (1) of *M. montispetrosi* nov. spec. is vestigial, whereas completely missing in *T. sanctialbani.* The sulcus extensorius (4) is shorter in *M. montispetrosi* nov. spec., reaching further distal in *T. sanctialbani*. The tuberositas m. tibialis cranialis (3) in *M. montispetrosi* nov. spec. is positioned slightly more distally on the shaft than in *Tyto sanctialbani.* The tuberculum m. fibularis brevis is directed plantolaterally in *M. montispetrosi* nov. spec. (15), while in *T. sanctialbani* it points in a purely plantar direction. In *M. montispetrosi* nov. spec. the trochlea III bulges less dorsally and its sulcus extends further proximally (5) than in *T. sanctialbani*. On the femur of *M. montispetrosi* nov. spec., the linea intermuscularis cranialis merges with the crista trochanteris (41) while in *T. sanctialbani* it reaches up to the facies articularis. The condylus lateralis on the tibiotarsus of *M. montispetrosi* nov. spec. is slanted proximolaterally (47) unlike in *T. sanctialbani.* The proportions of the pedal phalanges (57 and 59) in *M. montispetrosi* nov. spec. are diagnostic features, but cannot be compared to *T. sanctialbani* where the material is not complete enough.

Discussion and conclusions

The barn owl described here from the Middle Miocene (MN6) of the Nördlinger Ries represents a fossil genus near but not identical to *Tyto*. In a number of special characters (Tab. 2) it is distinct from *Tyto* and in some even resembles the Strigidae. *Prosybris antiqua* documented in the Early Miocene of Saint-Gérand-le-Puy (France), but possibly already present in the Oligocene of the Phosphorites of the Quercy

TABLE 5. Metrical comparison of *Miotyto montispetrosi* nov. spec. with *Tyto sanctialbani* from La Grive-Saint-Alban (measurements of the latter from Pavia & Mourer-Chauviré (2011)). Estimated measurements of slightly damaged bones are given in parenthesis.

	M. montispetrosi nov. spec from Steinberg and Goldberg			*T. sanctialbani* from La Grive-Saint-Alban		
	GL	**Wp**	**Wd**	**GL**	**Wp**	**Wd**
coracoid	(35)	–	(13)	37.8	–	–
humerus	*c.* 90	17.0	14.4	–	–	11.7–14.8 mean (n = 12) = 13.07
femur	55	10.8–11.1 (n = 2)	10.5	51.5–55.8 (n = 2)	9.5–11.4 mean (n = 3) = 10.13	8.9–11.8 mean (n = 13) = 10.08
tibiotarsus	90.5	–	10.9–11.0	–	–	9.0–10.3 mean (n = 10) 9.78
tarsometatarsus	55.1 (n = 2)	10.4–10.5 (n = 2)	11.8 (n = 2)	58.1–60.0 (n = 2)	9.3–10.0 mean (n = 6) = 9.6	10.4–11.9 mean (n = 17) = 11.06
phalanx I 1	12.5–12.7 (n = 2)	4.5–4.6 (n = 2)	3.4–3.5 (n = 2)	12.1	4.0	3.0
phalanx II 1	13.0–13.1 (n = 2)	7.0 (n = 2)	4.3–4.5 (n = 2)	13.1	6.6	4.2
index coracoid/femur	0.64			0.70		
index tmt/femur	1.00			1.08		

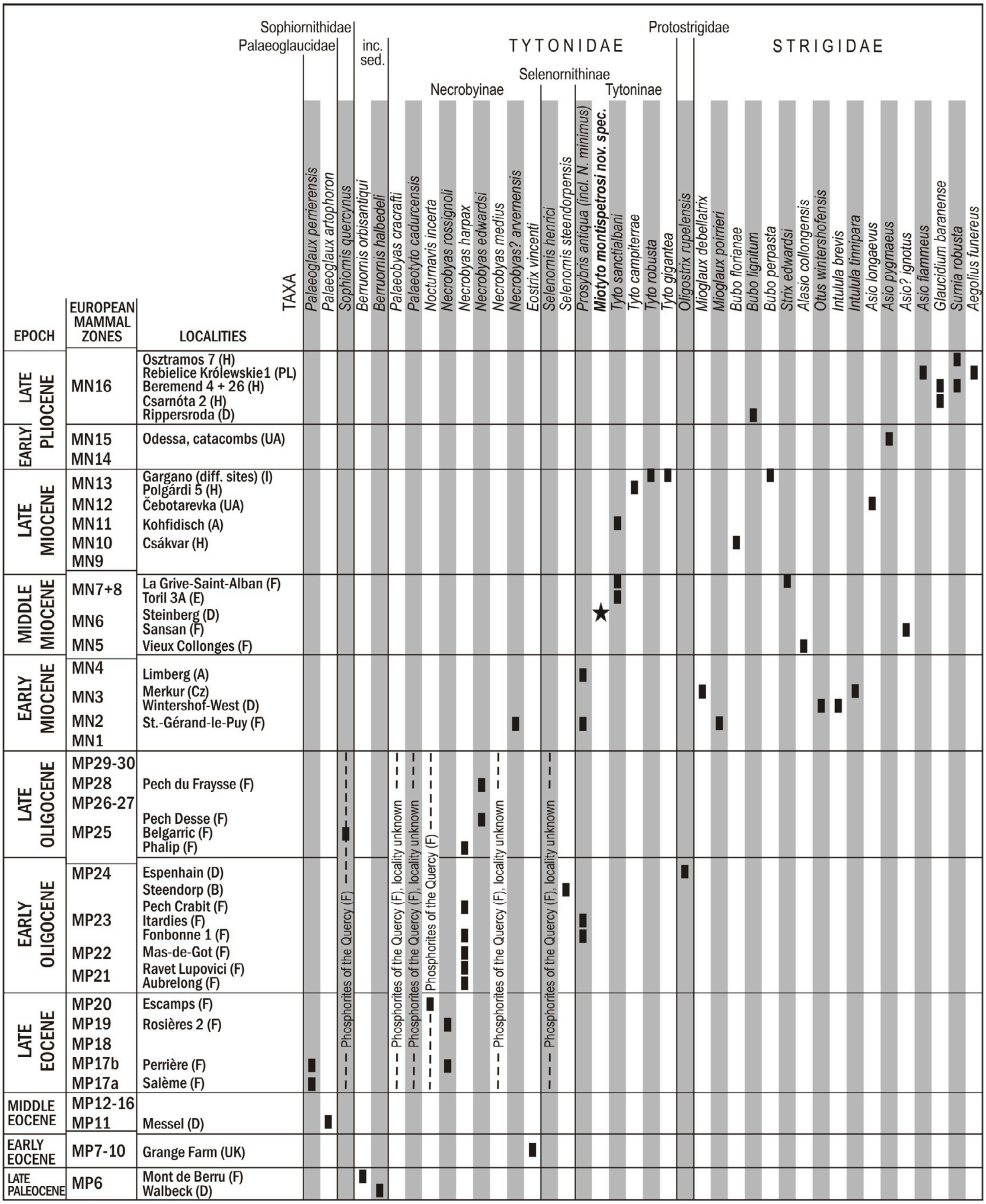

FIGURE 12. Fossil record of Paleogene and Neogene Strigiformes (taxa adjusted) in Europe. Stratigraphy of the Paleogene and Neogene and correlation between epochs and the European mammal zones follow Hilgen *et al.* (2012) and Vandenberghe *et al.* (2012), respectively. Epochs and mammal zones not to scale. Note: Following the Neogene Stratigraphy (Vandenberghe *et al.* 2012) of the International Stratigraphic Chart 2012, the Mammal Neogene unit MN17 is not part of the Pliocene anymore; therefore *T. balearica*, which can only be confirmed from MN17 on (Louchart 2002), is not considered in this figure.

(France) might be at the base of the Tytoninae. The Early Miocene Strigidae from Saint-Gérand-le-Puy (France), Wintershof-West (Germany), and Merkur (Czechia) can be considered to be the earliest typical owls known in Europe. We do not know when exactly the branching of the two families took place, but the Strigidae are younger. The extant genus *Phodilus* is credited with intermediate characters between the barn owls and the typical owls (Brodkorb, 1970). The comparison of *M. montispetrosi* nov. spec. with *Phodilus,* however, shows no special resemblance beyond the short tarsometatarsus without an ossified extensor loop (arcus extensorius). We may assume that *Phodilus* is a relict and that in the Middle Miocene and earlier a greater number of Strigiformes of intermediate systematic position existed.

Although distinguishable by several osteological details, as shown above, *M. montispetrosi* nov. spec. resembles most *T. sanctialbani* among European Miocene tytonids, especially in size and proportions; unfortunately, the proportions of the pedal phalanges (features 57 and 59) which are diagnostic for *M. montispetrosi* nov. spec., cannot be verified for *T. sanctialbani* as they are unknown to date.

M. montispetrosi nov. spec. is the only owl documented from the Middle Miocene deposits of the Nördlinger Ries and certainly most of the small-sized bird and small mammal remains (Heizmann & Fahlbusch 1983, Heizmann & Hesse 1995) originate from its regurgitated pellets. Probably the owl nested or had roosting places in crevices of the hills and spring mounds that emerged from the Ries crater lake.

At least one juvenile owl is documented by a tarsometatarsus and a tibiotarsus from the Goldberg 9 site. The presence of bones from a juvenile individual of *M. montispetrosi* nov. spec. indicates that the species was breeding at the Middle Miocene Ries Lake. A resident barn owl adds another species to the fossil bird fauna for the Nördlinger Ries indicative of warm climatic conditions.

Acknowledgements

We are grateful to the Bayerische Staatssammlung für Paläontologie und Geologie, Munich (BSPG), for putting the studied fossil material at our disposal. We thank A. Gamauf and H-M. Berg from the ornithological department of the Naturhistorisches Museum Wien (NHMW) and J. Dean from the National Museum of Natural History (Smithsonian Institution) Washington (NMNH) for providing skeletons of extant strigiforms for comparisons. We are grateful to M. Pavia (University Torino) for providing photos of fossils of *T. sanctialbani* and to G.W. Kaiser (Victoria, Canada) for improving the English of the manuscript. We thank C. Mourer-Chauviré (Université Claude Bernard Lyon1) for comments on a previous version of the manuscript. The manuscript profited from comments by the reviewers C. Mourer-Chauviré and M. Pavia.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

naturhistorisches museum wien

Who discovered the Phorusrhacidae? An episode in the history of avian palaeontology

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Abstract — Remains of giant predatory ground birds were first discovered in the Tertiary of Argentina at the end of the 1880s, within the context of a bitter competition between Florentino Ameghino (and his brother Carlos) and Francisco Pascasio Moreno, then director of the newly founded Museo de La Plata. The early stages in the discovery and description of the Phorusrhacidae were characterised by misidentifications, hurried publications, undue multiplication of taxa and a general climate of mutual distrust and hostility. One of the few positive points of the feud between Ameghino and Moreno was that it led to several palaeontological expeditions to southern Argentina, which resulted in the discovery of large quantities of important fossils. In many respects, the competition between the Argentinian palaeontologists parallels the well-known feud between E.D. Cope and O.C. Marsh, which took place in the United States at roughly the same time.

Key words: Phorusrhacidae, History, Argentina, Ameghino, Moreno, Mercerat

Introduction

At the end of the 19th century, the discovery of giant predatory flightless birds in the Cenozoic of South America attracted much attention in the palaeontological community and beyond, and can be considered as an important episode in the history of avian palaeontology. These birds are now generally known as Phorusrhacidae, although other names (*e.g.*, Stereornithes) were once used. They are mainly known from South America, with a record ranging from the Palaeogene to the Pleistocene (Alvarenga & Höfling 2003; Agnolin 2009; Alvarenga *et al.* 2011; Tambussi & Degrange 2013), and have also been reported from the Plio-Pleistocene of North America (Brodkorb 1963) and the Eocene of Africa (Mourer-Chauviré *et al.* 2011); they appear to be present in the Eocene of Europe as well (Angst & Buffetaut 2012). Reports of phorusrhacids from Antarctica were considered as unfounded by Cenizo (2012) and Tambussi & Degrange (2013). The first specimens were discovered in southern Argentina at the end of the 1880s, under rather peculiar circumstances. At that time, Argentine palaeontology was marked both by remarkably successful expeditions in various parts of the country, notably Patagonia, which revealed hitherto completely unknown vertebrate faunas, and by an acute feud between two of the leading Argentine researchers of the time, Florentino Ameghino and Francisco Pascasio Moreno. The discovery of the phorusrhacid birds is part of this wider story. Although its main outlines have been discussed in various reviews of the Phorusrhacidae (Alvarenga & Höfling 2003; Agnolin 2009), an examination of publications and correspondence by the protagonists

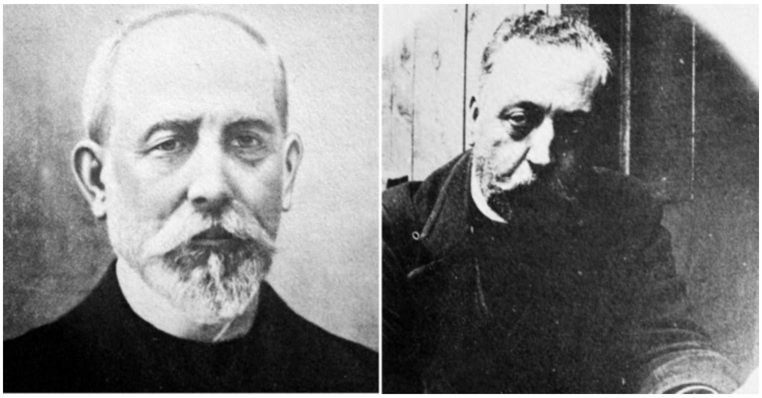

FIGURE 1. Florentino AMEGHINO (left) and Carlos AMEGHINO (right).

revealed various hitherto overlooked interesting points which are the topic of the present paper. For easier reading, quotations of papers in Spanish or French have been translated into English by the author.

The institutional and personal background

The palaeontological potential of southern Argentina had been revealed by Charles DARWIN during the voyage of the Beagle, when, in 1833, he discovered important fossil vertebrate localities in the vicinity of Bahía Blanca (DARWIN 1839). However, although subsequent travellers did occasionally collect fossils in Patagonia, it was not until the 1880s that systematic palaeontological research began to be carried out in what was then a remote and only partly explored part of Argentina.

This new development was largely a consequence of the establishment of the Museo de La Plata, a modern scientific institution that was launched in the then recently founded capital of Buenos Aires province thanks to an initiative of Francisco Pascasio MORENO (1852–1919), an active scientist, explorer and administrator, who had travelled extensively in Patagonia in the 1870s. Palaeontological research at the Museo de La Plata really started in 1886, when MORENO hired Florentino AMEGHINO (1854–1911) as subdirector and secretary of the museum. Although largely self-taught, AMEGHINO was a brilliant palaeontologist who had already made a name for himself internationally through his work on the fossil mammals of Argentina — although some of his interpretations were markedly idiosyncratic (for a recent biography of Florentino AMEGHINO, see CASINOS, 2012). Throughout his scientific career, Florentino AMEGHINO was seconded by his younger brother Carlos AMEGHINO (1865–1936), who from 1887 to 1903 conducted a total of 15 expeditions to Patagonia, in the course of which he collected a huge number of fossil vertebrate specimens which were described by his elder brother.

Carlos AMEGHINO had been employed by MORENO at the same time as his brother, as "travelling naturalist" for the Museo de La Plata. In that capacity, he was sent to southern Patagonia in January, 1887, to collect fossils, notably from localities that had been found by MORENO during some of his earlier visits to the Santa Cruz area (AMEGHINO 1887). Carlos's trip was enormously successful in terms of the number of fossils, mostly representing completely new taxa, that he collected. By the time he came back to La Plata in September, 1887, however, relations between his brother and MORENO had begun to deteriorate, for reasons involving both bureaucratic problems and a clash of personalities that have been discussed by various authors (FERNICOLA 2011; CASINOS 2012). In January 1888, Florentino AMEGHINO resigned from his position at the Museo de La Plata, and in February of the same year, he was officially dismissed from it. In addition, access to the palaeontological collections was denied him, although he had provided a large part of them.

From then on, and until he finally became director of the Museo Argentino de Ciencias Naturales in Buenos Aires in 1902, Florentino AMEGHINO

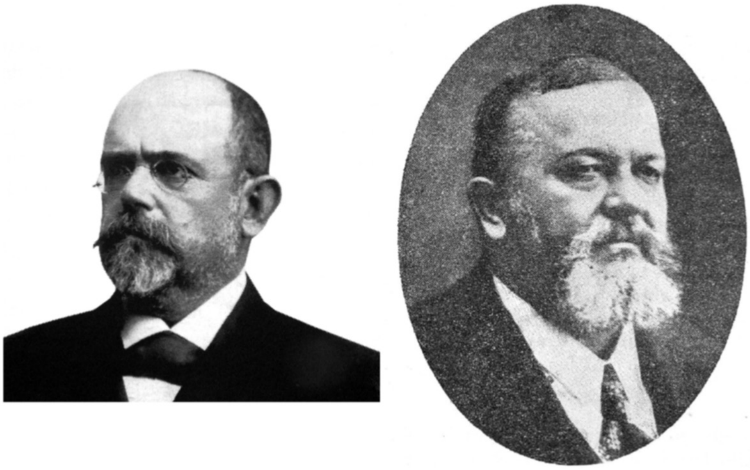

FIGURE 2. Francisco Pascasio Moreno (left) and Alcides Mercerat (right).

carried out his palaeontological researches without any permanent official support, which did not prevent him from sending his brother Carlos (who had left the Museo de La Plata together with him) on new collecting expeditions to Patagonia. Funding for them was provided by the book and stationary shop Florentino and his brother Juan ran in La Plata, supplemented by the occasional sale of fossil collections to European institutions (Casinos 2012). Meanwhile, competing expeditions were sent from the Museo de La Plata to Patagonia by Moreno, each trying to collect and describe as many new fossils as possible, before the hated competitor could do so (a situation rather reminiscent of the well-known feud between E.D. Cope and O.C. Marsh in North America at roughly the same time). It is within this peculiar scientific framework of intense competition that the discovery of the Phorusrhacidae took place.

***Phorusrhacos*, an edentulous mammal?**

When Carlos Ameghino came back from his first expedition to Patagonia in September 1887, he brought with him a considerable collection of fossil vertebrates, mainly from the Santa Cruz beds (now known to be Miocene in age, at that time considered as Eocene by Florentino Ameghino). In his own words, Florentino Ameghino worked "day and night" to produce preliminary descriptions of more than 120 species of fossil mammals collected by his brother, which were ready by 18th November, 1887 (Ameghino 1887). Possibly his relations with Moreno had already deteriorated and he wished to establish priority for the new taxa as quickly as possible — in any case he was in the habit of publishing very preliminary descriptions at a fast rate. Among the specimens described as new taxa was an incomplete large, edentulous lower jaw, which Ameghino placed among the Edentata under the heading "genera incertae sedis". He called the new taxon *Phorusrhacos longissimus* and stressed its considerable size and complete lack of teeth.

In 1889, Florentino Ameghino published a huge monograph on the fossil mammals of Argentina, partly based on material collected by Carlos in Patagonia in 1887, which should have been deposited in the Museo de La Plata, but apparently was appropriated by Florentino, and ultimately found its way into the Museo Argentino de Ciencias Naturales in Buenos Aires (Fernicola 2011). In that work, Ameghino (1889) described in more detail the mysterious toothless jaw. He emended the generic name to *Phororhacos* (however, the original spelling *Phorusrhacos* has priority and must be used, see Brodkorb 1963) *Phorusrhacos longissimus* was placed in a family of its own, the Phororhacosidae (later emended to Phorusrhacidae by Brodkorb 1963), itself placed among the Edentata and considered as completely extinct. Ameghino noted that the toothless tip of the jaw must have been covered by a horny sheath, similar to the beak of birds and turtles. No illustration was provided. On the basis of the first specimen discovered by Carlos

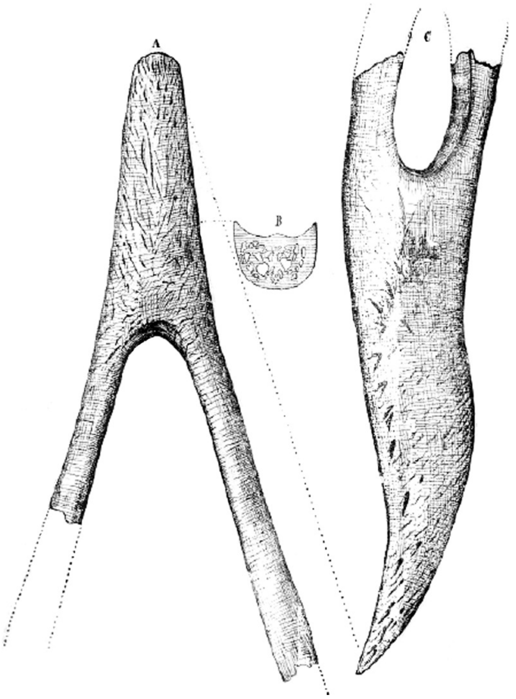

FIGURE 3. The type specimen of *Phorusrhacos longissimus* Ameghino, 1887: a lower jaw in ventral view (A), cross-section (B) and left lateral view (C), after Ameghino (1891a). The specimen was found in the Santa Cruz Formation of southern Patagonia by Carlos Ameghino in 1887.

Ameghino, the Phorusrhacidae were thus first interpreted by his brother Florentino as edentulous mammals.

It should be added that as late as June 1891, in a paper describing the characters of fifty new species of fossil mammals from Argentina, Florentino Ameghino described and figured a jaw fragment collected by Carlos in Patagonia as belonging to a new ground sloth, which he called *Tolmodus inflatus* (Ameghino 1891a). Only two months later, he reinterpreted it as a giant bird.

Moreno's large birds from Monte Hermoso and southern Patagonia

As noted above, after Florentino and Carlos Ameghino left the Museo de La Plata at the beginning of 1888, Moreno continued the palaeontological exploration of Argentina by sending parties from the museum to various fossil-bearing areas. Thus was accumulated a vast collection which in many ways paralleled that brought together by Carlos Ameghino from Patagonia. Moreno was fully aware of Carlos's continuing collecting activities, and in order to gain priority over his rivals, between 1888 and 1891 he published a number of brief reports on the development of the Museo de La Plata and especially the new palaeontological discoveries made by its teams of field researchers. Thus, in 1888, he published a preliminary report on the activities of the museum during the first semester of 1888. In it, he emphasized the discoveries made at Monte Hermoso, a locality on the south-eastern coast of Buenos Aires province (therefore not properly speaking in Patagonia) that had already been visited by Darwin, and more recently by Florentino Ameghino in 1887. There, fossiliferous beds now known to be Pliocene in age yielded an abundant vertebrate fauna. In his 1888 report, Moreno described in some detail the mammal assemblage and simply noted (Moreno 1888: p. 8) that 'large birds' ('grandes pájaros') were also present. This seems to be the first mention of giant birds in the Tertiary of South America.

In a later paper, Moreno (1889) provided more details about the large birds from Monte Hermoso. He mentioned that he had some remains of an enormous bird which he considered as "the largest to have taken flight in the South American region" (Moreno 1889: p. 29), and comparable only with *Gastornis* from Meudon (a giant flightless bird, at that time known mainly from fragmentary specimens from the Early Tertiary of Europe: see Buffetaut 1997). The available material consisted of part of a tibiotarsus, a fibula, parts of the femur and humerus and a cervical vertebra. The fragmentary tibiotarsus was 37 cm long and similar in size to that of an African ostrich. Moreno thought that these bones belonged to a "palmipedo lemelirostro" [*sic*] ("palmipèdes lamellirostres" was the name used by, among others, the French zoologist Alphonse Milne-Edwards (1835–1900) for the group comprising ducks and swans). For this giant bird, he coined the name *Mesembriornis Milne Edwardii* [sic], in honour of Milne-Edwards, the author of a monumental work on French fossil birds. That material from Monte Hermoso was described and figured two years later by Moreno & Mercerat (1891). In addition, Moreno (1889) reported a second new bird taxon from Monte Hermoso, based on an incomplete tarsometatarsal, which he called *Palaeociconia australis* and considered as a ciconiid. ALVARENGA & HÖFLING (2003) consider *Palaeociconia* as a junior synonym of *Mesembriornis*.

Although MORENO was mistaken about both the flight capabilities and the systematic position of the giant birds from Monte Hermoso, he was the first to clearly identify giant birds in the vertebrate faunas from the Tertiary of Argentina. Furthermore, in a report on the acquisitions and scientific results of the Museo de La Plata in 1889, MORENO (1890–1891) briefly mentioned that from October 1888 to August 1889 a party from the museum, led by Santiago POZZI and Clemente ONELLI, had explored fossil localities discovered by himself along the Rio Santa Cruz, in southern Patagonia. Among their most extraordinary finds were remains of giant birds. One of them, according to MORENO, was larger than the largest living bird, the African ostrich. Another one was even larger and apparently had affinities with the dinornithids of New Zealand, being as large as or larger than them. It therefore appears that by the end of 1889, MORENO had obtained phorusrhacid remains not only from Monte Hermoso, but also from southern Patagonia and soon thereafter had identified them as belonging to giant birds.

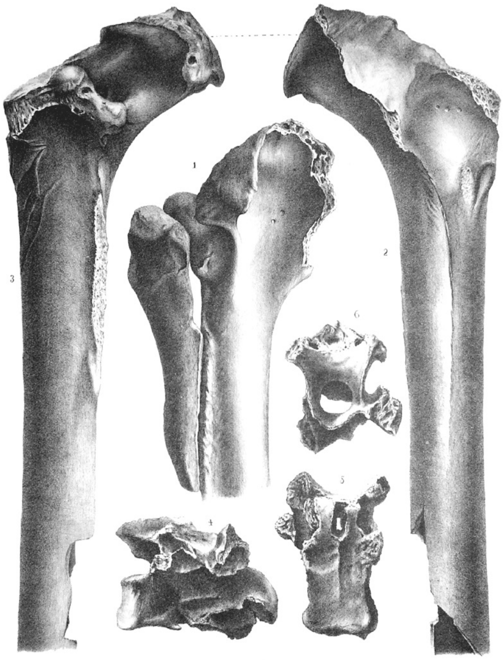

FIGURE 4. Bones of the giant bird *Mesembriornis* (tibiotarsus, fibula and vertebra) from Monte Hermoso, first reported by MORENO (1888, 1889), as figured by MORENO & MERCERAT (1891).

***Phorusrhacos* as a bird?**

Although Florentino AMEGHINO tried to hide this fact as much as possible in the papers he published in the early 1890s, the AMEGHINO brothers were at first much puzzled by MORENO's announcement of the discovery of giant birds in the Tertiary of Argentina. This is clearly shown by passages from the correspondence between Florentino and Carlos during some of the latter's early trips to Patagonia (TORCELLI 1935a, b; CHIARELLI 2006). A letter sent by Carlos from Rio Gallegos on 23rd December, 1890, during his long fourth expedition, is especially revealing. In it, Carlos first reflected on the position of *Phororhacos*, of which he had found an additional, more complete beak, and concluded that it was "an enigmatic animal". He clearly had read MORENO's 1889 paper, and went on to note (TORCELLI 1935a: p. 181; CHIARELLI 2006: p. 86):

> *"Moreno's large fossil birds, which so much puzzled us (Mesembriornis, etc.) have also appeared. They are indeed gigantic birds, some of them perhaps as large as the Gastornis. Could not the beak of Phororhacos belong to one of these birds?"*

Carlos, whose knowledge of anatomy and palaeontology was far from negligible, as shown by many of his letters to his brother, was thus the first to suggest that the mysterious *Phorusrhacos* was not a mammal, but a bird. However, he at first failed to convince his elder brother. In a reply sent from La Plata on 30th January, 1891 (TORCELLI 1935b: p. 10), the latter wrote:

> *"The possibility that the beak of Phororhacos belongs to a gigantic bird seems unlikely to me; because if it was so, they would be birds from groups completely distinct from those we presently know and without any relationship with the gigantic birds from Madagascar and New Holland. Personally, I tend to believe*

> *that it may well belong to an extinct giant monotreme".*

It is difficult to decide what exactly led Florentino to change his mind, but he obviously did so during the first few months of 1891. A new discovery made by Carlos later during his fourth trip to Patagonia may have contributed to this change of interpretation. In a letter sent from Santa Cruz on 28th April, 1891 (Torcelli 1935b: p. 19), he mentioned:

> *"A complete beak of Phororhacos, with which the head was also present, but could not be preserved. As measured in the field, it was 3 spans [about 69 cm] long".*

This is clearly the specimen of *Phorusrhacos longissimus* described in detail by Florentino Ameghino in 1895, about which he mentioned that "the skull which accompanied that mandible could not be preserved; it fell into small pieces" (Ameghino 1895: p. 12).

The complete mandible, with its fairly well preserved articular regions, was clearly avian and could not be mistaken for that of a mammal. However that may be, in several papers published in 1891 in the *Revista Argentina de Ciencias Naturales*, a journal he co-edited and which served as a convenient outlet for his abundant scientific production, Florentino Ameghino not only mentioned his brother's discovery of giant bird remains in Patagonia, but also completely revised his interpretation of both *Phorusrhacos* and *Tolmodus* (see below).

Carlos's discovery was mentioned in the "correspondence, travels and explorations" section of the *Revista Argentina de Ciencias Naturales*. In it, Florentino published (supposedly on 1st April, 1891) excerpts from the above-mentioned letter sent to him by Carlos on 23rd December, 1890 (C. Ameghino 1891), dealing with the "exploration of the fossiliferous deposits of southern Patagonia". While the section about the enigmatic nature of *Phororhacos* was reproduced almost *verbatim*, the part about fossil birds was printed with revealing changes (C. Ameghino 1891: p. 121), as follows:

> *"The large fossil birds that so much puzzled me have also appeared. They are indeed gigantic birds, some of them perhaps as large as the Epiornis [sic]".*

As can be seen, all mention of Moreno and his *Mesembriornis* had been deleted, as well as the question about *Phorusrhacos*. One can only suspect that Florentino Ameghino thus tried to deny Moreno any role in the discovery of the giant fossil birds of Argentina and to deflect attention from his misidentification of the *Phorusrhacos* jaw (perhaps the fact that his brother had been right about its avian nature, while he himself doubted it, was not a pleasant memory. Replacing "us" by "me" may reflect this). Why he chose to replace *Gastornis* by *Aepyornis* is unclear. Perhaps the huge recently extinct bird from Madagascar was more impressive than the poorly known *Gastornis*. Having tampered with Carlos's letter, Florentino later used it to claim priority for the discovery of the giant birds. In 1895, in a review of the fossil birds from Patagonia, he wrote that the first mention of the giant birds had been published by his brother Carlos in the above-mentioned 1891 note in the *Revista Argentina de Ciencias Naturales* (Ameghino 1895). Ameghino was rather disingenuous about this, since Moreno's mentions of the giant bird *Mesembriornis* from Monte Hermoso (Moreno 1888, 1889) and of huge fossil birds from southern Patagonia (Moreno 1890–1891) antedated the publication of Carlos's discoveries in southern Patagonia — as clearly shown by Carlos's December 1890 letter in which he mentioned Moreno's work.

Be that as it may, Florentino went on to reinterpret *Phorusrhacos* and *Tolmodus* in the light of the recent discoveries of giant bird remains. In a paper on new discoveries and reinterpretations of fossil mammals and birds, published in August, 1891 (Ameghino 1891a), he admitted that he had erroneously referred both to the Edentata, but that his brother's discoveries in Patagonia had convinced him of his error. He gave a longer description of *Phorusrhacos longissimus* (as "*Phororhacos*"), including the original mandible, which was figured for the first time, and various other bones such as several post-cranial elements (as well as the above-mentioned skull that had crumbled before it could be collected).Two addi-

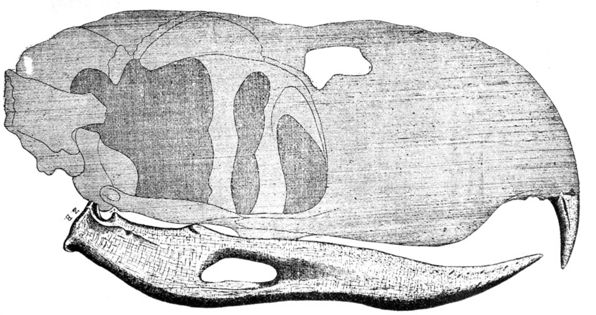

FIGURE 5. The *Phorusrhacos longissimus* specimen discovered by Carlos Ameghino in 1891, as illustrated by Florentino Ameghino (1895: Fig. 8). Except for the hook-like tip of the beak, the skull crumbled before it could be collected and was thus shaded on Ameghino's figure.

tional species of the genus (*P. Shenensis* and *P. delicatus*) were briefly described, and *Tolmodus inflatus* was referred to it, too, as *Phororhacos inflatus*. Ameghino added that these birds belonged to a family (previously considered by him as mammalian), the Phororhacosidae, which he was unable to place more precisely in avian classification. As to their size, he considered that by comparison with them the *Dinornis* from New Zealand were "dwarfs". Clearly, Florentino Ameghino was in a hurry to claim priority for as many giant bird taxa as possible, and he had good reason for that, as Moreno at that time was working on an ambitious editorial project concerning fossil birds.

Moreno and Mecerat's *magnum opus* and Ameghino's counter-attack

To replace Florentino Ameghino as subdirector and secretary of the Museo de La Plata, Moreno had hired a Swiss geologist, by the name of Alcides Mercerat (Vignati 1936). Although many aspects of his life remain obscure (including his date of birth; he died in 1934), both his personality and his contributions to the geology and palaeontology of Argentina have generally not been highly regarded (see Simpson 1984 and Casinos 2012 for details). Having been replaced at the Museo de La Plata by Santiago Roth in 1895, he eventually stopped his scientific activities to become a surveyor. In 1891, Moreno & Mercerat published in the *Anales del Museo de La Plata* a catalogue of the fossil birds of the Republic of Argentina, in the form of a large bilingual (Spanish and French) monograph, notable among other things for the huge size of its plates, which show the bones of various giant birds at their natural size (Moreno & Mercerat 1891). Moreno and Mercerat seized the opportunity to comment unfavourably on Florentino Ameghino's work, and did not fail to note that the latter had misidentified *Phororhacos* as a mammal. Although various types of fossil birds, including penguins and rheas, were described, much of the volume was devoted to phorusrhacids (for which the authors used the name "Stereornithes"). Besides a few already published taxa (including Ameghino's *Phorohacos longissimus*, with the type dentary incorrectly interpreted as a premaxilla) the catalogue included a large number of new ones, many of which based on very fragmentary material and of doubtful validity — a fact Ameghino was quick to point out, although he also was wont to erect new taxa on the basis of rather flimsy evidence. The fact that Moreno & Mercerat's large monograph was published hardly two years after Moreno's first mention of giant birds (from Monte Hermoso) shows that within that short time interval the collectors from the Museo de La Plata (including, for a time, Carlos Ameghino) had been very successful in their quest for avian fossils, mainly in Patagonia.

While Carlos was continuing his explorations in Patagonia, Florentino lost no time in launching a counter-attack against Moreno & Mercerat. At the end of 1891, he published in the *Revista Argentina de Ciencias Naturales* an "enumeration of the fossil birds from the Republic of Argentina" (Ameghino 1891b), which began with a fierce criticism of Moreno & Mercerat's work. According to Ameghino, that work was completely worthless and merely illustrated Moreno's megalomania. Most of the illustrations were of poor quality and the descriptions were "an innumerable succession of mistakes". Ameghino went on to provide a list of fossil birds from Argentina, never missing an opportunity to remind the reader that specimens described by Moreno & Mercerat were part of his "old collection" (which he had sold to the Museo de La Plata) or had been collected by his brother Carlos when he was working for the museum. A large part of the enumeration was devoted to phorusrhacids (which were placed among the ratites), Ameghino claiming that several of the taxa erected by Moreno & Mercerat in fact were junior synonyms of genera and species he had erected in several of his earlier publications. Thus, *Mesembriornis* and *Patagornis* were considered as junior synonyms of "*Phororhacos*", etc. As to the smaller form called *Psilopterus* by Moreno & Mercerat, Ameghino claimed that the name was preoccupied and proposed *Pelecyornis* as a substitute. With this paper, Florentino Ameghino clearly tried both to reassert his position as the leading expert on the fossil birds of Argentina and to demonstrate the utter lack of scientific significance of Moreno & Mercerat's work.

Curiously enough, there was no immediate reaction from Moreno & Mercerat to Ameghino's attack on their bird monograph. In 1895, Florentino Ameghino published one more paper on the topic, viz. a long bilingual (Spanish and French) review of the fossil birds of Patagonia, in which he provided more complete descriptions of the various taxa he had briefly mentioned in his 1891 papers, illustrated with accurate drawings of many specimens (Ameghino 1895). In the introduction to this work, he noted that the first mention of the existence of these giant birds had been made by his brother Carlos in his note of 1st April, 1891 in the *Revista Argentina de Historia Natural* (based on a letter which had been seriously tampered with by Florentino — see above). In fact, as noted above, Moreno had reported giant birds from Monte Hermoso as early as 1888, and had mentioned the discovery of enormous birds in southern Patagonia in a report on the activities of the Museo de La Plata for 1889, dated 1890–1891 (see above). Carlos had indeed found phorusrhacid remains in Patagonia as early as 1887, but, as mentioned above, Florentino had misinterpreted them as mammalian. He went on to claim that he had been the first to give descriptions and an illustration of some of these giant birds in his 1891 paper (Ameghino 1891a), which, according to him, had been published on 1st August, 1891. According to Ameghino's interpretation of publication chronology, Moreno & Mercerat's catalogue had appeared only "toward the end of the month" (August). Therefore, that catalogue not only was of poor scientific value (as Ameghino was pleased to remind his readers), it had also been published *after* Ameghino's own descriptions and names of giant birds, which therefore had priority over the names given by Moreno & Mercerat. This, as Ameghino noted, had already been pointed out in his December, 1891 paper on fossil birds (Ameghino 1891b).

This new paper by Florentino Ameghino eventually prompted a reaction by Mercerat, who in 1897 published a paper on fossil birds in which he thoroughly disagreed with the publication dates provided by Ameghino in his 1895 paper (Mercerat 1897). According to him, the text of the catalogue of fossil birds by Moreno & Mercerat had been published in May 1891, and the plates on 5th August. As to Ameghino's paper, it had been published on 11th August, not 1st August as claimed by its author. Mercerat even claimed that Ameghino had been seen perusing the text and plates of the catalogue at the Museo Argentino de Ciencias Naturales in Buenos Aires a few days before his own paper appeared in print. According to this chronology, Moreno & Mercerat clearly had priority over Ameghino. The dates provided by Mercerat have been accepted by some recent authors (*e.g.*, Alvarenga & Höfling 2003). Independent evidence would be useful to confirm Mercerat's assertions, as there is some evidence of unethical behaviour (including swindling) on his part (Simpson 1984; Vizcaíno *et al.* 2012).

The end of the controversy

The feud about giant fossil birds between Ameghino and Moreno & Mercerat seems to have petered out after 1897. A final paper on Stereornithes by Mercerat (1899), who was soon to stop his palaeontological researches, was essentially a reply to a review of the giant birds from Patagonia by the German palaeontologist Andreae (1899), some parts of which he did not agree with. As to Ameghino, he no longer had much avian material to work on, because in 1896 he had sold most of his fossil bird collection to the British Museum (Natural History). It is a well-known fact that between his resignation/dismissal from the Museo de La Plata in 1888 and his appointment as director of the Museo Argentino de Ciencias Naturales in Buenos Aires, Florentino Ameghino's financial situation was precarious, since he lacked any permanent institutional support and had to pay for his brother Carlos's travels in Patagonia (Simpson 1984; Casinos 2012). His stationery and bookshop business can hardly have been sufficient to cover all expenses, and it was supplemented by the sale of fossils to various European institutions (Casinos 2012). As recounted in detail by Casinos (2012), in 1895 Ameghino wrote to the director of the British Museum (Natural History), William Henry Flower, explaining that he was now concentrating on fossil mammals and was ready to sell his fossil bird collection, in order to support further work in Patagonia, for which he was short of funds. After some discussion about the sum requested by Ameghino (he eventually received 350 £), the collection was purchased by the London museum and arrived there in 1896. A few years later, this resulted in a monograph on the partial skeleton of "*Phororhacos inflatus*" by Andrews (1899). As pointed out by Casinos (2012), ten years later, once he had become director of the Museo Argentino de Ciencias Naturales, Ameghino had cause to regret the sale of his fossil bird collection, when he had to be content with a cast of that skeleton sent by the British Museum (Natural History) as part of an exchange of specimens.

By the end of the 1890s, Moreno and Mercerat had virtually ceased their palaeontological activities (Moreno left the Museo de La Plata in 1906 because he disagreed with its incorporation into the University of La Plata and, as mentioned above, Mercerat had turned to surveying). Florentino Ameghino became director of the Museo Argentino de Ciencias Naturales in Buenos Aires in 1902, which relieved him of the financial difficulties he had had to cope with for many years, and he continued his palaeontological researches until his death in 1911, but fossil birds no longer were one of his main fields of interest (he had become increasingly obsessed with his conceptions about the South American origins of most mammal groups, including man — see Casinos 2012). The giant birds of Patagonia were still occasionally mentioned in some of his general papers and books about the palaeontology of Argentina, but he did not publish any original descriptions after his 1895 monograph. Carlos Ameghino went on collecting in Patagonia until 1903. However, except for a letter to his brother dated 28 February 1893 (Torcelli 1935b: p. 47), in which he mentioned the discovery of an intact skull of *Phororhacos* with its mandible (probably that figured by Ameghino 1895: Fig. 1, as *Phororhacos inflatus*, and later sold to the British Museum), there is no indication that he found especially significant phorusrhacid material during his later expeditions. By that time, phorusrhacids had lost much of their novelty, although these spectacularly large and carnivorous birds have remained popular with both palaeontologists and the general public.

Conclusions

The main stages in the discovery of phorusrhacid birds can be summarised as follows:

Phorusrhacid bones were first discovered by Carlos Ameghino during his first trip to Patagonia, in 1887, but they were misinterpreted as remains of edentulous mammals by Florentino Ameghino.

The first published reports of giant birds from the Tertiary of Argentina were by Moreno in 1888–1889, with notably *Hermosiornis*, from the Pliocene of Monte Hermoso. Moreover, Moreno reported the discovery of giant birds in southern Patagonia as early as 1890–1891.

Carlos Ameghino was the first to realise, in 1890, that *Phorusrhacos* was not a mammal, but a bird, a conclusion that his brother Florentino did not accept until the following year. Florentino Ameghino's initial misinterpretation of phorusrhacids may reflect the fact that he was mainly interested in mammals and, at least at the beginning, had relatively little knowledge of fossil birds.

Whatever its shortcomings, the publication of Moreno & Mercerat's catalogue of fossil birds from Argentina in 1891 was a decisive element in the history of research on phorushacids, not only because it contained descriptions and illustrations of many new taxa, but also because it prompted Florentino Ameghino to quickly publish his own descriptions and interpretations of phorushacids.

In their fierce competition for Patagonian fossils, the Ameghino brothers on one side, Moreno and Mercerat on the other, sometimes resorted to rather dubious practices, one of them being the hurried publication of very preliminary and partial results in journals they completely controlled. Florentino Ameghino went even farther when he tampered with one of his brother's letters before he published it, and when he possibly manipulated publication dates to claim priority. All this is of course reminiscent of the feud between E.D. Cope and O.C. Marsh that was taking place in North America at roughly the same time (Shor 1974). As has been pointed out by many authors, the acrimonious competition between Cope and Marsh mostly had unpleasant aspects, but at least led to the discovery and description of large numbers of hitherto unknown fossil vertebrates. Similarly, the harsh competition between Ameghino and Moreno resulted in considerable progress in our knowledge of the extinct vertebrates of Argentina, including the hitherto unsuspected phorusrhacids. That this resulted in extremely tangled synonymy problems, some of which are still unresolved today, must be considered as one of the unwelcome consequences of this feud between two strong personalities.

Acknowledgments

Special thanks to Federico Agnolin (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires) for providing me with essential documents. I am grateful to Sebastian Apesteguia (Universidad Maimónides, Buenos Aires) for making possible my 2012–visit to Buenos Aires, which resulted in this paper, and to Adrià Casinos (Universitat de Barcelona) for useful discussions about Ameghino and for his comments on the first version of the present paper. Luis Chiappe (Los Angeles) also provided a constructive review.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

The Early Pliocene avifauna of Langebaanweg (South Africa): a review and update

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Abstract — The present paper provides an overview of the famous but still insufficiently known early Pliocene avifauna of the Varswater Formation at Langebaanweg (South Africa). This site produced one of the largest pre-Pleistocene bird bone accumulations worldwide. According to latest estimates, over 35 bird families with at least 90 species have been recorded and most of them mark the earliest family records for the African continent. There is a great diversity of both seabirds such as petrels, prions, and shearwaters (Procellariidae), penguins (Spheniscidae), and terrestrial taxa such as shorebirds (Charadriiformes) and songbirds (Oscines, Passeriformes). Recent identifications of new species shed new light on the palaeoenvironment and palaeoecology of the site and reveal the co-existence of two distinct terrestrial habitats. Honeyguides (Indicatoridae) and several cavity-nesting birds such as parrots (Psittaciformes) and woodpeckers (Picinae) indicate the presence of woodlands. Two species of sandgrouse (Pteroclidae) and at least one species of large ostriches (*Struthio* cf. *asiaticus*) are characteristic of arid to semi-arid landscapes.

Key words: Upper Varswater Formation, palaeoenvironmental reconstructions, palaeoecology, birds

Introduction

The Upper Varswater Formation of Langebaanweg, 110 km NNW of Cape Town, South Africa (32°58′ S, 18°7′ E) (Fig. 1), dates from the earliest Pliocene (5.2 Ma; Roberts *et al.* 2011) and ranks among the richest fossil vertebrate sites in Africa and the world (Werdelin 2010: p. 31). It stands out against other African fossil localities by the vast number of well preserved, though generally disarticulated bird remains (Rich 1980; Hendey 1981), which can be referred to at least 90 species representing both marine and terrestrial taxa, most of which have yet to be described (Tab. 1). The Upper Varswater Formation is also exposed at Duinefontein, *c*. 30 km N of Cape Town and at Ysterplaat Air Force Base, Cape Town, but these sites produced comparatively few and less well-preserved bones of mainly marine taxa (Simpson 1973, 1979b; Olson 1985b) (Fig. 1). Langebaanweg is one of the largest pre-Pleistocene bird bone accumulations worldwide (Rich 1980),

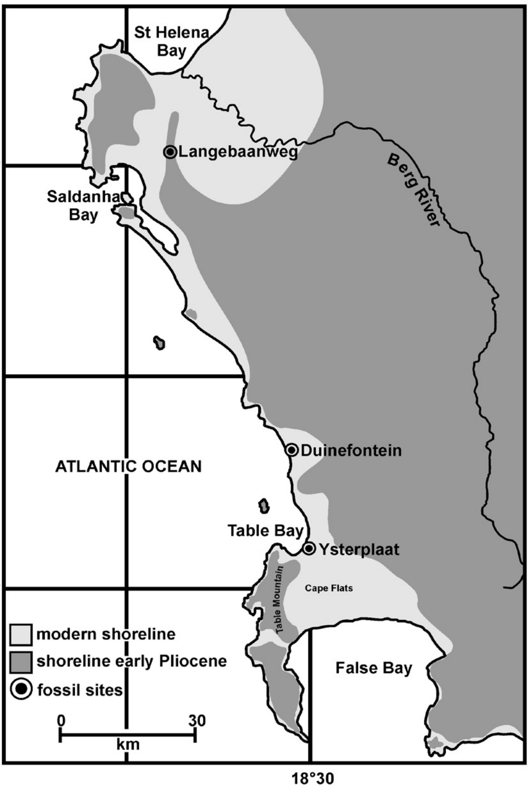

FIGURE 1. Map of Western Cape Province, South Africa showing fossil sites with outcrops of Early Pliocene Upper Varswater Formation, i.e. Langebaanweg, Duinefontein, and Ysterplaat. The modern shoreline is shown in comparison with shoreline at the climax of the Early Pliocene marine transgression with sea-levels *c.* 50 m higher than today resulting in a series of large offshore islands as suitable breeding sites for seabird colonies (after Olson 1983, 1985a).

comparable to other famous fossil localities such as Saint-Gérand-le-Puy (Early Miocene, France; Cheneval 1984; Mourer-Chauviré 1992) or Lee Creek Mine (Early Pliocene, North Carolina; Olson & Rasmussen 2001).

The fossil record of birds from the early Neogene of Africa is still very scarce (*e.g.*, Rich 1974; Harrison 1980; Brodkorb & Mourer-Chauviré 1982; Louchart *et al.* 2005a, b, 2008; Dyke & Walker 2008), and many findings at Langebaanweg represent the earliest evidence of certain taxa in Africa or even in the world, such as hamerkop (Scopidae), painted-snipe (Rostratulidae), honeyguides (Indicatoridae), mousebirds (Coliidae), parrots (Psittaciformes), penguins (Spheniscidae), and true woodpeckers (Picinae) (Simpson 1971; Rich 1980; Olson 1984, 1985d; Rich & Haarhoff 1985; Olson & Eller 1989; Manegold & Louchart 2012). Some bird taxa of the Upper Varswater Formation are today endemic to Africa (hamerkop, mousebirds) or evidently of African origin (honeyguides), but fossil evidence for a bird taxon of probable Eurasian origin (a malarpicine woodpecker) was reported only recently (Manegold & Louchart 2012).

Fossil assemblages close to the Miocene/Pliocene transition are particularly rare in Africa, so that Langebaanweg provides a rare insight into a period that is characterized by global cooling followed by the general spread of woodland savannahs and grasslands at the expense of forests (e.g., Cerling *et al.* 1997; Boisserie & Merceron 2011), by the first evidence for an already diverse fynbos flora in the south western Cape (Scott 1995) as well as by sea level changes and the establishment of the Benguela Upwelling System off the west coast of southern Africa (Hendey 1981; Diester-Haass *et al.* 2004; Heinrich *et al.* 2011; Rommerskirchen *et al.* 2011).

Fossil bearing units of the Upper Varswater Formation at Langebaanweg can be identified by characteristic sediments as tidal mud flats, floodplains, and salt marshes, respectively (Hendey 1981). Hypotheses on Early Pliocene palaeoenvironments at Langebaanweg and adjoining areas were largely based on the composition of the mammal fauna (Hendey 1981) and palynological studies (Scott 1995), but the composition of Langebaanweg's avifauna has also proven to be of great significance for palaeoenvironmental reconstructions (Rich 1980; Olson 1983, 1985a, c, 1994; Haarhoff 1988). The Early Pliocene seabird fauna, for example, is surprisingly diverse and can only be compared to the recent seabird diversity in the Subantarctic realm, which led Olson (1983, 1985a, b) to suppose that the Benguela Upwelling System was richer in nutrients and that its water temperatures were as cold or even colder than today. This would also be in accordance to certain morphological features of the seal *Homiphoca capensis* that were regarded as adaptations to low sea and ambient air temperatures (Hendey 1981: p. 69, but see Govender *et al.* 2012).

In comparison to the seabird fauna, the landbird fauna is less well studied, but seems dominated by two as yet unidentified species of francolins, one of them showing greatest overall similarity to the Crested Francolin, *Dendroperdix* (*Peliperdix*) *sephaena* (Rich 1980; Crowe 1992). The landbird fauna also comprises at least one species of a large ostrich (*Struthio* cf. *asiaticus*, see below), the large stork *Ciconia kahli*, the ibis *Geronticus apelex*, and the small mousebird *Colius hendeyi*, which are all supposed to be characteristic for rather open and dry habitats (Rich 1980; Hendey 1981; Olson 1985c; Rich & Haarhoff 1985; Haarhoff 1988). Evidence for a tree kingfisher *Halcyon* sp. could also indicate open savannah and bushlands, where most of its extant relatives occur (Olson 1994). Olson (1994) also tentatively referred an isolated humerus to the buttonquail *Turnix* cf. *hottentottus*, stating that the fossil could have been as characteristic for short, moist grasslands as its modern relative. Large grazers, such as the large, early hippopotamine (Hippopotaminae sp.), the rhino *Ceratotherium* sp., the gomphothere *Anacus capensis*, the elephantids *Loxodonta cookei* and *Mammuthus subplanifrons*, and the three-toed horse *Eurygnathohippus* cf. *baardi* also suggest the presence of grasslands (Hendey 1981; Franz-Odendaal *et al.* 2003; Sanders 2007; Boisserie & Merceron 2011). C_3 grasses apparently prevailed during the Late Miocene and Early Pliocene at Langebaanweg according to the study of isotopes (Franz-Odendaal *et al.* 2002) and of phytoliths (Rossouw *et al.* 2009), although in other parts of Africa C_4 grasses had already expanded considerably (Cerling *et al.* 1997).

Nevertheless, large browsers such as *Sivatherium* or the okapi-like *Paleotragus* in the fossil record imply the presence of woodlands as well (Hendey 1981, but see Franz-Odendaal & Solounias 2004; Boisserie & Merceron 2011: p. 356). Dental micro- and mesowear texture analyses of bovid teeth further indicate that six out of seven bovid species studied were browsers, not grazers as previously thought, and that *Simatherium demissum* probably was the only obligate grazer among Langebaanweg's bovids (Ungar *et al.* 2007; Stynder 2011). This might indicate that the palaeoenvironment was rather heavily wooded and not dominated by grass (Stynder 2011). Among the micromammals, two species of archaic *Myosorex* shrews were also supposed to be indicative of woodlands based on habitat preferences of their modern relatives (Matthews & Stynder 2011).

The presence of a slow-streaming river with a system of drainage channels and small pools, swamps, and marshes is indicated by fossil evidence for a hippopotamine, as yet unidentified species of ducks, geese, and allies (Anatidae), a few rails (Rallidae), a crane (Gruidae), the Dabchick *Tachybaptus ruficollis* and another species of grebe *Podiceps*? sp., an ibis *Threskiornis* aff. *aethiopicus*, numerous waders (Charadriiformes), among them an extinct species of painted-snipe *Rostratula minator*, a cerylid kingfisher *Ceryle* sp., intermediate in size between the African Pied Kingfisher *Ceryle rudis* and Giant Kingfisher *Megaceryle maxima* (Olson 1994), as well as numerous remains of several frog species (Rich 1980; Hendey 1981; Olson & Eller 1989; Olson 1994; Boisserie & Merceron 2011) and evidence for pollen referable to aquatic and semi aquatic Ranunculaceae (Scott 1995: p. 67).

Hendey (1982) proposed that the decrease in temperature and rainfall during the Miocene-Pliocene transition caused woodland to be increasingly confined to the immediate vicinity of the river whereas grasslands became more and more extensive. Accordingly, the palaeoenvironment at Langebaanweg could be imagined as a large "stream in a rather open savannah" (Olson 1994).

Evidence for one species of Gerbillinae, which are characteristic for deserts and savannahs, indicates open and rather dry habitats in the area, though it is unlikely that such habitats were very extensive (Matthews *et al.* 2007). However, the discovery of a new species of golden mole (Chrysochloridae) even suggests presence of arid, sandy habitats (Asher & Avery 2010). The humerus of the new species †*Chrysochloris arenosa* Asher & Avery, 2010 is very similar to that of its distant modern relative, the Grant's Golden Mole *Emeritalpa granti*, which could indicate similar adaptations for 'sand-swimming' in both of these species: Grant's Golden Mole dwells in large dune fields along the west coast of South Africa as well as in the Namib desert, where the sandy soil immediately collapses behind it while it moves through the sand.

Recent insights into the composition of the bird fauna (Stidham 2006; Manegold 2010a, b,

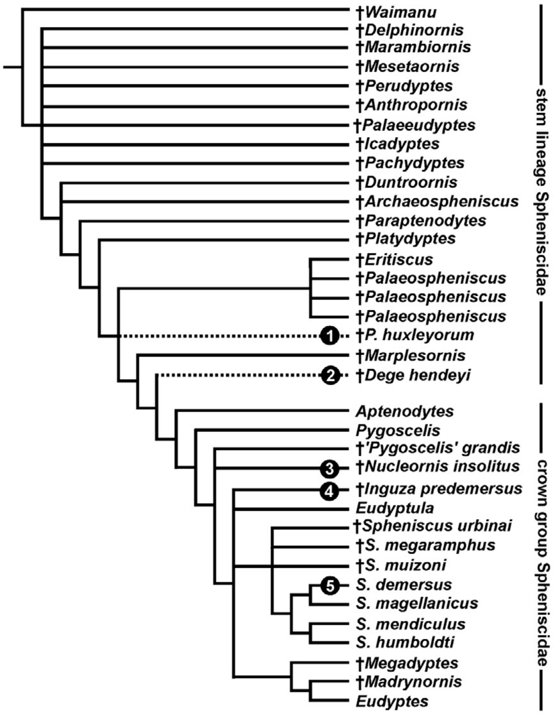

FIGURE 2. Simplified cladogram of stem-lineage and crown group penguins after Ksepka & Clarke (2010) and Ksepka & Thomas (2012). Note that †*Palaeospheniscus*? *huxleyorum* was not included in these phylogenetic analyses, but tentatively assigned by Ksepka & Clarke (2010) to a clade that also comprises other species of †*Palaeospheniscus* as well as †*Eritiscus*, †*Dege hendeyi*, †*Marplesornis*, and crown group Spheniscidae. The systematic position of †*Dege hendeyi* outside crown group Spheniscidae is based on one plesiomorphic character and regarded as being only tentative (Ksepka & Clarke 2010). Extinct species are indicated by a dagger (†), numbers (1–5) refer to the number of independent colonization events that occured by the late Miocene (1–4) and during the Plio-Pleistocene (5), respectively.

2013; Ksepka & Thomas 2012; Manegold & Louchart 2012; Louchart unpubl. data) also indicate that the palaeoenvironments were diverse and mosaic-like, and that the biogeographical history of certain taxa is more complex than previously thought. These findings are summarized and discussed in the following sections.

The Marine Avifauna

Penguins were the first fossil birds described from Langebaanweg by George Gaylord Simpson, who distinguished and named the four species *Dege hendeyi*, *Inguza predemersus*, *Nucleornis insolitus*, and *Palaeospheniscus*? *huxleyorum* (Simpson 1971, 1973, 1979a, b). All these species differ markedly in size, with *N. insolitus* being comparable in size to the largest modern penguins (*Aptenodytes*) and with *I. predemersus* being slightly smaller than the extant African Penguin (*Spheniscus demersus*) (Simpson 1971, 1973, 1979a, b; Olson 1985b). Although Simpson considered these species to be closely related, he nevertheless described them as four extinct genera. *N. insolitus*, and *P. huxleyorum* have been originally described from the Upper Varswater Formation exposed at Duinefontein and Ysterplaat, respectively, but all four species were subsequently recorded for Langebaanweg (Olson 1985b) with breeding evidence for *I. predemersus* at least (Ksepka & Thomas 2012).

Two recent cladistic analyses found no support for monophyletic Varswater penguins or for their close relationship to *S. demersus*, but indicate that probably neither *D. hendeyi* nor *P. huxleyorum* were part of crown group Spheniscidae (Ksepka & Clarke 2010: pp. 26–29), and that *Aptenodytes, Pygoscelis,* and *N. insolitus* are successive sister taxa to all the remaining crown group penguins, though the phylogenetic relationships of the aforementioned taxa to *'Pygoscelis' grandis* Walsh & Suarez, 2006 are still uncertain (Ksepka & Thomas 2012) (Fig. 2). *Inguza predemersus* turned out to be part of a clade that also comprises the extant genera *Eudyptes, Eudyptula,* and *Spheniscus* (Ksepka & Thomas 2012) (Fig. 2). Based on these hypotheses it seems evident that four penguin lineages colonized Southern Africa independently by the Late Miocene, whereas the ancestor of *S. demersus* arrived later sometime during the Plio-Pleistocene (Ksepka & Clarke 2010; Ksepka & Thomas 2012; Thomas & Ksepka 2013).

Aside from the four species of penguins, the marine avifauna of the Upper Varswater Formation comprises three species of cormorants (Phalacrocoracidae), a small booby (Sulidae; also known from Duinefontein; Olson 1985b), two species each of gulls and terns, and eight species of tubenoses (Procellariiformes) (Olson 1983; 1985a). However, some of the cormorants, gulls, and terns might also have been associated with fresh water habitats (Olson 1983).

Only tubenoses have been adequately described. Remains of juveniles indicate that an albatross, a storm-petrel, and at least one, but possibly three prion species bred close to the fossil site (Olson 1985a). Such a diverse marine avifauna is striking and comparable only to the present situation on certain Subantarctic islands (Olson 1983). Not a single species of tubenoses breeds on any African continental island today (Olson 1983), and only the African Penguin breeds along the Southern African coast with its small offshore islands, alongside with Cape Gannet (*Morus capensis*) and three cormorant species (*Phalacrocorax capensis*, *Miocarbo coronatus*, and *M. neglectus*) (Harrison *et al.* 1997).

One explanation for the past diversity in seabirds is the greater number of potential nest sites for these taxa at that time. At the beginning of the Pliocene, sea levels were about 50 m above present-day conditions turning the West Coast Peninsula as well as Table Mountain and other peaks of the Cape Peninsula into large islands and thus providing suitable breeding sites for marine birds (Olson 1983; Ksepka & Thomas 2012).

Furthermore, it was assumed that the past seabird diversity provides strong evidence that the Benguela Upwelling System off the southwest coast of Africa was both colder and richer in nutrients than today (Olson 1983: p. 400). Recent estimates of past sea surface and subsurface temperatures indicate, however, that the Benguela Current was in fact much warmer than today during a period between 6.5 and 5 Ma, because the exchange between Antarctic deep water mass and North Atlantic Deep Water was reduced and consequently the heat export from the South Atlantic decreased (Rommerskirchen *et al.* 2011). Water temperatures remained warmer than today – although began decreasing at the beginning of the Pliocene (Diester-Haass *et al.* 2002; Rommerskirchen *et al.* 2011). Marine productivity was nevertheless high and kept rising during this period (Rommerskirchen *et al.* 2011), and was obviously sufficient for sustaining large seabird colonies.

The Terrestrial Avifauna

Woodland species

Recent studies of several evidently woodland dwelling bird taxa such as a true woodpeckers (Picinae, Picidae), honeyguides (Indicatoridae), parrots (Psittacoidea), and several species of songbirds (Oscines, Passeriformes) strongly support current hypotheses that woodlands were more extensive at Langebaanweg than previously thought.

The recently described (Manegold & Louchart 2012) true woodpecker from Langebaanweg, *Australopicus nelsonmandelai* (Fig. 3A–F) was comparable in size with the Greater Spotted, *Dendrocopos major*, or Red-bellied Woodpecker, *Melanerpes carolinus*. A phylogenetic analysis of 50 morphological characters shows that the fossil species is not closely related to any of the extant African woodpecker taxa such as *Campethera*, *Geocolaptes* or *Dendropicos*, but to a clade that comprises woodpeckers that are primarily characteristic of dense woodlands or forests in the tropics of the Old and New World, such as *Celeus* and *Dryocopus* (Fig. 4). Furthermore, the tarsometatarsus of the fossil woodpecker is short and stout (Fig. 3D–E), which is characteristic of the more arboreal woodpecker species, whereas more terrestrial woodpeckers such as *Campethera* or *Geocolaptes* have more elongated tarsometatarsi. Thus, the fossil woodpecker represents a previously unknown lineage of Eurasian origin with a strong association to woodlands. *Australopicus* probably became separated from its relatives in Eurasia during the period of general expansion of grasslands at the expense of forests and woodlands in the Late Miocene (Manegold & Louchart 2012) that also led to the separation of other picine lineages (Fuchs *et al.* 2007), *Sasia*-piculets (Fuchs *et al.* 2006) and many other 'forest relicts' (Louchart 2003; Louchart *et al.* 2005a, 2008).

Extant honeyguides (Indicatoridae) also inhabit forests and various kinds of woodland, but avoid open savannah. Thus, evidence for Indicatoridae in the fossil record clearly indicates presence of wooded areas at or close to the fossil site. Langebaanweg honeyguides were first noticed by Olson (1985d), but only recently

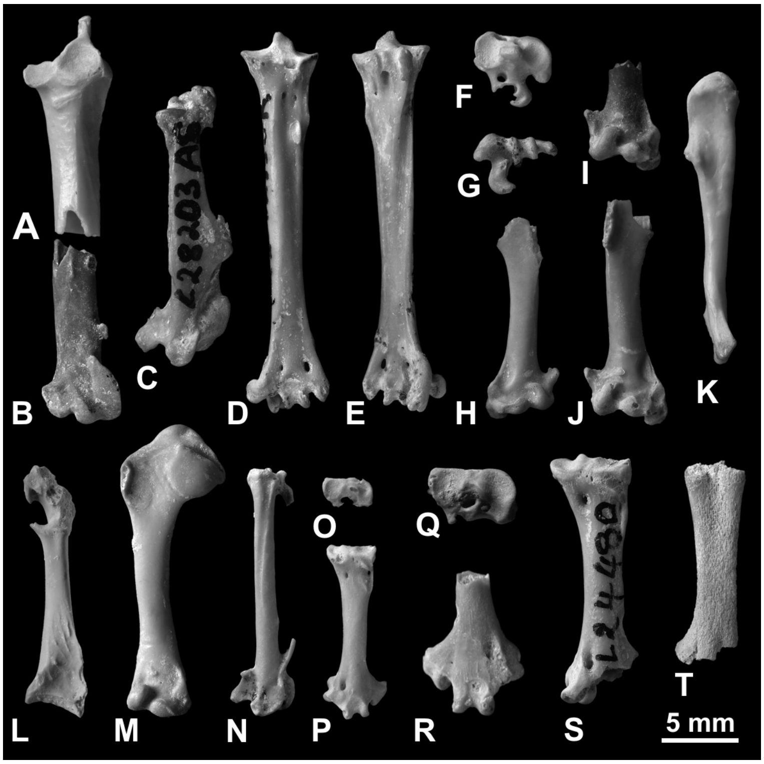

FIGURE 3. Recently described bird fossils from the Upper Varswater Formation, Langebaanweg (Early Pliocene, South Africa). (**A–F**) *Australopicus nelsonmandelai* (Picinae, Picidae): (**A**) right proximal ulna SAM PQ-L70284 in cranial view; (**B**) right distal ulna SAM PQ-L28428V in ventral view; (**C**) right carpometacarpus SAM PQ-L28203AS in dorsal view; (**D–E, G**) right tarsometatarsus L25293GR (holotype) in dorsal (**D**), plantar (**E**), and distal view (**G**); (**F**) right tarsometatarsus SAM PQ-L28199EE in proximal view. (**H–J**) Humeri of medium sized (**H**) and large (**I–J**) swallow species (Hirundinidae, Passeriformes) in cranial view: (**H**) left distal humerus SAM PQ-L 70289; (**I**) right distal humerus SAM PQ-L 70406; (**J**) right distal humerus SAM−PQ L 70288. (**K**) Left coracoid SAM PQ-L 20733N2 of a nightjar (Caprimulgidae) in medial view. (**L-P**) Lovebird *Agapornis attenboroughi* (Agapornithinae, Psittacoidea): (L) right coracoid SAM PQ-L704543 in dorsal view; (**M**) right humerus SAM PQ-L70432 in cranial view; (**N**) right carpometacarpus SAM PQ-L70451 in dorsal view; (**O–P**) right tarsometatarsus SAM-PQ-L70448 in proximal (**O**) and dorsal view (P). (**Q–T**) Psittacine parrot *Khwenena leopoldinae*: (**Q, S**) Right tarsometatarsus SAM PQ-L24480 in proximal (**Q**) and dorsal view (**S**); (**R**) left distal tarsometatarsus SAM PQ-L70432 in dorsal view; (**T**) left tarsometatarsus SAM PQ-L70441 of nestling parrot in dorsal view (Manegold 2010a, b, 2013; Manegold & Louchart 2012).

discovered material shows that in fact two species can be distinguished, which are tentatively referable to the genus *Indicator*. Both species were very small, but comparable to the tiny Least Honeyguide *I. exilis* and the only slightly larger Lesser Honeyguide *I. minor*, respectively. Although the biology and ecology of modern Indicatoridae are still insufficiently known, it seems evident that the last common ancestor of Indicatoridae was a brood parasite, and that the stem species of *Indicator* already had a strong preference for cavity nesting foster species, especially barbets (Short & Horne 2002). Thus, the fossil honeyguides could have benefited from the excavating activities of *Australopicus*. Surprisingly, barbets are as yet not evident in the fossil record of Langebaanweg, and probable foster species for the two indicatorids remain to be identified. The co-occurrence of two species of *Indicator* and the honey badger *Mellivora benfieldi* at Langebaanweg (Hendey 1978) is worth mentioning, although the alleged symbiotic relationship between the extant Greater Honeyguide *I. indicator* and Honey Badger *Mellivora capensis* is only a myth (Dean *et al.* 1990).

Previous studies supposed that two or three parrot species can be distinguished in the fossil record of Langebaanweg (Rich 1980; Stidham

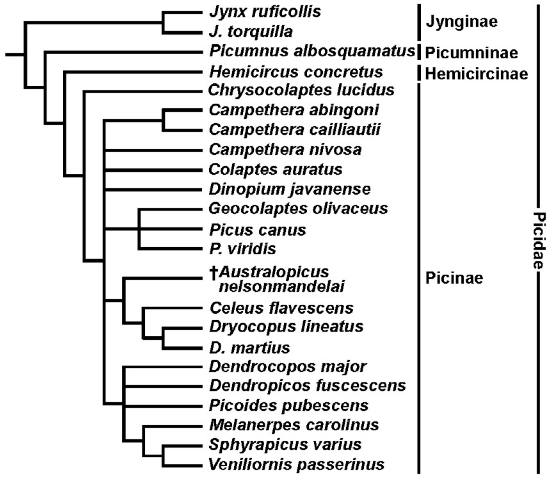

FIGURE 4. Simplified cladogram of woodpeckers (Picidae) based on a cladistic analysis of 50 morphological characters. *Australopicus nelsonmandelai* is sister taxon to a clade that comprises malarpicine woodpeckers primarily characteristic for tropical and subtropical forests (Manegold & Louchart 2012).

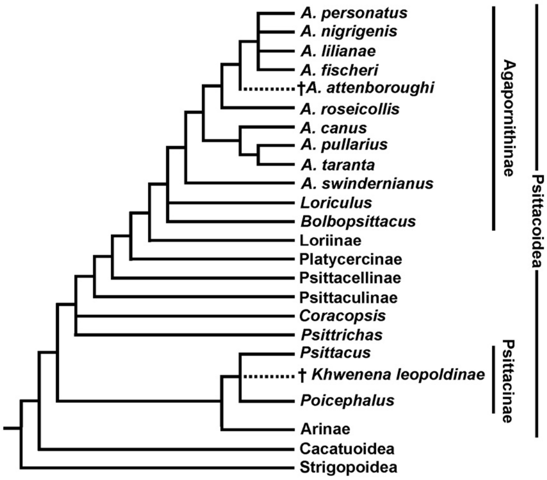

FIGURE 5. Simplified cladogram of parrots (Psittaciformes) after Joseph *et al*. (2012) indicating the phylogenetic position of the newly described lovebird and psittacine parrot from the Upper Varswater Formation, Langebaanweg (Manegold 2013). Phylogenetic position of *A. swindernianus* is only tentative and awaits further study.

2006). Stidham (2006) identified a species of lovebird (*Agapornis* sp.) and two other parrot species of uncertain affinities. Based on additional specimens (Fig. 3L–P), a new species of lovebird, *A. attenboroughi*, was described (Manegold 2013), which is comparable in size to the small species of the *A. personatus*-group and which probably is a stem lineage representative of this taxon (Fig. 5). Except for the Black-collared Lovebird *A. swindernianus*, all lovebirds avoid primary forest, but prefer different kinds of woodlands (Moreau 1948), and such habitat preferences might also apply to the fossil species. Although seeds of C_4 grasses play an important role in the diet of *A. roseicollis* and *A. nigrigenis* (Warburton & Perrin 2005; Ndithia & Perrin 2006) it would be premature to take the new species of lovebird as an indicator of C_4 grasslands.

Khwenena leopoldinae is the second, recently described species of fossil parrot from Langebaanweg (Fig. 3Q–T; Manegold 2013). It is of the size of the extant Ring-necked Parakeet *Psittacula krameri*, but is more closely related to the African Grey Parrot *Psittacus erithacus* and the genus *Poicephalus* (Fig. 4). Similarly to extant *Poicephalus* species, *K. leopoldinae* probably preferred woodlands with tall trees bearing suitable nest cavities – often provided by the Amethyst Starling *Cinnyricinclus leucogaster* and two additional species of Sturnidae, which are among the most common songbirds in the fossil record of Langebaanweg. *Cinnyricinclus leucogaster* is no longer part of the Western Cape avifauna, but common in different kinds of African woodlands, where it breeds in tree cavities like most sturnids. It seems likely that this breeding behaviour also applied for all three fossil starling species, although building of exposed globular or domed nests evolved independently in several, only distantly related lineages of Sturnidae (Lovette & Rubenstein 2007; Craig & Feare 2009).

A fragmentary tarsometatarsus of a tiny songbird shows all the features characteristic for the closely related Old World warblers and babblers (Sylviidae and Timaliidae *sensu* Gelang *et al.* 2009). Extant Sylviidae with African and Eurasian distribution are regarded as typical for drier habitats, but Timaliidae are in general more characteristic for different types of forest, woodland, and thickets (Gelang *et al.* 2009).

Non-marine aquatic and semi-aquatic birds

About one third of all bird species were typical for freshwater habitats. They comprise approximately 10–15% of all bird remains known from Langebaanweg and include predominantly members of the Charadriidae (ca. 15 species), and Anatidae (at least 4 species mainly by size groups). The latter family includes a large species, which probably represents the swan genus *Afrocygnus* Louchart *et al*., 2005b (Louchart unpubl. data), based on the morphology of the humerus (Louchart *et al.* 2005b). This extinct endemic African swan was hitherto known from northern Africa only, and today swans are absent from sub-Saharan Africa (Louchart *et al.* 2005b).

Species of dry open grasslands, savannah and/or arid habitats

Taxa characteristic for open habitats are the already mentioned ibis *Geronticus apelex* and stork *Ciconia kahli* (Olson 1985c; Haarhoff 1988), but also the as yet not described species of sandgrouse (Pteroclidae), bustards (Otididae), and thick-knees (Burhinidae) (Rich 1980; Louchart unpubl. data). Presence of fossil sandgrouse (Pteroclidae) and bustards (Otididae) at Langebaanweg was already mentioned by Rich (1980). More recent studies show that at least two species of *Pterocles* can be distinguished, which makes them the earliest record for crown group sandgrouse in the world (Louchart unpubl. data). Both *Pterocles* species differ in size, with the larger one being comparable to the extant Crowned Sandgrouse, *P. coronatus,* and the smaller species being even smaller than the modern Namaqua Sandgrouse, *P. namaqua* (Louchart unpubl. data). Today sandgrouse are among the most characteristic bird species of arid and semi-arid regions throughout Africa and Asia. Such preference for arid conditions might have been already present in stem-lineage representatives of modern Pteroclidae from the Palaeogene and Early Miocene of France (Mourer-Chauviré 1992). A thick-knee and two species of bustards, one of them as large as the huge Denham's Bustard, *Ardeotis denhami*, but the second smaller and of the size of extant *Afrotis* bustards (Louchart unpubl. data), are represented by a handful of fossil remains each. The bustards in particular (less clearly so the thick-knee as some today favour rather humid habitats) also indicate arid to semi-arid environments, i.e. deserts to semi-wooded savannah, at or quite close to Langebaanweg five million years ago (Louchart unpubl. data).

Ostriches are among the most characteristic bird species of open habitats. The extant *Struthio camelus*, with four living and one recently extinct subspecies, prefers open short-grass plains and semi-deserts, and avoids areas with tall grass as well as dense woodlands, although open mopane woodland seems to be suitable for *S. camelus australis* (Brown *et al.* 1982: p. 33). Fossil ostriches from SE Europe and the Middle East are characteristic elements of the *Hipparion*-fauna (Boev & Spassov 2009). The presence of fossil ostriches in the Langebaanweg Varswater Formation has long been known (Rich 1980; Hendey 1982: p. 70) but no study of this material has been undertaken before.

Thirteen among 17 leg bone fragments proved measurable in some dimensions except for the length of femur, tibiotarsus and tarsometatarsus as these bones are preserved only as proximal, distal or shaft fragments, which makes straightforward body size estimations impossible. However, all available measurement values of these bones are substantially higher than those of any *S. camelus*, indicating a larger body size. The tibiotarsal shaft depth is 107.1%–127.1% and the distal end measurements 105.6% (width) and 116.6% (lateral depth) of the mean values for extant ostriches. The values for the fibular shaft are 105% (width) and 122% (diameter), and those of the tarsometatarsal shaft about 114% (depth) and 123% (width) of the mean for *S. camelus*. These ranges (especially in shaft depth) exceed the adult variation between the extant ostrich subspecies (SD = 4.3%) and thus call for an explanation. Bone texture is not obviously unfinished in any of the five Langebaanweg tibiotarsi, which makes age-related variation unlikely to be responsible for the observed size ranges. The shaft depth reveals an indication of bimodality with two specimens measuring exactly 35.6 mm and two about 32 mm, which suggests either two (sub)species or sexual dimorphism. Except for size there is no evidence for two species and both larger and smaller specimens share the lateral trochlear crest that is more oblique than in Pleistocene and extant ostriches. Therefore, the observed size differences seem to be better accounted for by sexual dimorphism. In the extant ostriches the tibiotarsus (as well as femur and tarsometatarsus) tends to be wider and/or deeper in females (Elzanowski *et al.*, unpubl. data). In addition to the four discussed tibiotarsi, the smallest Langebaanweg tibiotarsus (SAM PQ-L50093A) has the shaft depth (30 mm, 107.1 % of the average for *S. camelus*) as in *S. barbarus* Arambourg, 1979 from the Villafranchian of North Africa thus leaving a possibility of a second, smaller ostrich (sub)species being represented at Langebaanweg.

In contrast to the other leg bones, the Langebaanweg phalanges are essentially of the same length as those of the largest *S. camelus*. Since the Langebaanweg ostriches were larger, their phalanges were shorter relative to body size than they are in the extant ostriches. The Langebaanweg III/1 phalanges are similar in proportions to those of *S. camelus* and differ from the prevailing type of Pleistocene phalanges that are much less waisted and thus more cylindrical or rod-shaped than the Langebaanweg and extant *S. camelus* specimens.

In both size and shape of the phalanges as well as the body size (as approximated form the measurements of other leg bones), the large Langebaanweg ostriches are comparable to *S. asiaticus* as described from the latest Pliocene of North Africa (Morocco) by Mourer-Chauviré & Geraads (2008). *Struthio asiaticus* is about 20 % larger than large *S. camelus* specimens and so are the shaft measurements of larger tibiotarsi, fibula, and tarsometatarsus from Langebaanweg. Growing larger (especially taller) is a common defence adaptation that is easiest to achieve developmentally. The Early Pliocene fauna of Langebaanweg abounded in large mammalian predators such as sabre-toothed felids, hyaenas, and giant civets (Hendey 1982; Werdelin 2006). However, the size dynamics of fossil ostriches needs to be discussed in a broader geographic and stratigraphic context. While in the post-Pliocene southern Africa the ostriches consistently decrease in size, even larger ostriches appeared in the Early Pleistocene of Kenya (Leakey 1965) and elsewhere. This suggests a role of local ecological factors that need to be analysed and compared against a paleogeographic background.

A guild of aerial insect hunters

Aerial insect hunters such as nightjars (Caprimulgidae) (Fig. 3K), swifts (Apodidae) and swallows (Hirundinidae) (Fig. 3H–J) are rarely described from pre-Pleistocene fossil localities, and evidence for all three taxa at Langebaanweg represents their first occurrence in the fossil record of Africa. Unfortunately, their use for palaeoenvironmental reconstructions is only limited. Habitat preferences of the Langebaanweg's nightjar cannot be deduced from the isolated coracoid referred to this species (Manegold 2010a), and although open woodlands might have been the ancestral habitat of Caprimulgidae, few more forest adapted nightjars occur in Central Africa (*Caprimulgus batesi*, *Veles binotatus*) and Madagascar (*Gactornis enarratus*) (Cleere & Nurney 1998, Han *et al.* 2010). The swift, known from a single humerus only and with strong resemblance to extant Alpine Swift *Tachymarptis melba* and Mottled Swift *T. aequatorialis* (Louchart unpubl. data) probably exploited food resources at Langebaanweg, but might have relied on the presence of rock crevices for nest building like most of the extant Apodidae (Chantler 1999). The rocky escarpments of the Piketberg massif, 50 km E of Langebaanweg, were already proposed as possible breeding site for the putative cliff nesting ibis *Geronticus apelex* (Olson 1985c), but might also have been used by swifts. The same might also apply for the two unidentified species of Hirundinidae (Manegold 2010b), because many extant swallows and martins breed in rock crevices or attach their mud nests to rock surfaces, but based on the limited fossil material it cannot be ruled out that the fossils retained the ancestral behaviour of Hirundinidae of excavating burrows in riverbanks (Winkler & Sheldon 1993; Manegold 2010b).

Discussion

A palaeoecological analysis of the highly diverse fossil avifauna indicates that the Early Pliocene Langebaanweg area was characterized by a mosaic of many fairly diversified habitats ranging from almost arid regions and open grasslands to floodplains, marshes, and woodlands. Evidence for typical inhabitants of tropical and subtropical forests such as pittas (Pittidae), broadbills (Eurylaimidae) and trogons (Trogonidae) is missing. This is in line with the lack of other key indicators of tropical or subtropical climate such as crocodiles (Crocodylia) (HENDEY 1973), and the general temperate character of the rest of the fauna and flora. Other groups of primarily forest taxa with a few secondarily dwellers of well-wooded savannah such as turacos (Musophagidae) and hornbills (Bucerotidae) are also missing. Apparently, precipitation at Langebaanweg was too low during the early Pliocene for sustaining forests that are suitable for these bird species. Surprisingly, there is still no evidence of barbets (Ramphastidae) and cuckoos (Cuculidae), which today are found in various habitats throughout sub-Saharan Africa. Even more remarkable is the absence of many aquatic taxa such as anhingas (Anhingidae), flamingos (Phoenicopteridae), herons (Ardeidae), or pelicans (Pelecanidae), which are known from the Miocene and Pliocene of sub-Saharan Africa (OLSON 1985c; LOUCHART *et al.* 2008). None of these taxa are strongly linked to tropical or subtropical climates, and it is hard to believe that they did not reach southern Africa in the early Pliocene. On the other hand, there is no obvious taphonomic phenomenon that might explain their absence from the fossil record. OLSON & ELLER (1989) supposed that the absence of these taxa could be explained by too small size and ephemeral nature of suitable aquatic habitats. However, the record of a hippopotamine, numerous anatids, charadriiforms, and rallids strongly suggests that fresh water habitats were present in the early Pliocene Langebaanweg area. The absence of flamingos alone (but not other missing groups) could be explained by the absence of alkaline or saline lakes that these birds require for feeding, and brackish lagoons or estuaries for their breeding colonies.

Birds continue to provide unique cues to the reconstruction of the Early Pliocene environment and local climate at Langebaanweg. Ongoing and future studies of certain bird groups will add more lines of evidence and help refine the present interpretations.

Acknowledgements

We thank S. TRÄNKNER (Senckenberg Forschungsinstitut Frankfurt) for taking the photographs as well as G. AVERY, R. GOVENDER, D. HAMERTON, T. MATTHEWS, R. SMITH, and K. VAN WILLINGH (Iziko South African Museum Cape Town), P. HAARHOFF (West Coast Fossil Park), and D. STYNDER (University of Cape Town) for allowing access to collections and for sharing information on Langebaanweg's faunas, taphonomy, and geology. We also thank T. CASSIDY and G. DAVIES (Ditsong Museum, Pretoria), G. LENGLET (Institut royal des Sciences naturelles de Belgique, Brussels), Z. BOCHEŃSKI (Instytut Systematyki i Ewolucji Zwierząt, Kraków), R. VAN DEN ELZEN and S. RICK (Museum Alexander Koenig Bonn), C. LEFÈVRE (Muséum national d'Histoire naturelle Paris), P. ECKHOFF, J. FIEBIG, and S. FRAHNERT (Museum für Naturkunde Berlin), M. LOUETTE (Musée royal de l'Afrique centrale Tervuren), L. MORUPEDI, R. NUTTALL, and D. DE SWARDT (National Museum, Bloemfontein, South Africa), J. COOPER and R. PRŶS-JONES (Natural History Museum, Tring), G. MAYR (Senckenberg Forschungsinstitut Frankfurt), as well as D. CHURCHES, P. HORTON, and M. PENCK (South Australian Museum, Adelaide) for allowing access to extant specimens and loans. Reviews by V. DE PIETRI and H. MEIJER helped to improve an earlier version of this paper. AE thanks C. MOURER-CHAUVIRÉ (CNRS, Lyon) for providing missing literature. AM thanks M. KOOPMAN (Niven Library, Percy FitzPatrick Institute, University of Cape Town) for forwarding important references. AE was supported by Poland's Ministry of Science and Higher Education grant N N303 549339. AL and AM were supported by postdoctoral grant of the South African NRF/African Origins Platform/West Coast Fossil Park Initiative, AL by NSF grant 0321893 HOMINID-RHOI, and Synthesys grant GB-TAF-1341, and AM by German Academy of Sciences Leopoldina Fellowship Programme grants BMBF-LPD 9901/8-183, LPDR-2009-1, and DFG grant MA 4809/1-1.

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Appendix

TABLE 1. Bird taxa of the Upper Varswater Formation at Langebaanweg, earliest Pliocene of South Africa, and their likely preferential habitat types. As far as possible, the number of specimens (n) followed by the estimated minimum number of individuals (mni) is given for each species. Only rough estimates are given for certain taxa such as ducks, geese and swans (Anatidae), cormorants (Phalacrocoracidae), and birds of prey (Accipitridae). No hypotheses on the probable habitat types of the fossil representatives of birds of prey, doves and pigeons (Columbidae), owls (Strigidae), swallows (Hirundinidae), and swifts (Apodidae) are given because of their diverse habitat preferences.

Taxon	Abundance n/mni	Habitat type	References
Struthioniformes, Struthionidae			
Struthio cf. *asiaticus* Milne-Edwards, 1871	24/ <5	dry open grasslands, savannah and/or arid habitats, fynbos, marginally open woodlands	Rich (1980); Elzanowski *et al.* (unpubl. data)
possibly another *Struthio* sp.	1/1		
Galliformes, Phasianidae			
Francolinus sp.	– / > 500	open savannah and bushlands	Rich (1980);Crowe (1992)
Dendroperdix aff. *sephaena* (A. Smith, 1836)			
cf. *Coturnix* sp.	Rare	open grasslands, fynbos	Rich (1980); Hendey (1981)
Anseriformes, Anatidae			
Anatidae gen. et sp. indet., sp. A, small	– / > 40	various fresh water habitats	Rich (1980, unpubl. data); Louchart, (unpubl. data)
Anatidae gen. et sp. indet., sp. B, small/ medium			
Anatidae gen. et sp. indet., sp. C, medium/ large			
cf. *Afrocygnus* sp.			
Sphenisciformes, Spheniscidae			
Inguza predemersus (Simpson, 1971)	7/2	marine	Simpson (1971, 1973, 1979a, b); Olson (1983, 1985b); Ksepka & Thomas (2012)
Dege hendeyi Simpson, 1979a	14/3		
Nucleornis insolitus Simpson, 1979b	2/2		
Palaeospheniscus? *huxleyorum* Simpson, 1973	Few		
Procellariiformes, Diomedeidae			
Diomedea sp.	1/1	marine	Olson (1985a)
Procellariiformes, Oceanitidae (Oceanitinae)			
Oceanites zaloscarthmus Olson, 1985a	176/23	marine	Olson (1985a)
Procellariiformes, Procellariidae			
Pachyptila salax Olson, 1985a	203/20	marine	Olson (1985a)
Pachyptila sp. B	2/2		
Pachyptila sp. C	4/3		
Puffinus sp.	3/3		
Procellariidae gen. et sp. indet.	1/1		

Taxon	Abundance n/mni	Habitat type	References
Procellariiformes, Pelecanoididae			
Pelecanoides cymatotrypetes Olson, 1985a	3/2	marine	Olson (1985a)
Podicipediformes, Podicipedidae			
Podiceps? sp.	3/1	various fresh water habitats	Olson (1994)
Tachybaptus ruficollis (Pallas, 1764)	56/16	various fresh water habitats	Olson (1994)
Ciconiiformes, Ciconiidae			
Ciconia kahli Haarhoff, 1988	30/2	open savannah and bushlands, fynbos?	Haarhoff (1988)
Ciconiiformes, Threskiornithidae			
Geronticus apelex Olson, 1985c	15/2	grasslands, open savannah and bushlands	Olson (1985c)
Threskiornis aff. *aethiopicus* (Latham, 1790)	1/1	various fresh water habitats, grasslands	Olson (1985c)
Pelecaniformes, Scopidae			
Scopus xenopus Olson, 1984	2/2	various fresh water habitats	Olson (1984)
Pelecaniformes, Sulidae			
Sula sp.	4/4	marine	Olson (1983, 1985b)
Pelecaniformes, Phalacrocoracidae			
Phalacrocorax sp. A, small	– / >25	marine?	Olson (1983, 1985b)
Phalacrocorax sp. B, medium sized			
Phalacrocorax sp. C, medium sized			
Falconiformes, Falconidae			
Falconidae gen. et sp. indet.	– / ca. 5	–	Rich (1980)
Accipitriformes, Accipitridae		–	
Accipitridae, Aegypiinae gen. et. sp. indet., sp. A	– /10	–	Rich (1980)
Accipitridae gen. et. sp. indet., sp. B			
Accipitridae gen. et. sp. indet., sp. C			
Accipitridae gen. et. sp. indet., sp. D			
Accipitridae gen. et. sp. indet., sp. E			
Gruiformes, Otitidae			
Otitidae gen. et sp. indet., sp. A, small	16/ < 5	dry open grasslands, scrubland, fynbos, savannah and/or arid habitats, marginally open woodlands	Rich (1980); Louchart (unpubl. data)
Otitidae gen. et sp. indet., sp. B, larger			
Gruiformes, Rallidae			
several species; ranging from crake to *Porphyrio* size	– / <10	various fresh water habitats	Rich (1980); Olson (unpubl. data)
Gruiformes, Gruidae			
Gruidae gen et. sp. indet.	2/2	wetlands, open grasslands	Rich (1980); Louchart (unpubl. data)

Taxon	Abundance n/mni	Habitat type	References
Charadriiformes, Turnicidae			
Turnix cf. *hottentottus* Temminck, 1815	1/1	short, moist grasslands	Olson (1994)
Charadriiformes, Burhinidae			
Burhinidae gen. et sp. indet.		dry open grasslands, fynbos, savannah and/or arid habitats	Rich (1980); Olson (unpubl. data), Louchart (unpubl. data.)
Charadriiformes, Recurvirostridae			
Himantopus sp.		wetlands	Rich (1980); Olson (unpubl. data)
Charadriiformes, Scolopacidae			
aff. *Gallinago* sp.		open wetlands, swamps, marshes	Rich (1980); Olson (unpubl. data)
Charadriiformes, Charadriidae			
Charadrius sp. A, similar in size to *C. pecuarius*	mni > 50	open wetlands, grasslands, seashores	Rich (1980); Olson (unpubl. data)
Charadrius sp. B, similar in size to *Pluvialis apricaria*			
Charadrius sp. C, smallest of all fossil *Charadrius*			
Charadrius sp. D, of the size of *C. marginatus*			
Charadrius sp. E, of the size of *C. placidus*			
Charadrius sp. F, of the size of *C. leschenaultii*			
Charadrius sp. H, of the size of *C. tricollaris*			
Charadrius sp. I, of the size of *C. mongolus*			
cf. *Vanellus senegallus* (Linneaus, 1766)			
cf. *Vanellus crassirostris* (Hartlaub, 1855)			
cf. *Vanellus albiceps* Gould, 1834			
cf. *Vanellus armatus* (Burchell, 1822)			
Charadriidae gen. et sp. indet., similar to *Vanellus* (*Stephanibyx*) spp.			
Charadriidae gen. et sp. indet., similar in size to *P. apricaria* or larger			
Charadriiformes, Rostratulidae			
Rostratula minator Olson & Eller, 1989	16/4	open wetlands, swamps, marshes	Olson & Eller (1989)
Charadriiformes, Laridae			
Larus sp. A, medium sized	Rare	marine?	Olson (1983, 1985b)
Larus sp. B, large sp.	1/1		
Sterna sp. A, medium sized	Few		
Sterna sp. B, larger	Few		

Taxon	Abundance n/mni	Habitat type	References
Columbiformes, Pteroclidae			
Pterocles sp. A *Pterocles* sp. B	– / < 5	grasslands, open arid/ semiarid habitats	Rich (1980); Louchart (unpubl. data)
Columbiformes, Columbidae			
Columbidae gen. et sp. indet., sp. A Columbidae gen. et sp. indet., sp. B	– /10	–	Rich (1980)
Psittaciformes, Psittacoidea			
Agapornis attenboroughi Manegold, 2013	30/4	woodlands	Rich (1980, unpubl. data); Stidham (2006); Manegold (2013),
Khwenena leopoldinae Manegold, 2013	6/5	woodland	Rich (1980, unpubl. data); Stidham (2006); Manegold (2013)
Psittacoidea gen. et sp. indet., large	1/1	woodlands	Stidham (2006); Louchart (unpubl. data)
Strigiformes, Strigidae			
Strigidae gen. et sp. indet., sp. A Strigidae gen. et sp. indet., sp. B	– /10–15	–	Rich (1980)
Coliiformes, Coliidae			
Colius hendeyi Rich & Haarhoff, 1985	124/26	open savannah and bushlands	Rich & Haarhoff (1985)
Alcediniformes, Alcedinidae			
Ceryle sp.	2/1	wetlands	Olson (1994)
Halcyon sp.	1/1	open savannah and bushlands	Olson (1994)
Piciformes, Picidae			
Australopicus nelsonmandelai Manegold & Louchart, 2012	14/4	woodlands, forest	Manegold & Louchart (2012)
Piciformes, Indicatoridae			
cf. *Indicator* sp. A cf. *Indicator* sp. B	– /4	woodlands, forest	Olson (1985d); Louchart & Manegold (unpubl. data)
Apodiformes, Apodidae			
cf. *Tachymarptis* sp.	1/1	–	Rich (1980); Louchart (unpubl. data)
Caprimulgiformes, Caprimulgidae			
Caprimulgidae gen. et sp. indet.	1/1	open woodlands?	Manegold (2010a)
Passeriformes	– / >100		
Hirundinidae gen. et sp. indet., sp. A	3/3	–	Manegold (2010b)
Hirundinidae gen. et sp. indet., sp. B	2/2	–	Manegold (2010b)
Sturnidae gen. et sp. indet., sp. A		woodlands?	
Sturnidae gen. et sp. indet., sp. B		woodlands?	
Sturnidae gen. et sp. indet., sp. C, aff. *Cinnyricinclus leucogaster*	1/1	woodlands	
Sylvioidea, gen. et sp. indet.	1/1	woodlands?	

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New finds and revised taxa of Early Pliocene birds from Western Mongolia

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Abstract — The Late Miocene-Early Pliocene Hyargas-Nuur formation in Western Mongolia yielded a rich fauna of birds which contributes significantly to our knowledge of the Neogene avian diversity in Asia. A study of new fossil remains, collected during the last 20 years, and a revision of several previously described taxa are presented in this paper. *Cygnus pristinus* is shown to be clearly separable from extant *C. olor*. *Podiceps solidus* and *Haliaeetus fortis*, initially described from the Late Miocene sediments, were found in the Early Pliocene. *Probalearica mongolica* is moved to the genus *Grus*, and a new genus *Pastushkinia* nov. gen. is erected for *Crex zazhigini*. Several new finds – a lapwing *Vanellus* cf. *V. leucurus*, two species of gulls (*Larus* spp.), and large *Gypaetus*-like accipitrid – represent the oldest records of the corresponding bird groups in Asia. A complete list of taxa known from the Early Pliocene of Western Mongolia is also presented.

Key words: Aves, Early Pliocene, Neogene, Central Asia, Fauna

Introduction

The fossil record of Neogene birds in Asia is very scanty, and Pliocene birds are especially poorly known. A small number of taxa (*Struthio asiaticus* Milne-Edwards, 1871; *Pelecanus sivalensis* Davies, 1880; *P. cautleyi* Davis, 1880; *Leptoptilos falconeri* Milne-Edwards, 1868; *L. siwalikensis* Harrison, 1974; *Cryptociconia indica* Harrison, 1974; *Mergus* sp.) has been described long ago from the Pliocene of Siwalik Hills in the Indian region (Milne-Edwards 1871; Davies 1880; Lydekker 1879, 1891; Harrison 1974, 1979; see also Louchart *et al.* 2005 for review of Siwalik Leptoptiline storks). Several Pliocene birds were reported from Japan (Rich *et al.* 1986), but they were identified just up to family level. An isolated ilium from the Pliocene of Tuva (Siberia) was recently assigned to *Buteo* sp. (Panteleev *et al.* 2006). Several non-passeriform taxa and a representative fauna of songbirds are known from the Late Pliocene of Northern Mongolia and adjacent territory of Russia (Kurochkin 1985; Zelenkov & Kurochkin 2009, 2010, 2012). The famous Chinese localities Ertemte and Baode, which yielded avian remains previously regarded as being Pliocene in age (Rich *et al.* 1986), are now placed in the terminal Miocene (Qiu & Qiu 1995). Thus the largest and by far the only representative fauna of Pliocene birds in Asia is that from Western Mongolia. It was thoroughly studied by Kurochkin (1971, 1976, 1980, 1985), but unfortunately was published mainly in Russian and due to this fact is very poorly known outside paleornithological community.

Neogene birds of Western Mongolia are known from a small number of relatively closely positioned localities in the Great Lake Depression (Fig. 1). Neogene sediments in this area are several hundred meters thick (Devjatkin 1981)

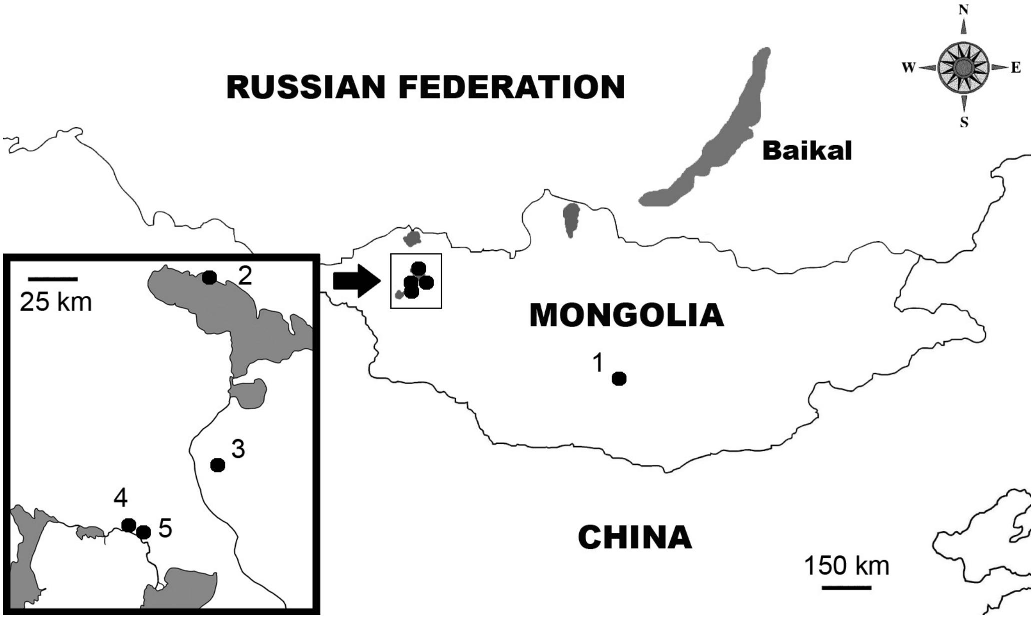

FIGURE 1. Map showing the location of the basic Late Miocene and Pliocene avian localities discussed in this paper. 1 – Hung-Kureh; 2 – Hyargas-Nuur 2; 3 – Zogsoo-Harhan 1 and 4; 4 – Chono-Harayah 1; 5 – Chono-Harayah 2.

and have been divided into several formations. Bird remains are most common in the youngest Hyargas-Nuur formation ("svita Khirgiz-Nur" of Soviet geologists), which is presumably roughly synchronous with previously described Hung-Kureh formation in Central Mongolia (Berkey & Morris 1927; Devjatkin 1981). The Hyargas-Nuur formation was once thought to be Early-Middle Pliocene (Devjatkin 1981); this age was accepted by Kurochkin (1985 and earlier works). Later paleomagnitic and biostratigraphic data however provided evidence for the Late Miocene-Early Pliocene age of the Hyargas-Nuur formation (Pevzner *et al*. 1983; Devyatkin 1994). The two most important late Neogene avian localities of the Western Mongolia, Hyargas-Nuur 2 and Chono-Harayah (also known as "Khirgiz-Nur" and "Chono-Khariakh"; both contain sediments of Hyargas-Nuur formation) are now being correlated with the well-studied Chinese mammalian localities Ertemte (MN 13) and Bilike (MN 14), respectively (Vangengeim *et al*. 2005). The fauna of Western Mongolian Neogene birds, previously thought to be of Pliocene age, thus should be revised in the light of new biostratigraphic data. Additionally, more avian remains were collected from the Hyargas-Nuur formation by the Joint Soviet-Mongolian expedition since the work of Kurochkin. These data may shed light on systematic position and taxonomy of several taxa.

A revision of Phasianidae and most Anatidae from Hyargas-Nuur formation was published elsewhere (Zelenkov & Kurochkin 2009, 2010; Zelenkov 2012). In this paper I present new finds and revise several species of birds previously described by Kurochkin (1985 and earlier works) from the Early Pliocene (as currently understood) of the Hyargas-Nuur formation. This revision was possible because of both broader taxonomic comparisons and more fossil material available. In order to reduce the length of the paper, I am not discussing here species with unquestionable taxonomic or nomenclature status. A complete list of Early Pliocene birds from Western Mongolia is given in Table 1.

Materials and methods

A comprehensive description of geology and associated fauna of the Western Mongolian Pliocene avian localities can be found in Devjatkin (1981). The main avian localities are Hyargas-

Nuur 2 (MN 13) and Chono-Harayah 1 and 2 (MN 14). Several bone remains come from the localities Zavhan, Zogsoo-Harhan 1 and 4 (MN 14–15). The material is stored at the Borissiak Paleontological Institute of Russian Academy of Sciences in Moscow. The osteological terminology in this work follows Baumel *et al*. (1993). All measurements are in mm.

Abbreviations: CMC: Carpometacarpus, COR: Coracoid, FEM: Femur, HUM: Humerus, PIN: Borissiak Paleontological Institute of Russian Academy of Sciences, RAD: Radius, SCA: Scapula, TMT: Tarsometatarsus, TT: Tibiotarsus, ULN: Ulna.

Systematic Paleontology

Order Anseriformes Wagler, 1831
Family Anatidae Vigors, 1825

Cygnus pristinus Kurochkin, 1971

(Fig. 2)

v. *Cygnus pristinus* Kurochkin, 1971: p. 60, fig. 2.
v. *Cygnus pristinus* Kurochkin, 1976: p. 55, figs 3–5.
v. *Cygnus pristinus* Kurochkin, 1985: p. 58, text-fig. 27; pl. VII, figs 5–8.
v. *Cygnus olor* (Gmelin, 1789): Mlíkovský & Švec 1986, p. 264.

Type locality: Hung-Kureh, Central Mongolia, Late Miocene-Early Pliocene (MN 13–15).

Stratigraphical and geographical distribution: Mongolia: Late Miocene (Hyargas-Nuur 2), Early Pliocene (Chono-Harayah 1 and 2; Zogsoo-Harhan 1 and 4).

Holotype: RAD sin., distal portion (PIN 2614/25). Figured in Kurochkin (1985) text-fig. 27; pl. VII, figs 5–8.

Emended diagnosis: Rather large swan, the size of extant *C. olor*, which can be distinguished from this species by the following characters. COR: processus acrocoracoideus not widening cranially in medial and lateral views; SCA: tuberculum coracoideum very large*, acromion oriented dorsocranially; HUM: distal end narrow with epicondylus ventralis weakly protruding ventrally; longitudinal axis of fossa m. brachialis oriented proximodistally; RAD: fovea ligamentalis very deep*; CMC: processus extensorius markedly shorter*; phalanx proximalis digiti majoris: dorsal and ventral surfaces very releif, with deep pit on ventral surface; proximal articular surface dorsoventrally elongated; TT: incisura intercondylaris wider; TMT: fossa infracotylaris deeper*; trochlea metatarsi III oval in medial view and slightly widening distally in dorsal view; trochlea metatarsi IV with narrow sulcus on distal surface. Characters indicated by an asterisk (*) represent autapomorphies of the taxon.

Measurements: COR: depth at the level of glenoid facet, 18.5 (PIN 3222/32); diameter of cotyla scapularis, 7.4 (PIN 3222/32); SCA: maximal dorsovental height of caput scapulae, 23.3 (PIN 2614/111); length of facies articularis humeralis together with tuberculum coracoideum, 18.1 (PIN 2614/111); HUM: distal width, 35.5 (PIN 2614/108); proximodistal height of condylus dorsalis, 16.4 (PIN 2614/108); depth across condylus dorsalis, 20.1 (PIN 2614/108); ULN: maximal distal width, 22.2 (PIN 2614/109); depth of condylus dorsalis, 19.4 (PIN 2614/109); RAD: distal width, 16.6 (holotype); maximal distal depth, 7.9 (holotype); CMC: proximal craniocaudal height, 32.6 (PIN 2614/159); length of metacarpale I, 17.0 (PIN 3222/38), 17.6 (PIN 3378/100), 18.7 (PIN 2614/159); dorsoventral depth of trochlea carpalis, 13.0 (PIN 2614/159); 12.8 (PIN 3222/38), 12.5 (PIN 3222/671); distal dorsoventral depth, 1.1 (PIN 3222/40); phalanx proximalis digiti majoris: total length, 48.1 (PIN 2614/26); TT: distal width ~ 23.1 (PIN 2614/70); depth across incisura intercondylaris, 13.9 (PIN 2614/70); TMT: proximal width, 24.2 (PIN 2614/154); depth of cotyla medialis, 12.6 (PIN 2614/154); width of trochlea metatarsi III, 10.7 (PIN 3222/54); depth of trochlea metatarsi III, 15.4 (PIN 2614/54).

Description and comparisons: The processus acrocoracoideus of the coracoid is not widening in medial and lateral views (markedly widening in *C. olor;* almost straight in *C. melanocoryphus*); the cranial angle of the facies articularis humeralis is obtuse (as in *C. olor*, *C. bewikii* and *C. melanocoryphus*), but this character slightly varies individually in swans; impressio lig. acrocoracohumeralis with a markedly curved apex

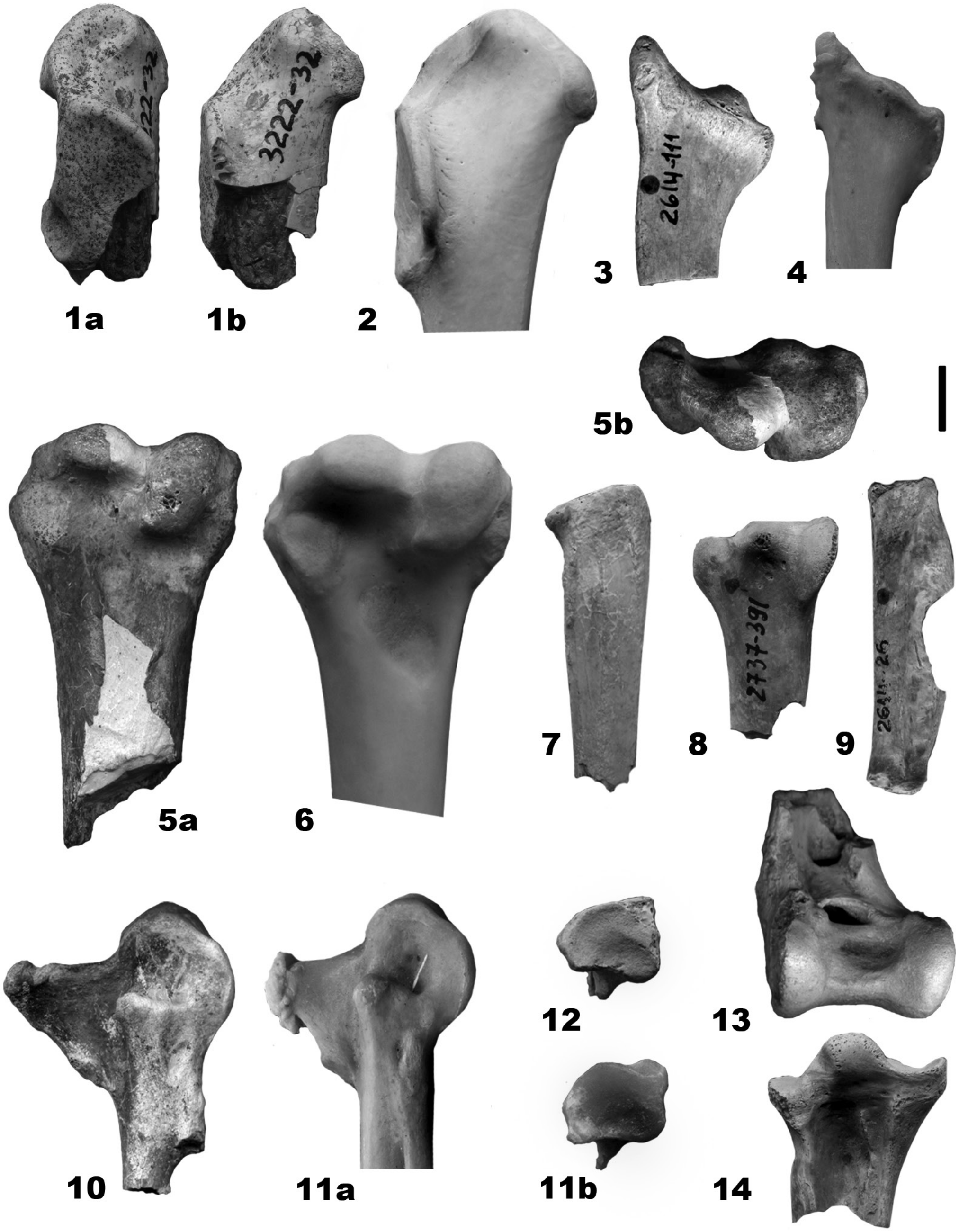

FIGURE 2. Selected remains of *Cygnus pristinus* Kurochkin, 1971 (**1, 3, 5, 7–10, 12–15**) from the Late Miocene and Early Pliocene of Western Mongolia compared with those of extant *C. olor* (**2, 4, 6, 11**). *Cygnus pristinus* Kurochkin, 1971: **1** cranial fragment of right coracoid, PIN 3222/32 in lateral (**a**) and ventral (**b**) views; **3**, cranial fragment of left scapula, PIN 2614/111 in medial view; **5**, distal fragment of right humerus, PIN 2614/108 in cranial (**5a**) and distal (**5b**) views; **7**, holotype, distal fragment of left radius, PIN, 2614/25 in dorsal view; **8**, distal fragment of left ulna, PIN 2737/391 in ventral view; **9**, basal phalanx of the major wing digit, PIN 2614/26 in dorsal view; **10**, proximal fragment of right carpometacarpus, PIN 2614/159 in ventral view; **12**, distal fragment of right carpometacarpus, PIN 3222/40 in distal view; **13**, distal fragment of right tibiotarsus, PIN 2614/70 in cranial view; **14**, proximal fragment of right tarsometatarsus, PIN 2614/154 in cranial view. *Cygnus olor,* extant: **2**, cranial fragment of right coracoid in ventral view; **4**, cranial fragment of left scapula in medial view; **6**, distal fragment of right humerus in cranial view; **11**, right carpometacarpus: ventral view of proximal part (**11a**) and distal view (**11b**). Scale bar equals 1 cm.

(as in *C. olor*), this impressio is more narrow and straight in other species; the cranial margin of the medial surface of the acrocoracoid is semicircular in medial view (as in *C. olor*), while this outline is more or less straight in other species. The most characteristic of the scapula of *C. pristinus* is the enlarged tuberculum coracoideum, unlike that of any of the extant species of swans. The acromion is pointing dorsocranially in *C. pristinus*, while it is oriented more cranially in *C. olor* and *C. buccinator*, and more dorsally in other species.

The distal humerus of *C. pristinus* resembles *C. cygnus* and differs from that of *C. olor* by weakly protruding ventrally epicondylus ventralis (the whole distal end is thus looks narrow in *C. pristinus* and *C. cygnus*); the fossa m. brachialis is oriented proximodistally in *C. pristinus* while it is angled in other swans; the epicondylus dorsalis is more strongly developed in *C. pristinus* than in *C. cygnus*, but less than that in *C. olor* and *C. melanocoryphus*; the fossa olecrani is deep as in *C. olor* and *C. bewikii.* The tuberculum carpale of ulna is proximodistally wide in *C. pristinus* as in *C. olor*. The most characteristic feature of the distal radius is its blunt distal outline (as in *C. olor*; pointed in other swans). Fovea ligamentalis is deeper than in other swans; sulcus ligamentosus is well marked (normally vestigial in other swans but weekly developed in *C. olor*). In the carpometacarpus, there is a pit just distal to the processus pisiformis and an indistinct notch in the ventral outline of the trochlea carpalis; the trochlea carpalis itself is roundish in ventral view and its dorsal half is weakly protruding proximally. In all of these four characters of the carpometacarpus, *C. pristinus* agrees with *C. olor*. The processus extensorius is however markedly proximodistally shorter in *C. pristinus* than in all extant species. The facies articularis dig. minoris is wide in *C. pristinus* as in *C. olor*. The proximal phalanx of the major wing digit is shortened, as in *C. olor*, but its surfaces are very relief and, in contrast to all other species, deep pits are present on both ventral and dorsal surfaces (the deep ventral pit is also characteristic of extant *C. cygnus*); the proximal articular surface is dorsoventrally elongated (as in *C. cygnus*) while it is roundish in *C. olor*.

The condylus medialis of the tibiotarsus in *C. pristinus* is thin in cranial view, close to the state of *C. olor*; KUROCHKIN (1985) used the shape of the distal aperture of the canalis extensorius to distinguish various swan species, but our study shows that this character is subject of individual variation. The incisura intercondylaris is wider in *C. pristinus* than in extant swans, although it is wide in some specimens of *C. olor*. The proximal end of tarsometatarsus is rather uniform in swans, but the fossa infracotylaris is deeper in *C. pristinus* than in other species; trochlea metatarsi III is oval in medial view (roundish in *C. olor*) and gently widens distally (as in *C. cygnus*). Trochlea metatarsi IV has a narrow furrow on the distal surface, as in *C. cygnus* and *C. melanocorhyphus* (lacking in *C. olor*). KUROCHKIN (1985) already mentioned that *C. pristinus* had shortened pedal phalanges, similar to those of extant *C. olor*.

Several other fossil species of swans have been described (reviewed by LOUCHART *et al.* 2005). *Cygnus verae* BOEV, 2000 is known from a proximal humerus and thus cannot be compared directly. *C. verae* is however smaller that *C. pristinus* (BOEV 2000). *C. herrenthalsii* VAN BENEDEN, 1871 has been described on the basis of a non-representative material (pedal phalange). *C. atavus* (FRAAS, 1870) from the middle Miocene of Germany is notably smaller than *C. pristinus*. *C. mariae* BICKART, 1990 is known from the Late Miocene of Arizona and is close in size to *C. pristinus*. *C. mariae* is also similar to extant *C. olor* (BICKART 1990) and thus can be a junior synonym of *C. pristinus*.

Remarks: *Cygnus pristinus* can be assigned to the genus *Cygnus* because of its large size (much larger than species of geese) and also based on the presence of several morphological features. For example, the cranial scapula is not pneumatized (pneumatic opening occurs in geese); the head of the coracoid has the typical crescentic outline in medial view, typical of swans; the distal humerus with a proximocaudally compressed ventral condyle (well visible in cranial view). In the distal tibiotarsus, *C. pristinus* agrees with *Cygnus* in having narrow condylus lateralis in distal view.

KUROCHKIN (1971) described *C. pristinus* on the basis of a distal radius and a few other very fragmentary remains. In 1982/1983, MLÍKOVSKÝ & ŠVEC (1986) studied the holotype of *C. pristinus* and transferred this species to *C. olor*. For unknown reason, they were unable to examine not only paratypes, but also materials described later, which include much more informative distal humerus and tibiotarsus (Kurochkin 1976). I agree with Mlíkovský & Švec (1986) that the distal radius of *C. pristinus* is practically indistinguishable from that of extant *C. olor;* but it is noteworthy that the distal radius alone is not informative enough to solve the taxonomic problem. *Cygnus pristinus* indeed resembles *C. olor* in many structural details and proportions (e.g., shortened wing and pedal phalanges) but differs from this and other species of the genus in several details of almost all of the known skeletal elements. Furthermore, *C. pristinus* is similar with *C. cygnus* in some details (morphology of the humerus; tarsometatarsus, phalanx proximalis digiti majoris). Although it is likely that *C. pristinus* is more closely related to *C. olor*, its specific identity seems obvious. The presence of a mixture of characters may indicate this species is more primitive than all extant species. Molecular phylogenetic data estimate the mean divergence time between swans and geese as relatively recent event, 19.5±4.8 Myr (Gonzalez *et al.* 2009), what probably corresponds to the Early or early Middle Miocene. The diversification of swans must have occurred later, probably not earlier than the second half of the middle Miocene (based on the appearance of the modern-type waterfowl fauna in the fossil record), and thus the presence of primitive taxa with a mixture of characters in the Late Miocene is expectable. A phylogenetic analysis of swans with inclusion of *C. pristinus* may add important information on the evolutionary history of swans and affinities of this species.

Material: *Cygnus pristinus* is the most common species of birds in the terminal Miocene-Lower Pliocene Hyargas-Nuur formation of Western Mongolia. For completeness, I include in this section all the known materials, even if they formally come from the layers below the Miocene-Pliocene boundary.

Latest Miocene material. Locality Hyargas-Nuur 1: proximal phalanx of the fourth toe of left foot (PIN 3222/599). Locality Hyargas-Nuur 2: COR dext., cranial fragment (PIN 3222/32); COR dext., caudal fragments (PIN 3222/53, 3222/705); SCA sin., cranial fragments (PIN 2614/27, 2614/111); ULN, distal fragment (PIN 3222/109); RAD dext., distal fragments (PIN 2614/115, 3222/25); ulnare sin. (PIN 2614/116); CMC dex., proximal fragments (PIN 3222/23, 3222/38); CMC sin., proximal fragment (PIN 322/671); CMC dext., distal fragments (PIN 3222/40, 3222/41); proximal phalanx of the major wing digit sin. (PIN 2614/26); TMT dext., proximal fragment (PIN 2614/154); isolated trochlea metatarsi III dext. (PIN 3222/54); isolated trochlea metatarsi IV dext. (PIN 3222/698); third phalanx of the third toe of left foot (PIN 2614/113); fourth phalanx of the fourth toe of right foot (PIN 2614/117).

Early Pliocene material. Locality Chono-Harayah 1: TT dext., distal portion (PIN 2614/70); second phalange of the third toe of left foot (PIN 2614/73). Locality Chono-Harayah 2: CMC sin., proximal portions (PIN 2614/159, 3378/100). Locality Zogsoo-Harhan 1: COR dext., cranial portion (PIN 2737/390); HUM dext., distal portion (PIN 2614/108); HUM, sin., distal fragment (PIN 3222/19); ULN, distal fragment (PIN 2737/391); TMT, dex., proximal fragment (PIN 2614/205). Locality Zogsoo-Harhan 4: TT dext., distal fragment (PIN 2614/153).

Order Podicipediformes Fürbringer, 1888
Family Podicipedidae Bonaparte, 1831

Podiceps solidus Kurochkin, 1985
(Fig. 3)

v. *Podiceps solidus* Kurochkin, 1985: p. 16, text-fig. 3; pl. I, figs 3, 4.

Type locality: Hyargas-Nuur 2, Western Mongolia, Late Miocene (MN 13).

Stratigraphical and geographical distribution: Mongolia: Late Miocene (Hyargas-Nuur 2), Early Pliocene (Chono-Harayah 1 and 2; Zogsoo-Harhan 1 and 4).

Holotype: HUM dext., distal portion (PIN 3222/37). Figured in Kurochkin (1985): text-fig. 3, pl. I, figs 3–4.

Original diagnosis: Distal end of humerus wide; impressio lig. collaterale ventrale inconspicuous; fossa m. brachialis shallow but broad; longitudinal axis of condylus ventralis oriented distocranially; dorsal part of fossa olecrani shallow (translated after Kurochkin 1985).

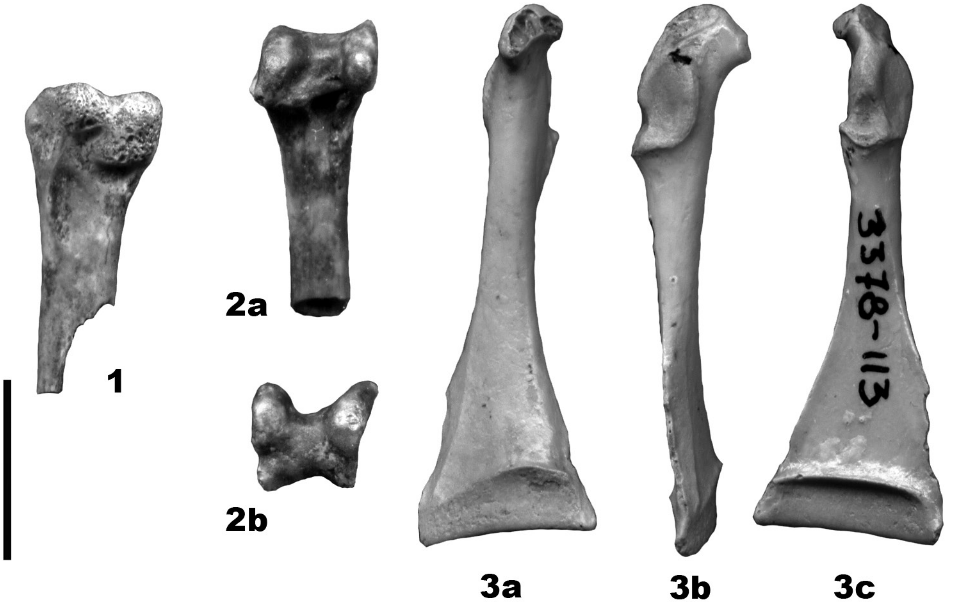

FIGURE 3. Remains of *Podiceps solidus* Kurochkin, 1985 from the Early Pliocene of Western Mongolia. **1**, holotype, distal fragment of right humerus, PIN, 3222/37 in cranial view; **2**, distal fragment of left tibiotarsus, PIN 3378/98 in cranial (**2a**) and distal (**2b**) views; **3**, right coracoid, PIN 3378/113 in ventral (**3a**), lateral (**3b**) and dorsal (**3c**) views. Scale bar equals 1 cm.

New materials: COR dext. (PIN 3378/113), locality Chono-Harayah 1; TT sin., distal portion (PIN 3378/98), locality Chono-Harayah 2; TMT sin., distal portion (PIN 3378/96), locality Chono-Harayah 2.

Measurements: COR: total length, 28.4; depth at the level of glenoid facet, 3.6; HUM: distal width, 7.2; TT: distal width, 6.6; distal depth, 6.2; depth across incisura intercondylaris, 4.2; TMT: distal width ~ 5.5; distal depth ~ 5.3.

Description and comparisons: I refer three new bones from the localities of Chono-Harayah to this species because of relative size and osteological similarity with extant *P. auritus* and *P. nigricollis*.

The fragmentary coracoid is morphologically similar to that of extant *P. nigricollis*, and differs only by the narrower dorsal portion of the facies articularis sternalis. The coracoid of extant *P. auritus* is more robust, with thicker shaft and wider impressio lig. acrocoracohumeralis. The fragmentary tibiotarsus, to the contrary, is similar to that of *P. auritus* in having the condylus lateralis truncated in lateral view. The condylus is more roundish in *P. nigricollis*. The tarsometatarsus belonged to an immature bird and thus displays few morphological details and cannot be compared with extant species.

Remarks: This species of a small grebe was established based on the distal end of humerus (Kurochkin 1985). Kurochkin (1985) noted that this species shared morphological features with both extant *P. nigricollis* and *P. auritus.* He further pointed that *P. solidus* was similar to *P. pisanus* from the Pliocene of Italy. Olson & Rasmussen 2001 and Mlíkovský 2002 later considered *P. pisanus* the junior synonym of extant *P. auritus*. However, *P. solidus* cannot be synonymized with *P. auritus* because it is more similar to *P. nigricollis* in some osteological details. The humerus of *P. solidus* is somewhat intermediate between the two extant species, the coracoid is more similar to those of *P. nigricollis*, and the tibiotarsus to that of *P. auritus*. Although there is a possibility that two species of similarly sized grebes inhabited the lakes of the Western Mongolia in the Late Miocene and Early Pliocene, I refer all of the known material to one species, in the absence of the contrary evidence. The intermediate morphology of *P. solidus* suggests that this species might be close to a lineage ancestral to both *P. auritus* and *P. nigricollis*.

Fossil grebes apparently related to this evolutionary lineage are known from the Pliocene

FIGURE 4. Bird remains from the Early Pliocene of Western Mongolia. 1, *Nyctanassa kobdoena* Kurochkin 1976, holotype, distal portion of right tarsometatarsus, PIN 2614/86 in dorsal (**1a**), ventral (**1b**) and distal (**1c**) views; 2, Otididae gen. indet., distal fragment of left tarsometatarsus, PIN 3378/129 in ventral (**2a**) and dorsal (**2b**) views. Scale bar equals 1 cm.

deposits of Europe and North America. *P. discors* Murray, 1967 was described from the Late Pliocene of Kansas (Murray 1967). A grebe similar to extant *P. nigricollis* was also found in the Late Miocene of Ukraine (Voinstvensky 1967). *P. auritus* is further known from the Early Pliocene of North Carolina (USA; Olson & Rassmussen 2001), Pliocene of Florida (USA; Brodkorb 1953) and Italia (sub. *P. pisanus*; Regàlia 1902).

P. solidus was initially described from the Late Miocene deposits of the locality Hyargas-Nuur 2 (Kurochkin 1985), but the new materials from Chono-Harayah expand its geological distribution to the Early Pliocene.

Order Ardeiformes Wagler, 1831
Family Ardeidae Vigors, 1825

***"Nyctanassa" kobdoena* Kurochkin, 1976**
(Fig. 4)

v. *Nyctanassa kobdoena* Kurochkin, 1979: p. 54, fig. 2.

v. *Nyctanassa kobdoena* Kurochkin: 1985, p. 23, text-fig. 6; pl. II, figs 5, 6.

Type locality: Chono-Harayah 1, Western Mongolia, Early Pliocene (MN 14–15).

Stratigraphical and geographical distribution: Mongolia: Late Miocene (Hyargas-Nuur 2; MN 13), Early Pliocene (Chono-Harayah 1 and 2).

Holotype: TMT dext., distal portion (PIN 2614/86). Figured in Kurochkin (1979): fig. 2; (1985): text-fig. 6; pl. II, figs 5, 6.

Emended diagnosis: Small heron the size of extant *Nyctanassa violacea* from which it can be distinguished by the following set of characters of distal tarsometatarsus: trochleae metatarsorum (especially trochlea metatarsi II) narrow; trochlea metatarsi II gradually widening distally; incisura intertrochlearis lateralis wide; sagittal plane of trochlea metatarsi II only slightly inclined with respect to sagittal plane of trochlea metatarsi III; distal margin of trochlea metatarsi IV positioned notably proximally than distal margin of trochlea metatarsi III; ventral articular surface of trochlea metatarsi II convex.

New materials: fragmentary cervical (11th to 14th) vertebra (PIN 3378/112), locality Chono-Harayah 2.

Measurements: maximum distal width, 9.5; width at the level of foramen vasculare distale, 6.4; maximal distal depth, 5.7.

Description and comparisons: Kurochkin (1976, 1985) provided detailed description and broad taxonomic comparisons of the holotype, but some of his characters are not suitable to diagnose this taxon. The characters mentioned above in the diagnosis allow distinguishing *N. kobdoena* from *N. violacea*. In the latter species, dorsal part of the articular surface of trochlea metatarsi II is widened and therefore the outer margin of this trochlea in distal view is inclined with respect to the sagittal plane of the trochlea metatarsi III at an angle about 40°, while this angle is much smaller in *N. kobdoena*. Ventral articular surface of the trochlea metatarsi II is concave in *N. violacea* while it is convex in *N. kobdoena*.

The most striking features in which this form differs from extant *Nyctanassa* and *Nycticorax* is the gradually widening trochlea metatarsi II in dorsal view (as in *Cochlearius*) and trochlea metatarsi IV protruding considerably less distally than trochlea metatarsi III (as in *Butorides*). Both of these features are present in the fossil genus *Matuku* from the Early Miocene of New Zealand. *Matuku* was shown to be basal with respect to all living herons (Scofield *et al.* 2010) and so these features may be plesiomorphic within Ardeidae.

Remarks: Olson & Wingate (2006) doubted the validity of the generic assignment of this species because of the fragmentary nature of the holotype. The two genera of herons (*Nycticorax* and *Nyctanassa*) are however strikingly different in the proportions of tarsometatarsi what evidently reflects their somewhat different adaptations. Locomotor apparatus of Ardeidae is very flexible so that osteological correlates with feeding and locomotion styles can be easily found (Boev 1988, 1989). Given these facts, it is unsurprising that the two genera are easily distinguishable on the basis of the distal tarsometatarsus alone. *Nyctanassa violacea* is the specialist in crustacean, particularly crabs, while *Nycticorax* herons are opportunist feeders with generally very diverse diet. *Nyctanassa violacea* spend much time in walking (Rodgers 1983) while *Nycticorax nycticorax* normally just stands and waits during feeding (Rusev 2011). I agree with Kurochkin (1976, 1985) that *N. kobdoena* is much more similar to extant *Nyctanassa* than to *Nycticorax* (in the fossil species, the trochleae metatarsorum are narrow and more splayed as in *Nyctanassa*), which may indicate that this fossil species was more generalized in its feeding behavior (although not necessarily in its diet) than extant *Nycticorax* species, but observed differences (see above) possibly indicate that *N. kobdoena* belongs to a more primitive extinct genus. New material is however necessary to confirm this hypothesis. At present, the generic status of *N. kobdoena* should be regarded as uncertain.

Order Otidiformes Sibley *et al.*, 1988
Family Otididae Gray, 1840

Otididae gen. indet.
(Fig. 4)

Material: TMT dext., distal fragment (PIN 3378/129), locality Chono-Harayah 2.

Measurements: depth of trochlea metatarsi III, 8.3.

Remarks. The fragmentary tarsometatarsus can be assigned to Otididae because of a characteristic widening of the shaft near the base of the trochlea metatarsi II in combination with flat dorsal surface and nearly symmetrical trochlea metatarsi III. The specimen however is very fragmentary which precludes from assigning it to any particular genus, but it may have belonged to the genus *Gryzaja* previously known from the Pliocene of Ukraine and Moldavia (Kurochkin & Khozatskij 1972). The Mongolian form is however larger then *G. odessana* Zubareva, 1939 and thus may represent another species. Very large bustard *Ioriotis gabunii* Burchak-Abramovich & Vekua, 1981 has been described from the Late Pliocene of Georgia based on a fragmentary proximal humerus (Burchak-Abramovich & Vekua 1981) and thus cannot be compared with the Mongolian form.

Order Gruiformes Bonaparte, 1854
Family Gruidae Vigors, 1825

Grus mongolica (Kurochkin, 1985) comb. nov.
(Fig. 5)

v. *Probalearica mongolica* Kurochkin, 1985: p. 58, text-fig. 27, pl. VII, figs 5–8.

Type locality: Chono-Harayah 1, Western Mongolia, Early Pliocene (MN 14–15).

Stratigraphical and geographical distribution: Mongolia: Late Miocene (Hyargas-Nuur 2), Early Pliocene (Chono-Harayah 1).

Holotype: TT sin., distal portion (PIN 3378/45). Figured in Kurochkin (1985): text-fig. 27, pl. VII, figs 5–8.

Emended diagnosis: Large crane, the size of extant *G. leucogeranus*, which can be distinguished from this and other large cranes by thin condylus medialis; roundish distal foramen of canalis extensorius; short and obliquely oriented ligamental scar on the medial margin of

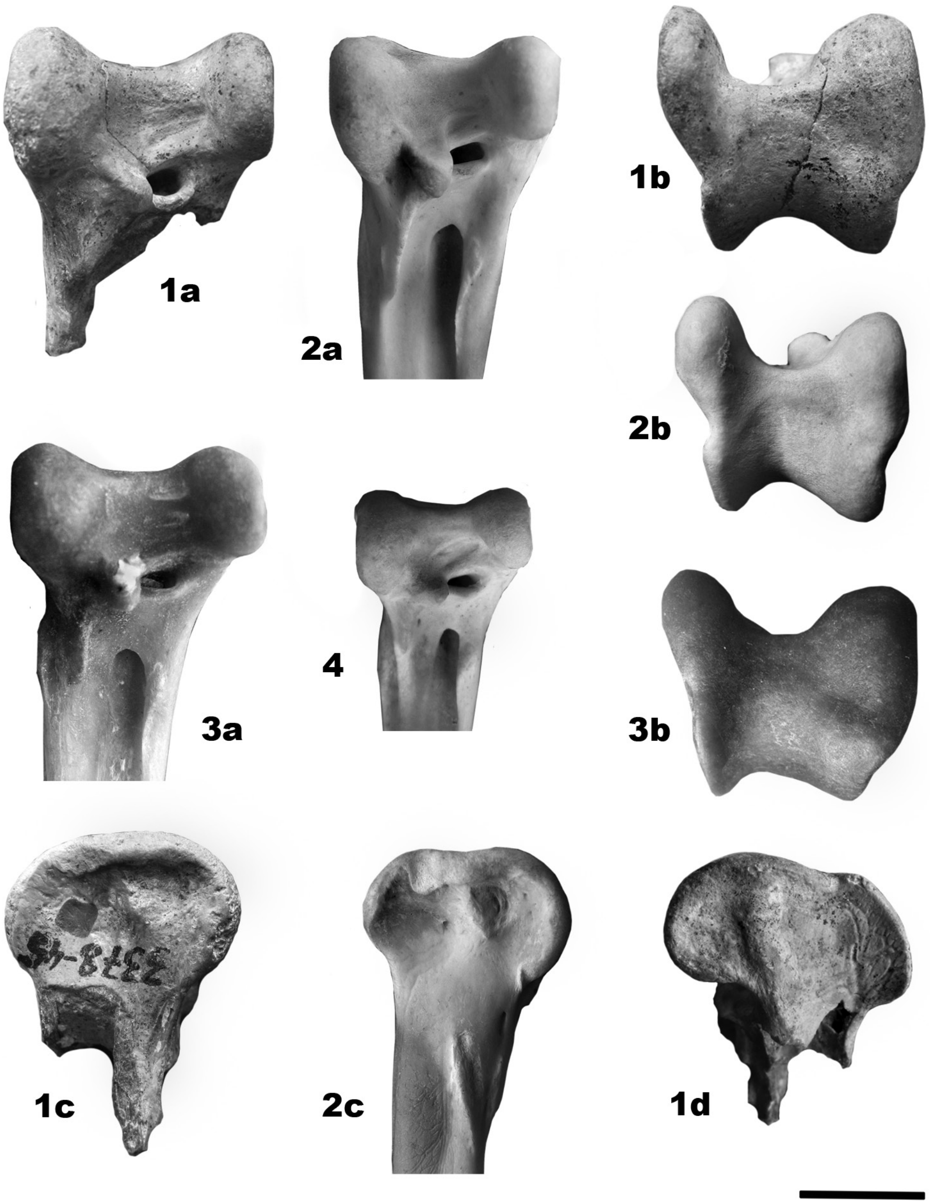

FIGURE 5. *Grus moldavicus* (Kurochkin, 1985) from the Early Pliocene of Western Mongolia compared with extant Gruidae. 1, *Grus moldavicus,* holotype, PIN 3378/45, distal tibiotarsus in cranial (**1a**), distal (**1b**), lateral (**1c**) and medial (**1d**) views; 2, *Grus grus*, extant, distal tibiotarsus in cranial (**2a**), distal (**2b**) and lateral (**2c**) views; 3, *Balearica regulorum*, extant, distal tibiotarsus in cranial (**3a**) and distal (**3b**) views; 4, *Anthropoides virgo*, extant, distal tibiotarsus in distal view. Scale bar equals 1 cm.

the cranial surface of the shaft; sulcus cartilaginis tibiotarsi narrow.

Measurements: maximal distal width, 21.8; maximal distal depth, 23.2; depth across incisura intercondylaris, 11.5;

Description and comparisons: The condylus lateralis is rather wide (as in *G. japonensis*, *G. vipio*), while it is notably narrower in other cranes and fossil genus *Pliogrus*; condylus medialis is unusually thin and proximodistally elongated in both cranial and distal view, this condyle is normally thicker in cranes although it is also somewhat thin in *G. vipio*, *G. monacha* and *G. leucogeranus*. The apophysis lig. externi is moderately developed, as in extant *G. japonensis* and *G. leucogeranus,* while it is bulbous in other cranes. The ligamental scar on the cranial surface just proximal to apophysis is unusually short and obliquely oriented (it is normally very long in cranes and usually is subparallel to the long axis of the bone). Somewhat similar morphology of the scar was found just in one specimen of *G. monacha*. A pit on the medial surface of the condylus medialis is very weakly developed; it is normally deep in cranes (shallow – but still deeper than in *G. mongolica* – pit is observed in *G. leucogeranus* and *G. japonensis*). The epicondylus medialis is weakly expressed.

Grus mongolica differs from *Anthropoides* and *Balearica* (including fossil "*Probalearica*" *crataegensis* Brodkorb, 1963) in that the condylus lateralis is not shifted laterally with respect to the shaft and also by the very thin condylus medialis. The ledge in the lateral outline of the bone in distal view is very caudally positioned in *Balearica* while it is shifted cranially in *Grus* (including *G. mongolica*). *G. mongolica* is further similar to extant *Grus* and differs from *Balearica* in having condylus medialis strongly shifted medially (well visible in distal view) and in the shape of the lateral outline of the bone in distal view.

Grus mongolica easily differs from the genus *Palaeogrus*, known from the Paleogene and Neogene of Europe, by the truncated distal surface of the condylus lateralis (flat in *Palaeogrus*) and by the presence of a well-developed ledge in the lateral outline of the bone in distal view (completely absent in *Palaeogrus*). In the putative crane *Geranopsis*, the distal surface of the condylus lateralis is also flat (Harrison & Walker 1979).

Another fossil genus *Pliogrus* contains two species from the Early Pliocene of Germany; distal tibiotarsus is known for one of them. The validity of this genus is not obvious; Cracraft (1973) and Mlíkovský (2002) consider *Pliogrus* the junior synonym of extant *Grus*. As can be judged from a picture in Lambrecht (1933), the condylus lateralis in *Pliogrus* is even narrower than in *Grus*, while in *Grus mongolica* it is wider than in most extant *Grus*.

Remarks: *Grus mongolica* was initially assigned to the genus *Probalearica*, which was erected by Lambrecht (1933) for the supposed crane *Grus problematica* Milne-Edwards, 1871 known from a fragmentary skull and sternum from the Late Oligocene-Early Miocene of France. Since the work of Lambrecht, three more species were assigned to this genus, all of them just because of supposed similarity to the extant cranes *Balearica*. *Probalearica crataegensis* Brodkorb, 1963, *P. moldavica* Kurochkin & Ganya, 1972 and *P. mongolica* Kurochkin, 1985 are all known from just distal tibiotarsi and thus cannot be directly compared to *G. problematica.* The type species of *Probalearica* was shown (Cheneval & Escuillié, 1992; Mourer-Chauviré, 2001) to be the junior synonym of the phoenicopteriform *Palaelodus ambiguous* Milne-Edwards, 1863, and thus the generic name *Probalearica* should be treated as the junior synonym of *Palaelodus*. Mourer-Chauviré (2001) gave a number of characters to distinguish *P. crataegensis* from *Balearica* and considered this species a member of the genus *Palaeogrus*. *P. moldavica* should be excluded from Gruidae (Mourer-Chauviré 2001); I agree with the latter author that the familiar or even ordinal affinity of this taxon requires confirmation. *Probalearica mongolica* was thus the only remaining species within the former genus *Probalearica,* and this one also should be moved to the genus *Grus*.

Family Rallidae Reichenbach, 1854

Pastushkinia Zelenkov, gen. nov.

Etymology: After "Pastushok", a common Russian name for rails.

Type species: *Crex zazhigini* Kurochkin, 1980.

Diagnosis: The genus can be diagnosed on the basis of the following features: distal humerus is more than twice wider (measured dorsoventrally) than deep (measured craniocaudally); cranial surface between tuberculum supracondylare ventrally and dorsal margin of the bone markedly concave; sulcus m. humerotricipitalis wide and shallow; epicondylus ventralis moderately protruding ventrally relatively to the shaft.

Comparisons: The distal humerus of *Pastushkinia* is unusually narrow in distal view (Fig. 6). It is more than twice wider that deep, while in most extant and all fossil rails the distal humerus is at maximum two times wider that deep (usually even less than that). The moderately protruding ventrally condylus ventralis and shallow and wide sulcus m. humerotricipitalis are obviously connected with the general craniocau-

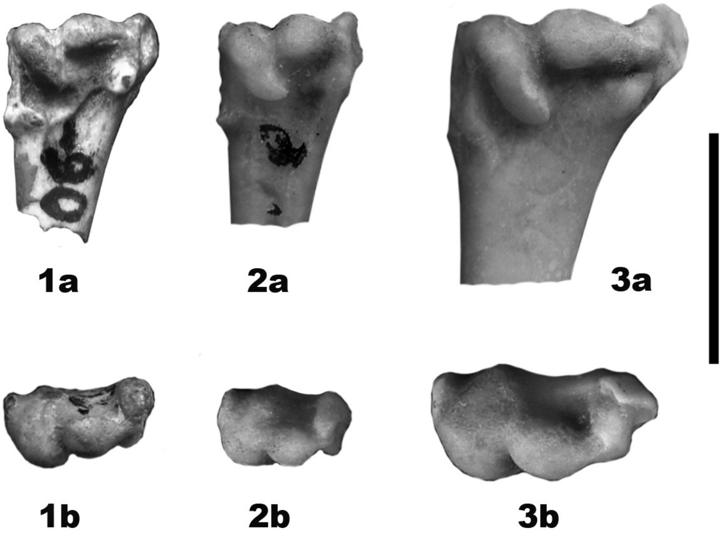

FIGURE 6. Distal humerus of *Pastushkinia zazhigini* (Kurochkin, 1980) in comparison with extant rails. **1**, *Pastushkinia zazhigini,* holotype, PIN 2614/90, distal end of left humerus in cranial (**1a**) and distal (**1b**) views; **2**, *Crex crex*, extant, in cranial (**2a**) and distal (**2b**) views; **3**, *Aramides saracura*, extant, in cranial (**3a**) and distal (**3b**) views. Scal bar equals 1 cm.

dal flatness of the distal end. A similar condition (narrow distal end with shallow sulcus) is found in *Aramides* and *Gallinula* – in both, however, the epicondylus ventralis is much more strongly protruding ventrally, in contrast to the condition of *Pastushkinia,* in which the distal end in cranial view is almost as narrow as in *Crex*. The new genus also differs from *Gallinula* and *Rallus* by unusually concave cranial surface of the distal end. This surface is however somewhat concave in *Crex* and *Aramides,* but it is absolutely flat in *Gallinula*.

Unusual flatness of the distal end further allows for distinguishing *Pastushkinia* from *Palaeoaramides* and other Neogene rail genera from which humeri are known (see Cracraft 1973; Cheneval 2000). *Pastushkinia* is similar in proportions to the genus *Belgirallus* from the Early Oligocene of Belgium (Mayr & Smith 2001), but differs from that genus by strongly protruding processus flexorius and weakly developed tuberculum supracondylare ventrale. The latter tuberculum is developed as rather broad elevated area in *Belgirallus*, while there is just a small tubercle in this position in *Pastushkinia*.

***Pastushkinia zazhigini* (Kurochkin, 1980), comb. nov.**
(Fig. 6)

v. *Crex zazhigini* Kurochkin, 1980: p. 72, figs 4, 5f.
v. *Crex zazhigini* Kurochkin: 1985, p. 69, text-fig. 31, pl. IX, figs 1, 2.

Type locality: Chono-Harayah 1, Western Mongolia, Early Pliocene (MN 14–15).

Stratigraphical and geographical distribution: Type locality only.

Holotype: HUM sin., distal portion (PIN 2614/90). Figured in Kurochkin (1980): figs 4, 5f; (1985): text-fig. 31, pl. IX, figs 1, 2.

Diagnosis: as for the genus.

Measurements: Maximum distal width, 6,2; depth of condylus dorsalis, 3.1; depth of condylus ventralis, 1.8.

Remarks: Unusual flatness of the distal end of the humerus precludes from referring the species to the extant genus *Crex* (see above). The original diagnosis (Kurochkin 1980) was based on comparisons with the extant *Crex crex* alone and as such is not valid.

Rallidae gen. indet.
(Fig. 7)

v. *Asio* aff. *otus*: Kurochkin 1985, p. 76, text.-fig. 76.

Material: Rostral fragment of sternum (PIN

2614/89), locality Chono-Harayah 1.

Remarks: The specimen was previously referred to a small owl (Kurochkin 1985), but in Strigidae a notch in the cranial outline of the sternum is visible in dorsal view. This notch is further not concave in cranial view in owls. Additionally, the cranial surface of the keel bears a ridge which is absent in the specimen from Chono-Harayah. All extant Rallidae except *Gallinula* have a pair of deep pits on the dorsal surface of the sternum just near its cranial margin. These pits are nearly absent in *Gallinula* and in the specimen in question. I however refrain from assigning this specimen to extant *Gallinula*, because such fragmentary sternum is not diagnostic enough at the genus level in birds. The oldest currently known find of this genus (*Gallinula kansarum* Brodkorb, 1967) comes from the late Early-early Late Pliocene of North America (Becker 1987). The genus has been further documented in the Early and Late Pliocene of Europe (Boev 1999; Mayr & Gregor 1999; Mlíkovský 2002).

Order Charadriiformes Fürbringer, 1888
Family Charadriidae Vigors, 1825

***Vanellus* cf. *V. leucurus* (Lichtenstein, 1823)**
(Fig. 7)

Material: COR sin. (PIN 3378/107), locality Chono-Harayah 2.

Measurements: Maximal length of the fragment, 20.5; minimal shaft width, 3.0; depth of facies articularis humeralis, 3.3.

Description and comparisons: This specimen can be assigned to Charadriidae because of presence of the foramen n. supracoracoidei and widened base of the angulus medialis. It is similar to the subfamily Vanellinae in having narrow central part of the facies articularis sternalis (well visible in caudal view) and sub-rectangle facies articularis humeralis. In Charadriinae, the facies articularis sternalis is not narrow in its central part, and facies articularis humeralis is angled cranially. The specimen from Chono-Harayah 2 is similar to *Vanellus leucurus* because of angulus medialis not curved dorsally (the angulus is curved in other *Vanellus,* including *V. gregarius*).

Remarks. The White-tailed lapwing *Vanellus leucurus* inhabits river valleys and swamps in Asian deserts. It is morphologically distinct from other *Vanellus* and once was placed into a monotypic genus *Vanellochettusia* (Kozlova 1961).

Family Laridae Bonaparte, 1831

Larus* magn. *L. ichthyaetus
(Fig. 7)

Material: Ulnare (PIN 3378/133), locality Chono-Harayah 2.

Measurements: Maximal length, 14.2.

Remarks: Extant species of the genus *Larus* can hardly be distinguished on the basis of morphology of ulnare, and thus the exact taxonomic status of this large Early Pliocene gull remains uncertain. The specimen can be referred to Laridae because of the short ramus dorsalis, and to the genus *Larus* due to the well-defined concavity on the proximal surface.

Larus* magn. *L. canus
(Fig. 7)

Material: CMC dext., distal portion (PIN 3378/85), locality Chono-Harayah 1.

Measurements: Craniocaudal depth of the distal end, 7.7.

Remarks: This specimen belonged to a gull the size of extant *L. canus,* but its fragmentary nature precludes from detailed comparisons.

Order Accipitriformes Savigny, 1809
Family Accipitridae Savigny, 1809

***Haliaeetus fortis* Kurochkin, 1985**
(Fig. 7)

Type locality: Hyargas-Nuur 2, Western Mongolia, Late Miocene (MN 13).

Stratigraphical and geographical distribution: Mongolia: Late Miocene (Hyargas-Nuur 2), Early Pliocene (Chono-Harayah 1 and 2; Tataly; MN 14–15).

Holotype: COR sin., cranial portion (PIN 3222/31). Figured in Kurochkin (1985): text.-fig. 23, pl. II, figs 9, 10.

Newly referred material: basal phalanx of the first toe sin. (PIN 3378/89+91), locality Chono-Harayah 2; second phalanx of the

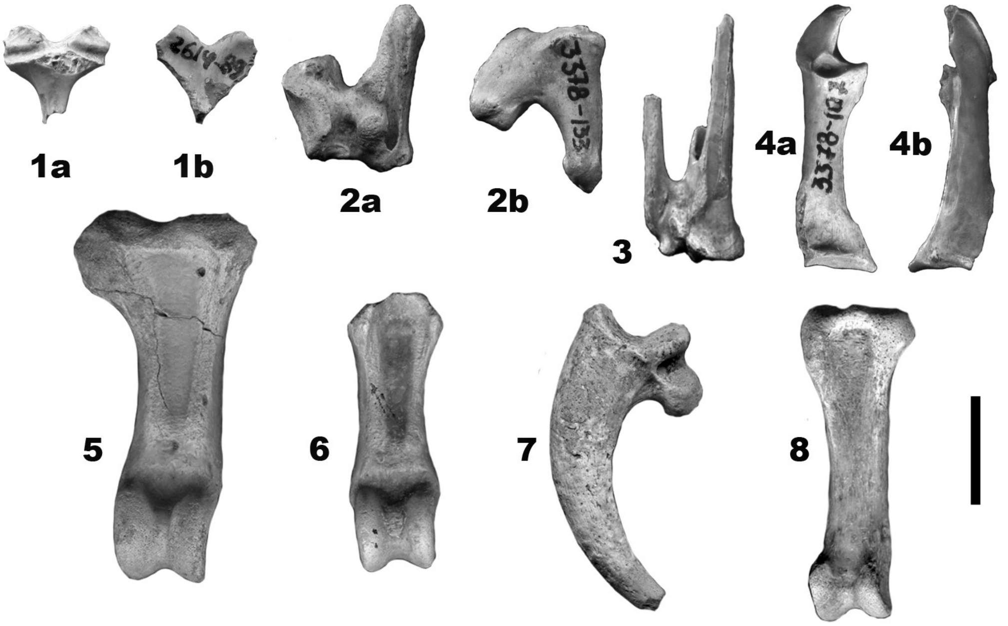

FIGURE 7. Various bird remains from the Early Pliocene of Western Mongolia. **1**, Rallidae gen. indet., fragmentary sternum, PIN 2614/89 in cranial (**1a**) and dorsal (**1b**) views; 2, *Larus* magn. *L. ichthyaetus*, left ulnare, PIN 3378/133 in ventrocaudal (**2a**) and dorsocranial (**2b**) views; **3**, *Larus* magn. *L. canus*, right distal carpometacarpus, PIN 3378/85, in ventral view; **4**, *Vanellus* cf. *V. leucurus*, left coracoid, PIN 3378/107, in dorsal (**4a**) and ventral (**4b**) views; **5–7**, *Haliaeetus fortis* (Kurochkin, 1985): **5**, basal phalanx of the first toe of left foot, PIN 3378/89+91, in ventral view; **6**, second phalanx of the second toe of right foot, PIN 3378/126, in ventral view; **7**, ungulate phalange, PIN 2614/161 in lateral view; **8**, Accipitridae gen. indet., proximal phalanx of the third digit of left foot, PIN 3378/105, in ventral view. Scale bar equals 1 cm.

second toe dext. (PIN 3378/126), locality Chono-Harayah; ungual phalanges (PIN 2614/161), locality Chono-Harayah 2 and (PIN 3376/64), locality Tataly.

Measurements of the new material: specimen PIN, 3378/89: total length, 34.6; proximal width, 17.4; proximal depth, 8.3; distal width, 8.8; distal depth, 8.4; specimen PIN, 3378/126: total length, 27.5; proximal width, 8.9; proximal depth, 10.3; distal width, 7.3; distal depth, 7.6; specimen PIN, 2614/161: proximal depth, 13.4; proximal width, 8.5; specimen PIN 3376/64: proximal depth, 11.9.

Remarks: *Haliaeetus fortis* was described from the Latest Miocene of Western Mongolia (Kurochkin 1985). Newly referred phalanges from the Early Pliocene beds agree with the holotype in relative size (roughly similar to extant *H. leucocephalus*) and on this basis are assigned to this species. The avian faunas of the Late Miocene and Early Pliocene sections of the Hyargas-Nuur formation are very similar and contain many common species (Kurochkin 1985; Zelenkov 2012), so such assignment seems to be plausible. The proximal phalanx of the first toe is somewhat larger than the corresponding bone from the Hyargas-Nuur 2 (see Kurochkin 1985) but such differences can be explained by sexual dimorphism. The first phalanx of the first digit agrees with that of extant *Haliaeetus* in its proportions and short medial (internal) process on the proximal part. The process is also short in *Gyps*, but the distal end of the phalanx in *Gyps* is twisted. The second phalanx of the second toe is also similar to those of extant *Haliaeetus* in its proportions and high articular surfaces. The ungual phalanges agrees with those of extant *Haliaeetus* in its curvature (unguals are normally considerably less curvated in other large Accipitines) and well developed (but not as robust as in *Aegypius*) flexor tubercles.

Gypaetinae indet.

Material: Proximal phalanx of the third digit sin. (PIN 3378/105), locality Chono-Harayah 2.

Measurements: total length, 29.5; proximal depth, 8.1; proximal width, 10.7; distal depth, 8.5; distal width, 7.1.

Description and comparisons: The proximal phalanx of the third toe is similar to that of extant *Gypaetus barbatus* in being elongated and relatively narrow, but differs by smaller size and considerably more asymmetrical distal articular surface and more elongated flexor tubercle. It clearly differs from those of *Haliaeetus* by its narrower proportions and thus cannot be assigned to *Haliaeetus fortis*. The specimen significantly differs from the corresponding elements of *Aegypius* and *Gyps* in several characters, including asymmetrical distal articular surface with the condyles strongly protruding ventrally.

Conclusions

The study of the new material and revision of the previously described remains of the Early

TABLE 1. A full list of taxa currently known from the Pliocene of Western Mongolia. Localities: 1 – Chono-Harayah 1; 2 – Chono-Harayah 2; 3 – Chono-Harayah 3; 4 – Zavhan; 5 – Tataly; 6 – Hung-Kureh; 7 – Zogsoo-Harhan 1; 8 – Zogsoo-Harhan 4. References: 1 – Kurochkin 1971; 2 – Kurochkin 1976; 3 – Kurochkin 1980; 4 – Kurochkin 1985; 5 – Mlíkovský & Švec 1986; 6 – Zelenkov & Kurochkin 2010; 7 – Zelenkov 2012. Taxa marked with an asterisk (*) are also recorded from the latest Miocene of Mongolia (see Kurochkin 1982, 1985; Zelenkov 2012).

Taxon name	Localities	References
**Syrmaticus kozlovae* Kurochkin, 1985	1, 2	4, 6
Perdicinae gen. indet.	2	4 (sub. *Alectoris* sp.), 6 (sub. Phasianidae gen. indet.)
**Anser* (*Chen*) *devjatkini* Kurochkin,1971	1	1, 7
**Anser* (*Chen*) *liskunae* Kurochkin, 1976	4	2, 4, 5 (sub *Olor liskunae*), 7
**Cygnus pristinus* Kurochkin, 1971	1, 2, 6, 7, 8	1, 2, 4, 5 (sub *Cygnus olor*), this study
**Cygnus* sp.	1, 2, 4, 8	4
Anserinae/Tadorninae gen. indet.	2, 5	4 (sub Tadorninae gen.)
Aix sp.	1	7
**Anas* cf. *A. pullulans* Brodkorb, 1961	2	4, 7
**Anas* magn. *A. strepera*	1, 4	4, 7
**Anas* sp.	2, 8	4 (sub *Anas molesta*), 7
**Aythya molesta* Kurochkin, 1985	3	4 (sub *Anas molesta*), 7
Aythya? *spatiosa* Kurochkin, 1976	1	2, 4, 5, 7
Podiceps solidus Kurochkin, 1985	1, 2	4; this study
**Phalacrocorax reliquus* Kurochkin, 1976	1	2, 4
Phalacrocorax mongoliensis Kurochkin, 1971	1	1, 4
**Nyctanassa kobdoena* Kurochkin, 1976	1	2, 4; this study
**Ciconia lucida* Kurochkin, 1982	1	4
**Urmiornis dzabghanensis* (Kurochkin, 1985)	2; 4; 8	4
Otididae gen. indet.	2	this study
Grus mongolicus (Kurochkin, 1985)	1	4; this study
Pastushkinia zazhigini (Kurochkin, 1980)	1	3, 4 (sub. *Crex zazhigini*), this study
Rallidae gen. indet.	1	4 (sub *Asio* aff. *otus*), this study
Vanellus cf. *V. leucurus*	2	this study
Limosa lacrimosa Kurochkin, 1985	1	4
Larus magn. *L. ichthyaetus*	2	this study
Larus magn. *L. canus*	1	this study
**Haliaeetus fortis* Kurochkin, 1985	1, 2, 5	this study
Accipitridae indet. (aff. ?*Gypaetus*)	2	this study
**Syrrhaptes* sp.	1	4

Pliocene birds from Western Mongolia broaden the list of taxa currently known from the Hyargas-Nuur formation and provide evidence for systematic position of some taxa described earlier. A bustard, two species of gulls, a gypaetine raptor, and a lapwing are for the first time documented in the Early Pliocene of Asia and represent the oldest finds of the corresponding evolutionary lineages in Asia. The find of a lapwing very similar to extant *V. leucurus* is especially interesting and present evidence for a long history of this charadriid bird in Asia, now inhabiting only arid zone. Two more bird taxa, *Podiceps solidus* and *Haliaeetus fortis* were initially described from the Late Miocene sediments but are now known from the Early Pliocene of the same area. The crane *Probalearica mongolica* belongs to the extant genus *Grus*; the presumed corncrake *Crex zazhigini* is moved to a separate genus *Pastushkinia*; the generic position of the heron *Nyctanassa kobdoena* remains uncertain, but further materials may prove its separate generic status. Owls are not yet reported from the Pliocene of Asia since the presence of the genus *Asio* in the Early Pliocene of Mongolia is deleted.

Acknowledgements

I am grateful to Zlatozar Boev (National Museum of Natural History, Bulgarian Academy of Sciences, Sofia) and Federico Agnolin (Museo Argentino de Ciencias Naturales „Bernardino Rivadavia“, Buenos Aires) for their reviews of the manuscript, and also to Albrecht Manegold (Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt/Main) for useful taxonomic comments. The study was supported by the grants from the Russian Foundation of the Basic Research and from a grant from the President of Russian Federation (MK-7463.2013.4).

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

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Early Pleistocene fossil birds from Cava Sud, Soave (Verona, North-Eastern Italy)

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Abstract — The analysis of the fossil bird remains found in the Early Pleistocene deposits of Cava Sud, one of the localities of the so-called "Brecce di Soave", is presented. The fossil remains have been found in some fissure fillings opened in the Eocene limestone and exploited by quarry activities. The fossil bird bones were associated with macro- and micromammals and the whole association is referred to the late Early Pleistocene MNQ 19 on the basis of the taxonomy and evolutionary degree of the micromammals. This study reveals the presence of at least 14 taxa and Cava Sud testifies the oldest occurrence of some of them, particularly *Rallus aquaticus* and *Strix nebulosa*, and the oldest Italian record of *Carduelis chloris*. The species identity of *Corvus pliocaenus* is also discussed and confirmed. Our results also support the hypothesis that the late Early Pleistocene represents the beginning of the present-day European avifauna, as the fossil associations of this age comprise mostly extant taxa. The bird taxa found at Cava Sud allow making palaeoenvironmental reconstructions of the area, suggesting the presence of dense woodlands and open grassy environment.

Key words: Birds, Early Pleistocene, Italy, paleoenvironment, *Strix nebulosa*

Introduction

The locality of Cava Sud is one of the various localities of the so-called "Brecce di Soave". This term is used to define a karst filling complex occurring in the Eocene limestone exposed and extensively quarried near the village of Soave (Verona, NE Italy). The fissures are filled by white or reddish not cemented calcareous sands and locally contain fossil vertebrates (Pasa 1947; Bona & Sardella 2012). The fossiliferous deposits have been described and studied since the first half of the 19th century (Scortegagna 1844).

The deposits of Cava Sud are the oldest of the entire karst network and are referable to the late Early Pleistocene, as Cava Sud is the type-locality of the Arvicolinae *Microtus* (*Allophaiomys*) *ruffoi* described by Pasa (1947), a key species for the biochronology of the Italian late Early Pleistocene (Sala & Masini 2007; Marcolini *et al.* 2013). In particular, Cava Sud is one of the localities referred to the "Pirro Nord Faunal Unit" of the Italian biochronological scheme (Gliozzi *et al.* 1997), corresponding to the MNQ 19, around 1.5 Ma. The complete list of mammals from Cava Sud is listed in Bon *et al.* (1991).

Most of the fossil remains collected at Cava Sud are of small dimensions, resulting that the association is dominated by small-sized taxa and/or small-sized bones of bigger taxa. Most of the bird bones are presented by very fragmented long bones, so they can only be referred to small-sized Passeriformes or Aves indeterminate. In addition, the bones are not very well preserved, as they are slightly decalcified, and the complete long bones are extremely rare, except for some pedal phalanges, explaining the relatively scarce number of taxa identified at specific level.

FIGURE 1. Geographic location of Cava Sud, near the village of Soave, Verona County, in the North-Eastern Italy.

Mourer-Chauviré (1980) partially analysed the fossil birds from Cava Sud and reported the presence of *Palaeocryptonyx* sp., Alaudidae and *Corvus pliocaenus*. More recently, one of us (CB) studied the complete fossil bird assemblage and reported the presence of 16 taxa (Bedetti 2003). Aim of this paper is the completion of the study of the fossil of birds collected by Pasa during the first half of the 20th Century (Pasa 1947) and stored at the Museo di Storia Naturale of Verona, Italy.

Material and Methods

The bird material collected at Cava Sud is entirely stored at the Museo Civico di Storia Naturale of Verona (MCSN V). The fossil bones were compared with recent bird skeletons stored in the Dipartimento di Scienze della Terra, Universiy of Torino, Italy (Marco Pavia Ornithological Collection, MPOC), in the Museo Civico di Storia Naturale di Carmagnola, Torino, and in the Laboratoire de Géologie de Lyon, Université Claude Bernard Lyon 1, Villeurbanne, France. Osteological terminology used in this publication principally follows Baumel & Witmer (1993); measurements were taken after von den Driesch (1976) and Göhlich & Mourer-Chauviré (2005). The systematic order and the nomenclature for the extant taxa is following del Hoyo *et al*. (1992, 1994, 1996, 1999, 2004, 2009, 2011), including the author names of the extant bird taxa.

Systematic Paleontology

The present analysis refines the conclusions reached by Bedetti (2003) and allows us to define the fossil bird assemblage of Cava Sud. It is constituted by 14 taxa: *Branta* sp., *Palaeocryptonyx donnezani*, cf Tetraoninae indet., *Aquila* sp., *Rallus aquaticus*, Charadriiformes indet., *Bubo bubo*, *Strix nebulosa*, Strigidae indet., *Alauda arvensis*, *Corvus pliocaenus*, *Carduelis chloris*, *Emberiza* sp., Passeriformes indet. Synonymy lists have been provided only for the fossil species.

Order Anseriformes Wagler, 1831
Family Anatidae Vigors, 1825
Genus Branta Scopoli, 1769

***Branta* sp.**

Material: Cranial fragment of left scapula (MCSN V12400); distal right radius (MCSN V12420); left os carpi ulnare (MCSN V12328a).

Remarks: The three fragments are of a middle- to big-sized Anatidae thus comparable with the genera *Branta* and *Tadorna* among the Palaearctic Pleistocene taxa. The fossil can be referred to the genus *Branta* for the size, bigger than *Tadorna*, and the following characteristics, which are absent in *Tadorna*: a small fossa on the lateral surface of the scapula, just below the facies articularis humeralis; a shallow sulcus tendinosus in the distal radius and the wider incisura metacarpale in the os carpi ulnare. The dimensions of the bones are comparable with *Branta leucopsis*, the biggest European species of the genus (Bacher 1967), but their fragmentary status do not allow to better the determination above the genus level.

Order Galliformes Temminck, 1820
Family Phasianidae Vigors, 1825
Genus *Palaeocryptonyx* Depéret, 1892

Palaeocryptonyx donnezani Depéret, 1892
(Fig. 2A–E, G–H)

*1892 *Palaeocryptonyx donnezani* – Depéret: 691.
*pars 1897 *Palaeocryptonyx Donnezani* Depéret, 1892 – Depéret: 131–134; pl. 13, figs 2–10 [non pl. 13, figs 3–3a, 4–4a, 7–7a, 10–10a].
*pars 1897 *Turdus* aff. *cyaneus* [sic *Turdus cyanus* = *Monticola solitarius*] Linnaeus, 1766 – Depéret: 137–138, pl. 13, figs 23–23a.
1933 *Palaeocryptonyx donnezani* Depéret, 1890 [sic] – Lambrecht: 438.
1954 ?*Palaeocryptonyx donnezani* Depéret, 1892 – Thenius: 49–50.
1964 *Palaeocryptonyx donnezani* Depéret, 1892 – Brodkorb: 316–317.
* 1980 *Palaeocryptonyx* sp. – Mourer-Chauviré: 355.
1996 *Palaeocryptonyx donnezani* Depéret, 1892 – Mlíkovský: 188.
1997 *Palaeocryptonyx donnezani* Depéret, 1892– Bocheński: 309.
1998 *Palaeocryptonyx donnezani* Depéret, 1892 – Mlíkovský: 136.
1998 *Palaeocryptonyx donnezani* Depéret, 1892 – Tyrberg: 522.
pars 2002a *Alectoris donnezani* (Depéret, 1892) – Mlíkovský: 159–161.
2002b *Coturnix donnezani* (Depéret, 1892) – Mlíkovský: 60.
* 2003 *Palaeocryptonyx donnezani* Depéret, 1892 – Bedetti: 78–79, Pl. 3, Figs n, q.
*pars 2003 *Perdix* n. sp. – Bedetti: 78–79.
2009 *Palaeocryptonyx donnezani* Depéret, 1892 – Sánchez-Marco: 1150, fig 2a–c.
* 2012a *Palaeocryptonyx donnezani* Depéret, 1892 – Pavia *et al.*: 258–262, figs 1, 2B.
* 2013 *Palaeocryptonyx donnezani* Depéret, 1892 – Bedetti & Pavia: 36–37, pl. 1, figs o–p.

Material: Two proximal right humeri (MCSN V12322c, MCSN V12340); left ulna (MCSN V12341), proximal right ulna (MCSN V12319d); two left carpometacarpi (MCSN V12339a, MCSN V12339d), distal left carpometacarpus (MCSN V12339e), right carpometacarpus (MCSN V12319e), two distal right carpometacarpi (MCSN V12339d, MCSN V12339f); three distal tibiotarsi (MCSN V12322d, MCSN V12333, MCSN V12344a), right tibiotarsus (MCSN V12319c); proximal left tarsometatarsus (MCSN V12334), distal left tarsometatarsus (MCSN V12322e), right tarsometatarsus (MCSN V12318d).

Measurements: See Table 1.

Description: In the fossil bones from Cava Sud there are some bone of a small-size Phasianidae, smaller than the extant *Perdix perdix* and larger than *Coturnix coturnix*. All the bones can be referred to *Palaeocryptonyx donnezani* following the characteristics pointed out by Pavia *et al*. (2012). In particular, the coracoid is not pneumatised, the humerus shows the two pneumatic fossae pneumotricipitalis with lamella and substantia spongiosa in the ventral one, the carpometacarpus shows a well-developed processus intermetacarpalis and the facies articularis digitalis more distally than the convex part of the facies articularis digitalis major, and the distal tibiotarsus is slender. It is also noteworthy to note that the material of Cava Sud allow us to describe and illustrate for the first time the ulna and the tarsometatarsus of *P. donnezani*, as the latter is not present in the type-series while the former is only represented by the distal part (Pavia *et al.* 2012a). The ulna is relatively short and bent with the proximal end ventrodorsally compressed and the cross section triangular; the margo interossea is well developed and the olecranon is sharp in caudal view and in continuation of the shaft bending; the impressio musculi brachialis is superficially and clearly bordered. In the distal end, the condylus ventralis ulnae is well developed and pointed distally and the tuberculum carpale tends cranially. The tarsometatarsus is slender, with the proximal end narrower than the distal one and no evidence of spur; the crista medianoplantaris is absent with the hypotarsus situated slightly laterally; the fossa infracotylaris dorsalis is well pronounced and the sulcus extensorius is shallow. The plantar side of the shaft is raised and smooth, with the cristae slightly evident; in the distal part, the throchlea 4 distally surpassed trochlea II and the trochlea II and IV are equally bent plantarly.

Remarks: After the present study we can better precise the specific attribution of the material from Cava Sud, previously indicated as *Palaeocrytonyx* sp. by Mourer-Chauviré (1980). The type-series of *P. donnezani* has recently been re-examined by Pavia *et al.* (2012a) with the selection of lectotype and paralectotypes and also the assessment of the systematic identity of the species. The recently described *Palaeocryptonyx novacki* Sánchez-Marco, 2009 from the Late Pliocene of Spain can be excluded because it is overall smaller and shows some morphological

FIGURE 2. Bones of non-Passeriformes from the late Early Pleistocene of Cava Sud (Verona, N-E Italy). *Palaeocryptonyx donnezani*: A, proximal right humerus (MCSNV V12322c), caudal view; B-C, right carpometacarpus (MCSNV V12319e), ventral (B) and dorsal (C) views; D-E, left ulna (MCSNV V12341), ventral (D) and medial (E) views; G-H, right tarsometatarsus (MCSNV V12318d), dorsal (G) and plantar (H) views. *Strix nebulosa*: F, distal right tarsometatarsus (MCSNV V12422), dorsal view; I, right phalanx 1-III (MCSNV V12328h), dorsal view. *Aquila* sp.: J, right phalanx 1-II (MCSNV V12328b), dorsal view. *Rallus aquaticus*: K, distal right tibiotarsus (MCSNV V12344b), cranial view. The scale bars represent 5 mm.

differences in many of the long bones (Sánchez-Marco 2009: 1152–1153). The present analysis adds some important information to the knowledge of the species, as we described some bones previously unknown. *Palaeocryptonyx donnezani* is the only small-sized Galliformes found at Cava Sud, as the remains of *Perdix* n. sp. reported by Bedetti (2003) have been referred here to *P. donnezani*.

This species is reported from the Early Pliocene, Ruscinian MN 15, of France to the Early/Middle Pleistocene, late Villafranchian/Biharian MNQ 20–21, of various localities (Sanchez-Marco 2009; Pavia *et al*. 2012a; Bedetti & Pavia 2013).

Subfamily Tetraoninae Vigors, 1825

cf. Tetraoninae indet.

Material: distal right tarsometatarsus (MCSN V12348).

Remarks: The bone is very poorly preserved with also the trochlea II and IV broken off. However, the general morphology recalls that of Phasianidae and, in particular, its robustness suggests the taxonomic attribution to the Tetraoninae, even if only tentatively.

Order Accipitriformes Vieillot, 1816
Family Accipitridae Vieillot, 1816
Genus *Aquila* Brisson, 1760

Aquila sp.
(Fig. 2J)

Material: right distal tarsometatarsus (MCSN V12318a); left phalanx 1-II (MCSN V12328b); two left phalages 3-III (MCSN V12328c, MCSN V12328d); left phalanx 4-III (MCSN V12319a).

Remarks: The tarsometatarsus was previously referred to *Circaetus gallicus* by Bedetti (2003), but the morphology of the lateral side of the distal part of the bone, in particular the shape of the groove proximally to the foramen vasculare distale is more similar to *Aquila* than to *Circaetus*. The five bones can be referred to a small sized *Aquila*, such as *Aquila clanga*, but their scarce number and the quality of preservation do not allow referring these specimens to specific-level taxon.

Order Gruiformes Bonaparte, 1854
Family Rallidae Vigors, 1825
Genus *Rallus* Linnaeus, 1758

Rallus aquaticus Linnaeus, 1758
(Fig. 2K)

Material: Cranial fragment of a left coracoid (MCSN V12411); distal right tibiotarsus (MCSN V12344b).

Measurements: See Table 1.

Remarks: The morphology of the two bones clearly reflects that of the Rallidae. In particular the coracoid shows a shallow sulcus on the cranial surface of the diaphisys and the facies articularis humeralis is laterally well expanded; the tibiotarsus shows the condylus medialis clearly smaller and thinner than the condylus lateralis with the incisura intercondylaris asymmetrical in dorsal view. Among the Rallidae the bones are similar in size to *Rallus aquaticus* or *Crex crex*, but match better in dimension with the first, which is overall smaller than those of *C. crex*, and because the sulcus on the cranial surface of the coracoid is as deep as in *R. aquaticus*, whereas it is less deep in *Crex crex*.

Rallus aquaticus is reported from the Early Pleistocene of Ubeidiya in Israel (Tchernov 1980), a site little younger in age than Cava Sud. Thus, the Italian record represents the oldest occurrence of the species, given that the record from the Late Pliocene of Csarnóta, Hungary (Jánossy 1979) is only dubious.

Order Charadriiformes Huxley, 1867

Charadriiformes indet.

Material: left scapula (MCSN V12407); caudal fragment of a right coracoid (MCSN V12410).

Remarks: The bones can be referred to a middle-sized Charadriiformes, similar in size to *Pluvialis apricaria*, but the remains are too fragmentary to better define their taxonomic affinities.

Order Strigiformes Wagler, 1830
Family Strigidae Vigors, 1825
Genus *Bubo* Duméril, 1806

Bubo bubo (Linnaeus, 1758)

Material: distal right humerus (MCSN V12423); distal left tarsometatarsus (MCSN V12425).

Remarks: The bones described here can easily be referred to a big-sized Strigidae. The osteological morphology of this species is quite unique in the Palaearctic avifauna and it can only be confused with *Bubo scandiacus* (former

Nyctea scandiaca, recently placed in the genus *Bubo* by Sangster *et al.* 2004). A detailed analysis of the osteological differences between these two species has been made by Bedetti & Pavia (2007), based on which the bones from Cava Sud can be referred to *Bubo bubo*.

This species is known from the Early Pliocene of various European localities (Mlíkovský 2002a).

Genus *Strix* Linnaeus, 1758

Strix nebulosa Forster, 1772

(Fig. 2F, I)

Material: distal left tibiotarsus (MCSN V12421); distal right tarsometatarsus (MCSN V12422); left phalanx 2-II (MCSN V12328i); right phalanx 1-III (MCSN V12328h); right phalanx 3-IV (MCSN V12328j); right phalanx 4-IV (MCSN V12328k); right phalanx 5-V (MCSN V12328l).

Measurements: See Table 1.

Remarks: The fossils described here belong to a large-sized Strigidae, smaller than *Bubo bubo*. The morphological characteristics recall those to the genus *Strix*, also according to Langer (1980). In the Palaearctic, six species of the genus *Strix* have been recorded, both living and fossils (Mourer-Chauviré 1975; Ballmann 1976; del Hoyo *et al.* 1999). The size of the remains from Cava Sud is comparable only to those of *Strix nebulosa*, the biggest species of the genus (del Hoyo *et al.* 1999).

Strix nebulosa is known from the Middle Pleistocene, MNQ 21, of Stránská Skála, Czech Republic (Mlíkovský 2002b), and in general it is rarely reported as a fossil (Tyrberg 1998, 2012). The record from Cava Sud represents the oldest occurrence of the species.

Strigidae indet.

Material: Right phalanx 1-II (MCSN V12328g); left phalanx 5-IV (MCSN V12319f).

Remarks: The two posterior phalanges clearly belong to a small-sized Strigidae, slightly bigger in size to both *Athene noctua* and *Aegolius funereus*. Unfortunately the bones are not very well preserved and thus we are not able to refer these specimens to a more precise taxon, even at generic level.

Order Passeriformes Linnaeus, 1758
Family Alaudidae Vigors, 1825
Genus *Alauda* Linnaeus, 1758

Alauda arvensis Linnaeus, 1758

(Fig. 3H)

Material: right humerus (MCSN V12364); three proximal right humeri (MCSN V12361a, MCSN V12361b, MCSN V12362); proximal left humerus (MCSN V12361c).

Remarks: The humeri listed above can clearly be attributed to an Alaudidae, following the morphological characteristics listed by Jánossy (1983) and Moreno (1985). The overall size of the bones is comparable with both *Alauda arvensis* and *Galerida* spp. (Jánossy 1983), but the morphology of the caput humeri, which is — like in *Alauda arvensis* — less prominent and of the crista deltopectoralis, which is gradually joining the diaphysis and not forming a step like in *Galerida* spp., allow us to refer these bones to *Alauda arvensis*. In addition, many of the bones of Passeriformes indet. could be referred to Alaudidae, but their fragmentary status does not allow their better taxonomic attribution.

The species has already been reported from the Italian locality of Pirro Nord (Bedetti & Pavia 2013), similar in age with Cava Sud, thus the present record is a confirmation of the occurrence of this taxon from the Early Pleistocene onwards.

Family Corvidae Vigors, 1825
Genus *Corvus* Linnaeus, 1758

Corvus pliocaenus (Portis, 1889)

(Fig. 3A–D, G)

* 1887 *Numenius* sp. (*Pliocaenus*) – Portis: 195 [nomen nudum].
* 1889 *Numenius* sp. (*pliocaenus*) – Portis: 13, pl. I, figs 26a–26b.
* 1902 *Corvus* [*pliocaenus* ?] Portis, 1889 – Regàlia: 220, pl. 27 (1), fig. 1.
1975 *Corvus pliocaenus* Portis, 1889 – Mourer-Chauviré: 236.
1978 *Corvus pliocaenus* Portis, 1889 – Brodkorb: 158.
* 1980 *Corvus pliocaenus* Portis, 1889 – Mourer-Chauviré: 355.
1997 *Corvus pliocaenus* Portis, 1889 – Bocheński: 325.
1998 *Corvus pliocaenus* Portis, 1889 – Tyrberg: 582.
*pars 2002a *Corvus corone* Linnaeus, 1758 – Mlíko-

FIGURE 3. Bones of Passeriformes from the late Early Pleistocene of Cava Sud (Verona, N-E Italy). *Corvus pliocaenus*: A-B, distal left ulna (MCSNV V12332b), ventral (A) and dorsal (B) views; C, proximal left ulna (MCSNV V12343), medial view; D, distal left tarsometatarsus (MCSNV V12336), dorsal view; G, right phalanx 1-I (MCSNV V12323a), dorsal view. *Carduelis chloris*: E, maxillary fragment (MCSNV V12338), dorsal view; F, recent skull for comparison (MPOC 153), dorsal view. *Alauda arvensis*: H, right humerus (MCSNV V12364), caudal view. The scale bars represent 5 mm.

vský: 232.
* 2003 *Corvus pliocaenus* Portis, 1889 – Bedetti: 78, pl. V, figs m–n and p–r.
* 2012 *Corvus pliocaenus* Portis, 1889 – Rook *et al.*: 7, figs 8F–8G.
* 2013 *Corvus pliocaenus* Portis, 1889 – Bedetti & Pavia: 45, pl. 2, figs r–v.

Material: left quadratum (MCSN V12413a); three right quadrata (MCSN V12389, MCSN V12405, MCSN V12413); cranial fragment of a right coracoid (MCSN V12311); left scapula (MCSN V12404); distal left humerus (MCSN V12342a); distal right humerus (MCSN V12342b); proximal left ulna (MCSN V12343); distal left ulna (MCSN V12332a); two distal right ulnae (MCSN V12332b, MCSN V12424); three left ossa carpalia (MCSN V12331a, MCSN V12331b, MCSN V12322b); three distal left carpometacarpi (MCSN V12317, MCSN V12330a, MCSN V12330b); right proximal carpometacarpus (MCSN V12319b); right phalanx 1 digiti majoris (MCSN V12401); three distal right femora (MCSN V12346, MCSN V12347a,

TABLE 1. Measurements (in mm) of the bones of selected taxa from the Early Pleistocene of Cava Sud. Measurements of bones that are slightly worn or damaged are given in parentheses.
Abbreviations: GL, greatest length; Wp, proximal width; Dp, proximal depth; Wd, distal width; Dd, distal depth; Ws, smallest width of shaft; Ds, depth of the shaft; Dpm, smallest proximal depth without hypotarsus; Dpt, proximal depth with tuberculum flexorius; Wtf, width of tuberculum flexorius.

	GL	Wp	Dp	Wd	Dd	Ws	Ds	Dpm	Dpt	Wtf
Palaeocryptonyx donnezani										
Humerus MCSNV V12322c	–	10.8	5.0	–	–	–	–	–	–	–
Ulna MCSNV V12319d	–	4.9	6.9	–	–	–	–	–	–	–
Ulna MCSNV V12341	38.4	4.9	6.8	5.4	4.3	2.4	3.2	–	–	–
Carpometacarpus MCSNV V12319e	24.5	6.5	3.7	4.9	2.7	2.1	2.4	–	–	–
Carpometacarpus MCSNV V12339a	25.9	6.5	4.0	5.5	2.7	2.3	2.7	–	–	–
Carpometacarpus MCSNV V12339b	24.7	7.1	3.8	5.4	3.1	2.3	3.9	–	–	–
Carpometacarpus MCSNV V12339c	–	–	–	5.1	2.6	2.3	2.4	–	–	–
Carpometacarpus MCSNV V12339d	–	–	–	5.2	3.1	2.3	2.6	–	–	–
Tibiotarsus MCSNV V12319c	–	–	–	6.0	5.7	(3.0)	–	–	–	–
Tibiotarsus MCSNV V12322d	–	–	–	6.4	3.6	–	–	–	–	–
Tibiotarsus MCSNV V12333	–	–	–	5.5	5.7	–	–	–	–	–
Tarsometatarsus MCSNV V12318d	36.8	6.4	6.1	7.1	5.1	2.9	2.5	3.9	–	–
Tarsometatarsus MCSNV V12322e	–	–	–	7.5	5.1	–	–	–	–	–
Tarsometatarsus MCSNV V12334	–	7.1	6.1	–	–	3.4	2.9	4.1	–	–
Rallus aquaticus										
Tibiotarsus MCSNV V12344b	–	–	–	5.4	5.7	–	–	–	–	–
Strix nebulosa										
Tarsometatarsus MCSNV V12422	–	–	–	15.7	11.9	–	–	–	–	–
Phalanx 2-II MCSNV V12328i	25.1	6.1	6.5	4.6	5.4	5.1	4.2	–	–	–
Phalanx 1-III MCSNV V12328h	10.4	8.8	7.5	7.2	5.8	6.3	4.6	–	–	–
Phalanx 3-IV MCSNV V12328j	7.2	5.4	5.5	4.7	4.9	4.6	4.1	–	–	–
Phalanx 5-V MCSNV V12328l	–	4.8	6.4	–	–	–	–	–	8.9	3.8
Corvus pliocaenus										
Coracoid MCSNV V12311	–	6.6	8.4	–	–	3.9	3.5	–	–	–
Humerus MCSNV V12342a	–	–	–	16.9	8.1	–	–	–	–	–
Humerus MCSNV V12342b	–	–	–	15.2	7.8	–	–	–	–	–
Ulna MCSNV V12332a	–	–	–	8.2	7.1	4.8	4.8	–	–	–
Ulna MCSNV V12343	–	11.5	10.7	–	–	–	–	–	–	–
Ulna MCSNV V12424	–	–	–	9.8	6.9	–	–	–	–	–
Carpometacarpus MCSNV V12319b	–	11.5	10.7	–	–	–	–	–	–	–
Carpometacarpus MCSNV V12330b	–	–	–	11.4	4.9	4.0	4.9	–	–	–
Carpometacarpus MCSNV V12330c	–	–	–	10.3	4.6	4.1	4.2	–	–	–
Carpometacarpus MCSNV V12343	–	11.7	6.7	–	–	–	–	–	–	–
Femur MCSNV V12347a	–	10.5	5.9	–	–	–	–	–	–	–
Femur MCSNV V12347b	–	10.9	5.6	–	–	4.8	4.7	–	–	–
Tarsometatarsus MCSNV V12336	–	–	–	6.5	4.4	3.8	4.4	–	–	–
Phal, 1 digit I MCSNV V12323a	21.7	6.1	4.6	4.2	3.2	3.7	2.6	–	–	–

MCSN V12347b); distal left tarsometatarsus (MCSN V12336); two left phalanges 1-I (MCSN V12379a, MCSN V12379b); right phalanges 1-I (MCSN V12323a).

Measurements: See Table 1.

Description: The measurements of the bones of *Corvus pliocaenus* fall within the same size-class of *Corvus corone* but, on average, are slightly bigger in all elements (Tomek & Bocheński 2000), whereas the general morphology is more similar to that of *Corvus corax* (also according to Bedetti & Pavia 2013). More in detail, the coracoid of *C. pliocaenus* is stouter than the one of *C. corone* with the processus acrocoracoideus not pointed as in *C. corone*. The tuberculum coracoideum in the scapula is wider and less developed than in *C. corone*. In the proximal ulna the ventral side of the cotyla ventralis is more pronounced in *C. pliocaenus* and the notch on the olecranon is absent (Tomek & Bocheński 2000); the incisura tendinosa in the distal ulna is deeper than in *C. corone* and the tuberculum carpale is pointed cranially as in *C. corax* and not proximally as in *C. corone*. In the carpometacarpus of *C. pliocaenus* the processus extensorius is bigger than in *C. corone* and the processus intermetacarpalis more proximal than *C. corax* and *C. corone* with the spatium intermetacrpalis thinner. The long depressio along the shaft of the phalax 1 digitorum majoris in *C. pliocaenus* is deep and begins very close to the proximal part of the bones, more than in *C. corone* and *C. corax*, the proximal surface is more similar to the other two species than previously indicated by Bedetti & Pavia (2013). The tarsometatarsus is more similar to that of *C. corax* in having a broader groove in the plantar side of the trochlea metatarsi III and a small tuberculum in the distal part of the small crest on the medial side of the bone in plantar view. The phalanx 1-I is stouter than in *C. corone* with the proximal end proportionately wider.

Remarks: This species has been reported from various European localities since the Late Pliocene (Portis 1889; Mlíkovský 2002a) and survives up to the Middle Pleistocene (Tyrberg 1998). From the Middle Pleistocene of France, Mourer-Chauviré (1975) described the subspecies *Corvus pliocaenus janossyi*, slightly bigger than the nominate one, only reported from three localities. Mlíkovský (2002a) considered *C. pliocaenus* as a junior synonym of *C. corone*, whereas *C. p. janossy* was synonymized with *C. corax*, both on the basis of the measurements, without considering the morphology. Mlíkovský (2002a) also followed Brodkorb (1978) in considering both *C. praecorax* and *C. betfianus* as synonyms of *C. pliocaenus*. The relationships among the various extinct big-sized species of the genus *Corvus* is beside the aim of this paper, and also we are not able to discuss here the validity of the Middle Pleistocene subspecies *Corvus pliocaenus janossy* and its systematic rank, but the morphological characteristics shown by the Cava Sud remains, together with the material recently described from the coeval locality of Pirro Nord (Bedetti & Pavia 2013) allow to confirm *Corvus pliocaenus* as a valid species.

Family Fringillidae Vigors, 1825
Genus *Carduelis* Brisson, 1760

Carduelis chloris (Linnaeus, 1758)
(Fig. 3E)

Material: fragmented maxilla (MCSN V12338).

Remarks: The conical morphology of the bill fragment clearly indicates its relationships with the Fringillidae. In particular, it is wider than any other species of the family except *Coccothraustes coccothraustes*, which is clearly bigger and more robust; thus this fragment can be attributed to *Carduelis chloris*, also following the indication of Moreno (1985).

This species is reported from coeval localities in France and Spain (Mlíkovský 2002a) but Cava Sud represents the oldest Italian record for this taxon.

Family Emberizidae Vigors, 1831
Genus *Emberiza* Linnaeus, 1758

Emberiza sp.

Material: Four proximal right humeri (MCSN V12314a, MCSN V12375a, MCSN V12375b, MCSN V12375c).

Remarks: The four humeri clearly show the morphological characteristics of the family Emberizidae, as described by Jánossy (1983) and Zelenkov & Kurochkin (2012), in particular the shape of the fossae pneumotricipitalis and the squared crista deltopectoralis. The various species of the genus *Emberiza* are morphologically very similar even in the humerus and the fragmentary status of the bones from Cava Sud do not allow to better the taxonomic attribution.

Discussion

The high degree of fragmentation of the bird material coming from Cava Sud is probably due to the taphonomic history of the deposits, as the fossils were found in fissure fillings with the bigger bones probably already fragmented by diagenesis, and to the excavation techniques possibly too aggressive for the preservation of fragile bird bones, as a greater attention was dedicated to the recovery of micro-mammal teeth. Because of their high fragmentation, which only allows us to determine a low percentage of the whole bird remains below the family level, the faunal composition of the Early Pleistocene of Cava Sud is not very rich, but we can make some palaeoenvironmental reconstruction, even if only qualitative as it is not possible to evaluate the relative importance of the various taxa. The palaeoenvironment reconstruction based on living bird taxa, which are the majority from Cava Sud, is normally extremely significant, as the ecological needs and characteristics of modern birds are very well studied and understood (Pavia & Bedetti 2004).

The relative abundance of Alaudidae recognized at Cava Sud allow to hypothesize the presence of an open grassy habitat, possibly inhabited also by the extinct *Palaeocryptonyx donnezani*. Other areas were probably covered by dense forest, as suggested by the Tetraoninae and *Strix nebulosa*, as the latter one only inhabits the taiga forest in the Boreal region (del Hoyo *et al.* 1999). Other taxa, such as *Bubo bubo* and probably the extinct *Corvus pliocaenus*, are generalist and so do not give any precise paleoenvironmental indication.

During the European Early Pleistocene we observe the extinction of most of the Pliocene bird taxa of Neogene origin, substituted by the modern taxa (Mourer-Chauviré 1993). In fact, the Pliocene fossil bird associations are normally characterized by a great number of extinct taxa, some of them on the lineage of the recent ones (Emslie 1998; Olson & Rassmussen 2001; Boev 2002; Zelenkov & Kurochkin 2012). On the other hand, starting from around 1.5 Ma on, one can observe that the European fossil bird association are composed mostly by extant taxa (Tyrberg 1998), with only few taxa already present in older sites, such as *Palaeocryptonyx donnezani* and *Corvus pliocaenus* (Tyrberg 1998; Bedetti 2003; Pavia *et al.* 2012a, b). This is particularly evident in the Italian site of Pirro Nord, where more than 40 bird taxa have been detected (Pavia *et al.* 2012b; Bedetti & Pavia 2013), but only three extinct species: *Perdix* n. sp., *Palaeocryptonyx donnezani* and *Corvus pliocaenus*. The site of Cava Sud is biochronogically coeval with Pirro Nord, only a little older, following the evolutionary degree of the micromammals (Marcolini *et al.* 2013) and confirms what was observed already at Pirro Nord: the scarce importance of birds as biochronological tool from the late Early Pleistocene onwards. As a matter of fact we report here the first occurrence of *Strix nebulosa* and *Rallus aquaticus* and the oldest Italian occurrence of *Carduelis chloris* (Tyrberg 1998, 2012; Bedetti 2003), adding new data on the early history of the extant bird species.

Conclusions

This paper updates the knowledge of the fossil bird association coming from the late Early Pleistocene fissure fillings of Cava Sud. In addition new information about the chronological and geographical distribution of some recent and fossil bird species is given from an area, the Northern Italy, with few fossiliferous localities of that time-span (Bedetti, 2003). The fossil bird association of Cava Sud shows the composition of a modern-type avifauna, also shown by other bird association of the Early Pleistocene around 1.5 Ma. Despite the low number of taxa determined at generic or specific level, some of them are congruent with the coeval site of Pirro Nord, Southern Italy (Bedetti & Pavia 2013) and Monte Argentario (Bedetti 2003; Pavia unpubl. data), with the exception of the Tetraoninae and *Strix nebulosa*. This difference is probably related to the paleoenvironment of Cava Sud around 1.5 Ma, characterized by open grassy habitat with dense Alpine woodlands, while the other sites were characterized by open, more arid, environment. The reconstruction of the environment of the late Early Pleistocene of Italy is also of particular importance, as this area is of interest concerning the early human colonisation of Europe, dating around 1.5 Ma (Arzarello *et al*. 2007).

Acknowledgements

We would like to thank Roberto Zorzin and Anna Vaccari, of the Museo Civico di Storia Naturale of Verona, for putting the material in their collections at our disposal. M. Pavia was financially supported by Synthesys Program (FR-TAF 2067 and NL-TAF 2255) and by Italian MIUR PRIN 2009MSSS9L 002 to Giulio Pavia. We also would like to thank Nikita Zelenkov (Borissiak Paleontological Institute of Russian Academy of Sciences), an anonymous reviewer and Ursula Göhlich (NHMW) for their comments and suggestions that greatly improved the manuscript.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

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Revisiting *Asio priscus*, the extinct eared owl of the California Channel Islands

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Abstract — *Asio priscus* was described on the basis of a single bone from upper Pleistocene (late Wisconsinan Glacial Episode) deposits of Santa Rosa Island, one of the Channel Islands in the Pacific Ocean off the coast of southwestern California. Several additional specimens referable to this extinct species have been recovered since the original description, including what appear to be several bones of one individual. The new specimens are described, and they substantiate the original description of the species as distinct from living eared owls. Wing bones associated with a leg bone suggest that *A. priscus* had smaller wings relative to its legs than does the similar-sized Short-eared Owl, *A. flammeus*, a condition not uncommon in island birds in comparison to mainland relatives.

Key words: *Asio priscus*, California, Channel Islands, eared owls, Pleistocene

Introduction

Hildegarde Howard (1964) described *Asio priscus* from upper Pleistocene (late Wisconsinan Glacial Episode) deposits of Santa Rosa Island, one of the Channel Islands in the Pacific Ocean off the coast of southwestern California. The holotypic, and only known, specimen at the time of description was a tibiotarsus collected between 1928 and 1931. Since the original description several additional specimens referable to this extinct species have been recovered from Santa Rosa Island and San Miguel Island, which lies ~6.0 km northwest of Santa Rosa Island (Fig. 1). The new specimens include several bones of what appears to be one individual that were collected together at one site. Some of these new specimens were mentioned, or listed in tables, by Guthrie (1980, 1998, 2005), although without osteological descriptions. Two fragmentary specimens referred to *A. flammeus* by Guthrie (1998) are referred herein to *A. priscus*. The purpose of this paper is to describe the new specimens for the record and comment on possible life history traits of *A. priscus*.

The living species of eared owls, *Asio flammeus* Pontoppidan, 1763, and *A. otus* Linnaeus, 1758, are listed as very rare visitors to the Northern Channel Islands, with the former being a transient fall visitor and the latter a summer visitor (Collins 2011). Two fossil specimens referable to *A. flammeus* are in collections from San Miguel Island stored at the SBMNH. Neither of the living species currently nests on the islands, and it is not known if they did so previously.

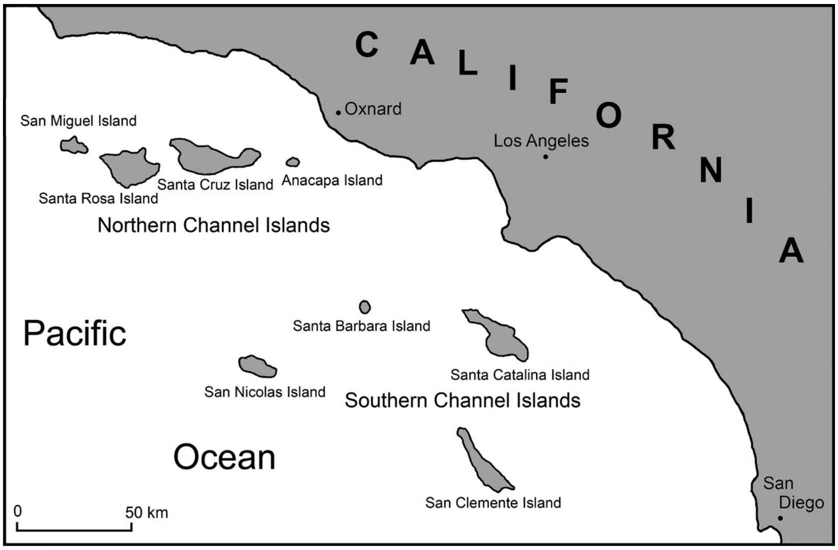

FIGURE 1. Map showing location of Channel Islands of California, USA.

Study area

The California Channels Islands comprise a group of eight continental islands in the Pacific Ocean off the coast of southwestern California (Fig. 1). The group is divided into the Southern Channel Islands and Northern Channel Islands, the latter comprising San Miguel Island, Santa Rosa Island, Santa Cruz Island, and Anacapa Island. Although today the nearest island to the mainland, Anacapa Island, is ~23 km distant, during the Pleistocene, when sea level was lowered by over 100 m (Miller *et al.* 2005), it would have been less than 10 km distant. Further, all four of the Northern Channel Islands were united during periods of low sea level during the Pleistocene, giving a single large island known as Santa Rosae Island. The current point of highest elevation (747 m) is found on Santa Cruz Island, and the topography of the four islands varies from steep, narrow canyons to broad plains representing ancient marine terraces.

Materials and Methods

The fossil specimens were compared with modern skeletons of *Asio flammeus* (n=11; 2♂, 4♀, 5?) and *A. otus* (n=13; 4♂, 5♀, 4?), as well as dozens of specimens of those two species from the upper Pleistocene Rancho La Brea asphalt deposits housed in the George C. Page Museum, a subsidiary of the Natural History Museum of Los Angeles County. Together, the two species of eared owls represent the third most common owls at Rancho La Brea, with a minimum number of individuals exceeding 175. Measurements were taken with digital calipers accurate to 0.01 mm, captured directly to computer, and rounded to nearest 0.1 mm. Some of the specimens are too fragmentary to provide meaningful measurements. Osteological terminology mostly follows Baumel & Witmer (1993) and Howard (1980).

Abbreviations: LACM, Natural History Museum of Los Angeles County; n, number; R, Range; RLB, Rancho La Brea; SBMNH, Santa Barbara Museum of Natural History; $\bar{x}$, mean.

Anatomical abbreviations used in the illustrations: am, Angulus medialis; Artic., Articularis; cb, Crus breve; Ccl, Crista cnemialis lateralis; ce, Condylus externis; cf, Crista fibularis; ci, Condylus internis; cl, Condylus lateralis of femur; cl, Crus longum; clh, Crista lateralis hypotarsi; cmh, Crista medialis hypotarsi; di, Depressio intercondylaris of Incisura intercondylaris; ei, Eminentia intercotylaris; ep, extension proximad of Condylus lateralis of tibiotarsus; Fac., Facies; fc, attachment for M. flexor carpi ulnaris; fe, Fac. externa of Crista articularis sternalis; fl, Fac. lateralis of Corpus coracoidei; fp, Fac. plantaris; iii, Os metacarpi III; iv, Os metacarpi IV; li, Linea intermuscularis; pa, Proc. acrocoracoideus; Proc., Processus; sf, Sulcus flexorius.; si, Sulcus intercondylaris; st, Sulcus tendinosus; ta, Tuberculum aponeurosis ventrale; tc, Tuberculum carpale; tf, Trochlea fibularis; ti, Tuberositas interna retinaculi extensori; tr, Tuberculum retinaculi m. fibularis [peronei]; um, distal attachment of Lig. ulnocarpo-metacarpale ventrale.

Systematic Paleontology

Order Strigiformes Wagler, 1830
Family Strigidae Leach, 1820
Genus *Asio* Brisson, 1760

Asio priscus Howard, 1964
(Figs 2–4)

Holotype: Right tibiotarsus, some portions of shaft and proximal end missing: LACM 106/4712. (Fig. 2).

Emended diagnosis: Similar to *Asio flammeus* and *A. otus* in general form and deep excavation of shaft anteroproximal to distal condyles. Howard (1964) noted the following diagnostic characters: 1) Crista fibularis flaring laterad distally; 2) Crista fibularis with broad longitudinal depression on anterior face medial to lateral edge, which gives a relatively narrow, convex Fac. anterior of shaft, in contrast to broadly convex Fac. anterior of shaft in *A. flammeus* and *A. otus*; 3) Linea intermuscularis extending proximad from proximal end of Crista fibularis slanting more abruptly posteriad from crest, in lateral view; 4) Crista cnemialis lateralis less excavated at its posterolateral edge; 5) Tuberositas interna retinaculi extensori prominent; 6) Condylus lateralis with posterior rim extending 5–15 percent more proximad relative to anterior rim than in modern species; 7) length greater. To those characters I add: 8) Crista cnemialis lateralis very broad at proximal end; 9) Fac. artic. lateralis of proximal end very prominent, more rounded; 10) Incisura tibialis of proximal end very narrow, with prominent ridge leading to it from Fac. artic. lateralis; 11) Depressio intercondylaris of Incisura intercondylaris much deeper; 12) Tuberculum retinaculi m. fibularis [peronei] longer and protruding more laterad; and 13) condyles broader.

Type locality: LACM(CIT) 106; Arlington Canyon, east of canyon mouth, Santa Rosa Island, Santa Barbara County, California, USA.

Type horizon and age: Tecolote Member of Santa Rosa Island Formation; upper Pleistocene (late Wisconsinan Glacial Episode).

Referred specimens: Santa Rosa Island: Presumed associated left coracoid, proximal right carpometacarpus, distal left and right ulnae, distal left femur, distal left radius, and right Os carpi ulnare, SBMNH 648; proximal left femur, SBMNH 420.

San Miguel Island: Distal end and shaft of left humerus, SBMNH 222; distal left femur, SBMHN 86; complete right tarsometatarsus, SBMNH 223. Distal end and shaft of left humerus (A.6431–6924) and distal end of right tibiotarsus (A.6431–6923), Archeology Collections, Anthropology Department, LACM.

Description: *Asio priscus* is closest in size to the Short-eared Owl, *A. flammeus*. The Long-eared Owl, *A. otus*, is generally a smaller, more slender bird, although the latter two species do overlap in size (Table 1). The characters noted above as diagnosing *A. priscus*, and below as differentiating it from other species, are based on limited fossil material and might not hold with a larger series of specimens.

Coracoid (Fig. 3E): Left, incomplete. Compared with *A. flammeus*: 1) Proc. acrocoracoideus not extending as far proximad, much narrower, and less robust; 2) Fac. artic. humeralis shorter and more rounded; 3) Cotyla scapularis more concave adjacent to Fac. artic. humeralis; 4) Angulus medialis longer and more pointed mediad, although broken and improperly glued back onto shaft; 5) Fac. lateralis of Corpus coracoidei flattened anterior to Angulus lateralis (tapers to thin edge in *A. flammeus*, but similarly flattened in *A. otus*). Similar in length to *A. otus*, but 1) more robust; 2) Proc. acrocoracoideus longer, less rounded; 3) Fac. artic. humeralis longer, broader; 4) Fac. externa of Crista artic. sternalis larger at medial end.

Humerus (Tab. 1): Proximal end missing, distal end and shaft abraded. Compared with *A. flammeus*: 1) Condylus dorsalis shorter anteroposteriorly, and more rounded, in dorsal view; 2) Condylus ventralis smaller; 3) Epicondylus ventralis small, not protruding as far ventrad, although more distinctly set off from shaft.

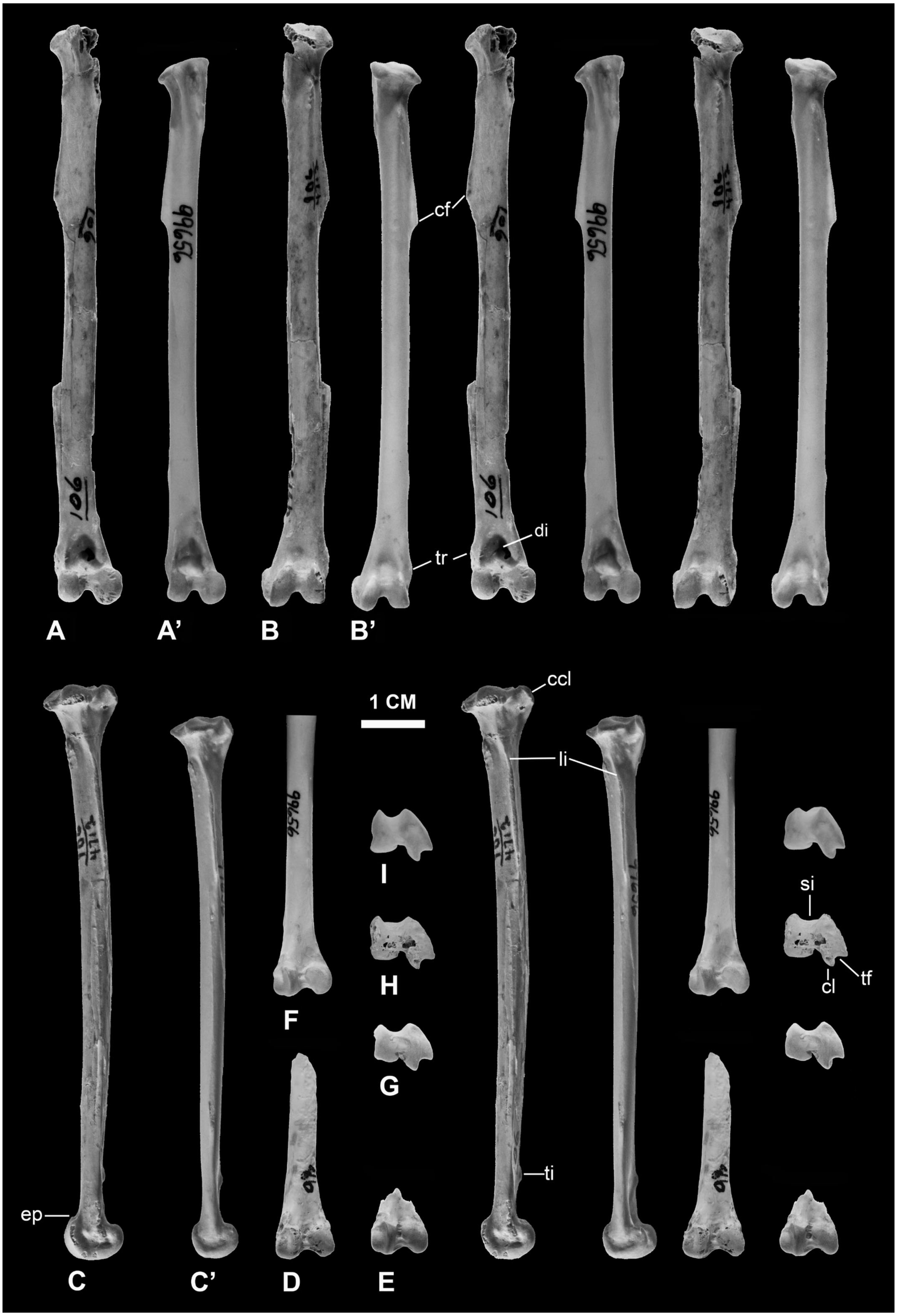

FIGURE 2. Stereopair photographs of holotypic right tibiotarsus of *Asio priscus* (LACM 106/4712, **A**–**C**), in comparison with that of *A. flammeus* (LACM 99656, **A’**–**C’**), in **A**, **A’**) anterior, **B**, **B’**) posterior, and **C**, **C’**) lateral views; and referred femora of *A. priscus* (SBMNH 86, **D**, **H**; SBMNH 648, **E**, **G**), in comparison with that of *A. flammeus* (LACM 99656, **F**, **I**) in **D**, **E**, **F**) posterior and **G**, **H**, **I**) distal views. Note the more robust shaft and condyles of the tibiotarsus of *A. priscus*.

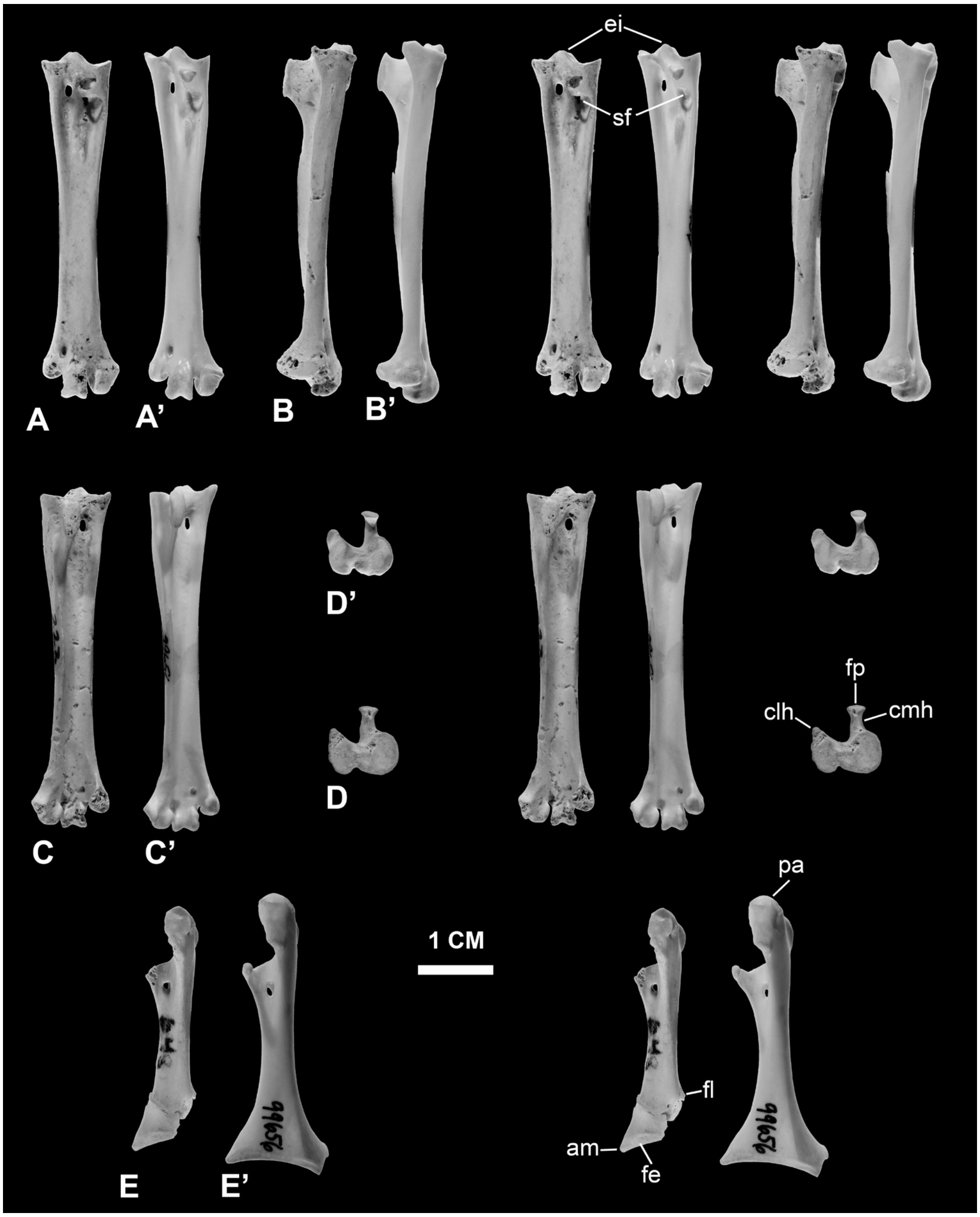

FIGURE 3. Stereopair photographs of right tarsometatarsus (SBMNH 223, **A–D**) referred to *A. priscus* in comparison with that of *A. flammeus* (LACM 99656, **A’–D’**) in **A**, **A’**) anterior, **B**, **B’**) lateral, **C**, **C’**) posterior, and **D**, **D’**) proximal views; and referred left coracoid (SBMNH 648, **E**), in comparison with that of *A. flammeus* (LACM 99656, **E’**), in **E**, **E’**) ventral view.

Ulna (Fig. 4D, Tab. 1): Distal end, right and left associated bones, identical. Compared with *A. flammeus*: 1) Condylus externis longer, thinner in ventral view and with rim more rounded in lateral view; 2) Condylus internis ulnaris undercut anteriad, not extending as far distad; 3) Sulcus intercondylaris not as prominent in ventral view; 4) Tuberculum carpale not extending as far anteriad; 5) shaft less robust. Distinctions with *A. otus* similar.

Radius (Fig. 4C, Tab. 1): Distal end, right. Compared with *A. flammeus*: 1) Sulcus tendinosus prominent, well marked; 2) Tuberculum aponeurosis ventrale angular, forming a prominent spur; 3) Fac. artic. radiocarpale set off more abruptly from shaft; 3) attachment for Lig. radioradiocarpale ventrale more prominent, elevated.

Os carpi ulnare (Fig. 4A, B): Right. Compared with *A. flammeus*: 1) length from tip of Crus breve to tip of Crus longum relatively

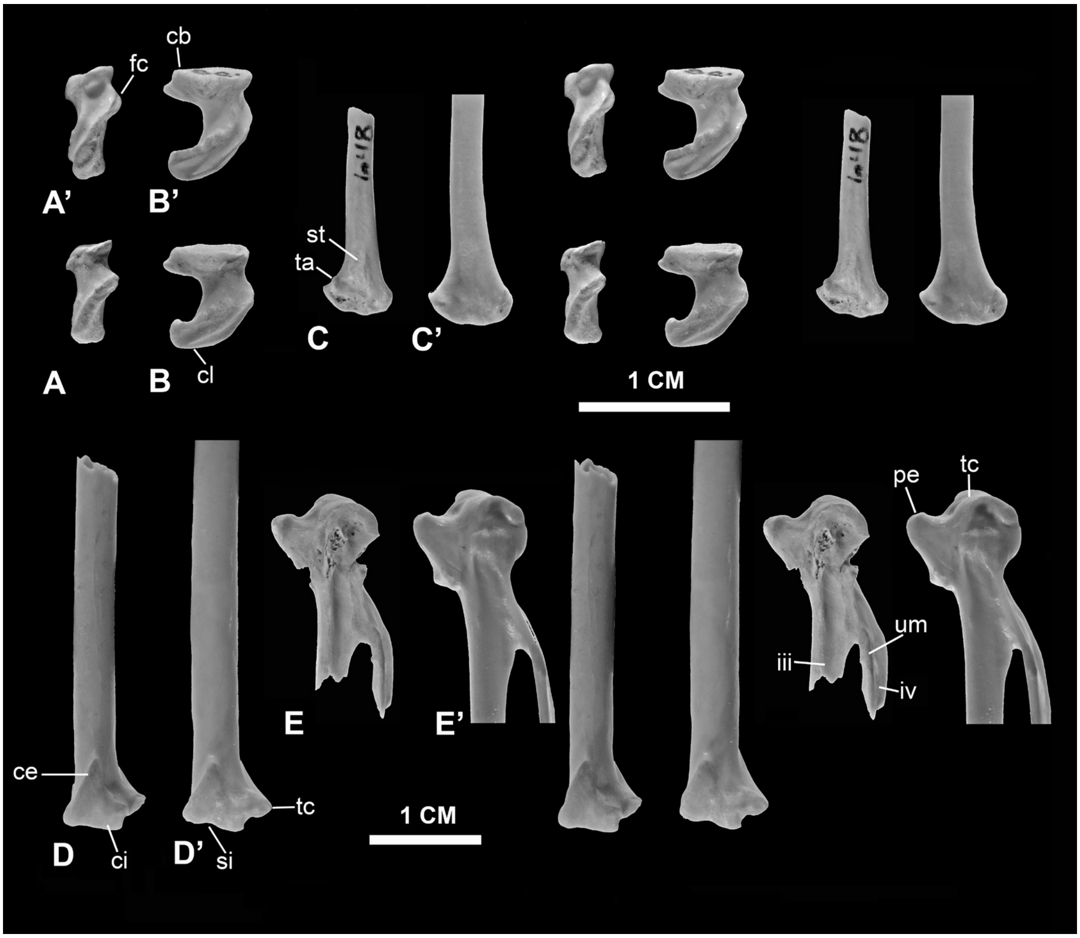

FIGURE 4. Stereopair photographs of referred specimens of *Asio priscus* in comparison with those of *A. flammeus*: right Os carpi ulnare (SBMNH 648, **A**, **B**; LACM 99656, **A'**, **B'**), in **A**, **A'**) posterior and **B**, **B'**) ventral views; distal right radius (SBMNH 648, **C**; LACM 87427, **C'**) in dorsal view; distal left ulna (SBMNH 648, **D**; LACM 99656, **D'**) in ventral view; and proximal right carpometacarpus (SBMNH 648, **E**; LACM 99656, **E'**) in ventral view. Scale bars equal 1 cm; long bar (x2.0) in reference to A and B only; short bar (x1.5).

shorter; overall smaller, less stout; 2) attachment for M. flexor carpi ulnaris not protruding as far dorsoproximad.

Carpometacarpus (Fig. 4E): Proximal end, right, broken. Compared with *A. flammeus*: 1) Trochlea carpalis does not lie as far proximal to Proc. extensorius; 2) Fac. artic. radiocarpalis does not extend as far proximad, giving less slope to Trochlea carpalis, in distal view; 3) Os metacarpale IV (minus) more separated from Os metacarpale III (majus) proximally, in dorsal view; 4) Os metacarpale IV (minus) narrows distal to proximal synostosis, but expands to comparable width seen in *A. flammeus* at distal attachment of Lig. ulnocarpo-metacarpale ventrale.

Femur (Tab. 1): Proximal end, left, abraded. Compared with *A. flammeus*: 1) Caput femoris larger, extending more proximad, and rotated more toward horizontal, in anterior view when held vertically; 2) Fac. artic. antitrochanterica not sloping as steeply relative to long axis of shaft, in anterior view when bone held vertically.

Distal ends, two left, one abraded, one unabraded. 1) Sulcus intercondylaris broader, flatter on bottom; 2) Trochlea fibularis broader, more open "U"-shape; 3) Condylus lateralis more in line with long axis of shaft proximodistally (*i.e.*, anteroproximal end does not turn as far laterad), in posterior view. The three femoral specimens appear to be more robust than those of *A. flammeus*, but they are too fragmentary to say definitively that they are.

Tarsometatarsus (Fig. 3A–D; Tab. 1):

Compared with *A. flammeus*: 1) Eminentia intercotylaris larger, probably more elevated, but abraded; 2) cotylae broader and more rounded, which agrees with broader condyles of tibiotarsus; 3) Crista medialis hypotarsi thicker, with medial side of base positioned more medially and with broad Fac. plantaris; 4) Crista lateralis hypotarsi (proximal surface missing, but posterior tip present) smaller, not extending as far posteriad; 5) shaft broader, more robust, with Sulcus flexorius broader; 6) trochleae (all broken at critical places) appear to be more robust and longer proximodistally; 7) Trochlea metatarsi III extends slightly farther distad relative to other two trochleae than in *A. flammeus*.

Discussion

The new specimens of *Asio priscus* substantiate the original description of the species as distinct from the living Short-eared Owl, *A. flammeus*, and Long-eared Owl, *A. otus*. There are still too few specimens to make any definitive statements to characterize the species, but the greater length and robustness of the holotypic and referred tibiotarsi and the greater least shaft width of the tarsometatarsus suggest that *A. priscus* had longer and more robust legs than the similar-sized *A. flammeus*. The greater width of the Sulcus intercondylaris and the combined width of the condylus lateralis and trochlea fibularis of the femur are also indicative of a more robust, more powerful leg. These features might also be an indication of greater body mass, but a larger

TABLE 1. Measurements (mm) of holotypic tibiotarsus and referred tarsometatarsus, humerus, ulna, radius, and femur of *Asio priscus* and fossil (Rancho La Brea) and modern specimens of *A. flammeus* and *A. otus*.

	A. priscus (n=1(2))	***A. flammeus*** (n=11)		**RLB *A. flammeus*** (n=10)		***A. otus*** (n=13)		**RLB *A. otus*** (n=5)	
	R	R	$\bar{x}$	R	$\bar{x}$	R	$\bar{x}$	R	$\bar{x}$
Tibiotarsus									
length	90.4	76.1–86.8	81.9	78.0–86.7	81.8	74.8–81.5	77.1	72.9–78.7	76.5
fibular crest width	6.5	4.5–6.3	5.5	5.3–5.7	5.5	4.3–5.3	4.9	4.6–5.2	4.8
least shaft width	4.9	3.5–4.6	4.1	4.0–4.3	4.2	3.2–3.9	3.8	3.5–4.1	3.9
distal width	10.1	8.8–9.4	9.1	8.2–9.8	9.1	7.9–9.1	8.5	7.9–8.7	8.2
Tarsometatarsus									
length	46.4	41.6–47.3	44.6	42.2–46.3	44.8	35.6–44.0	40.6	37.9–43.7	40.4
proximal width	9.4	8.2–9.2	8.7	8.6–9.4	8.9	7.7–8.8	8.3	7.4–8.5	8
least shaft width	5.1	4.3–4.7	4.5	4.3–4.9	4.6	3.6–4.4	4.2	3.8–4.4	4.2
distal width	10.6	9.8–10.7	10.2	10.0–10.8	10.4	8.4–10.2	9.4	8.8–10.1	9.3
Humerus									
least shaft width	5.9	5.3–6.0	5.7	5.3–5.9	5.6	4.8–5.4	5.1	4.8–5.5	5.1
distal width	13.0	12.5–14.4	13.7	12.8–14.2	13.4	11.6–13.4	12.4	11.6–12.4	12.0
Ulna									
depth through tub. carpale	7.2	7.0–8.1	7.7			6.5–7.6	7.0		
depth shaft. prox. to cond.externa	3.8	3.7–4.3	4.0			3.3–4.2	3.7		
Radius									
distal width	6.4	6.4–7.7	7.0			5.7–7.0	6.2		
Femur									
distal width	9.5–10.3	8.7–10.2	9.6			8.4–9.6	9.0		
least shaft width	4.5	3.8–4.4	4.2			3.7–4.1	3.9		

sample is required before that can be determined.

Note that all of the measurements of the holotypic tibiotarsus of *A. priscus* exceed the range of those of *A. flammeus* (Table 1), whereas the measurements of the tarsometatarsus fall within the range of those of *A. flammeus*, except for shaft width. Limited measurements of the referred tibiotarsus (not included in table) are identical to the holotype. There was very little difference recorded in the mean measurements of modern *A. flammeus* and *A. otus* and a sample of specimens of these species from the upper Pleistocene Rancho La Brea asphalt deposits selected for their completeness, although the range of measurements of the modern forms often exceeded those of the fossil forms.

Also, wing bones presumed to be associated with a distal femur suggest that *A. priscus* had smaller wings relative to its legs than does *A. flammeus.* This possibility is also suggested by the partial humerus, whose measurements fall within the range of those of *A. flammeus*. Such changes in relative proportions of wings and legs are not uncommon in island birds relative to mainland relatives, especially the lengthening of the legs (Grant, 1965a, 1965b, 1966). For owls in general, this condition was noted by Louchart (2005), and Campbell & Bocheński (2010) suggested that the extinct La Brea Owl, *Oraristrix brea* (Howard, 1933) might well have responded evolutionarily to isolation in southwestern California as if that geographic region were an island.

The alternative to viewing *Asio priscus* as having followed the allometric trends of many island birds in reducing wing size relative to leg size would be that there were two extinct species of *Asio* on Santa Rosae Island, one represented in collections only by leg elements and the other only by elements of the pectoral girdle. That is considered unlikely, especially given the presumed association of wing and leg bones.

The paleofauna of the Channel Islands is quite rich, with many species of reptiles, birds, and mammals reported. For example, according to Guthrie (2005), a total of ~17,000 specimens from 61 species of birds were recovered from San Miguel Island alone from 1980 to 2002. In addition to *Asio priscus*, there were three additional extinct species of birds: *Morus reyanus* Howard, 1936; *Chendytes lawi* Miller, 1925; and *Fratercula dowi* Guthrie, Thomas & Kennedy, 2000. Various extinct mammals have also been recorded from the Channel Islands, including *Mammuthus exilis* Stock and Furlong, 1928 (a dwarf mammoth), *M. columbi* Falconer, 1857 (the Columbian mammoth), *Desmodus stocki* Jones, 1958 (a vampire bat), and, of special interest to the strigid avifauna, two species of mice: *Peromyscus nesodytes* Wilson, 1936 (the “giant” deer mouse) and *Microtus miguelensis* Guthrie, 1998 (a vole). For more information on the paleofaunas, geological deposits, and excavations on the Northern Channel Islands, see Guthrie (1992, 1993, 1998, 2005).

Acknowledgments

I thank Dan A. Guthrie (Claremont Colleges, Claremont, CA; USA), collector of some of the specimens described here, for suggesting I pursue description of the material, Paul Collins (SBMNH) for loan of the material, and Chris Coleman for assistance with specimens in the Archaeology Collections of the Anthropology Department of the LACM. I also thank Alison Stenger (Institute for Archaeological Studies, Portland, OR, USA) for financial support, Fritz Hertel (California State University, Northridge, CA, USA) for comments on an early version of this paper, and Zbigniew Bocheński and Antoine Louchart for their helpful reviews.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

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A synopsis of the pre-human avifauna of the Mascarene Islands

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Abstract — The isolated Mascarene Islands of Mauritius, Réunion and Rodrigues are situated in the south-western Indian Ocean. All are volcanic in origin and have never been connected to each other or any other land mass. Despite their comparatively close proximity to each other, each island differs topographically and the islands have generally distinct avifaunas. The Mascarenes remained pristine until recently, resulting in some documentation of their ecology being made before they rapidly suffered severe degradation by humans. The first major fossil discoveries were made in 1865 on Mauritius and on Rodrigues and in the late 20th century on Réunion. However, for both Mauritius and Rodrigues, the documented fossil record initially was biased toward larger, non-passerine bird species, especially the dodo *Raphus cucullatus* and solitaire *Pezophaps solitaria*. This paper provides a synopsis of the fossil Mascarene avifauna, which demonstrates that it was more diverse than previously realised. Therefore, as the islands have suffered severe anthropogenic changes and the fossil record is far from complete, any conclusions based on present avian biogeography must be viewed with caution.

Key words: Mauritius, Réunion, Rodrigues, ecological history, biogeography, extinction

Introduction

The Mascarene Islands of Mauritius, Réunion and Rodrigues are situated in the south-western Indian Ocean (Fig. 1). Despite their comparatively close proximity to each other, each island differs topographically and the islands have generally distinct avifaunas. The Mascarenes were the last major group of islands to be colonised by humans, so remained in a comparatively pristine state into the era of written history. Arab traders were aware of them from at least the 13th century and the Portuguese in the early 16th century (NORTH-COOMBES 1980, 1994a; HALL 1996), but as far as known no attempt at settlement was made by either. It was with the chance discovery by a Dutch East India Company (VOC) fleet under Vice-Admiral Wybrandt Warwijck in September 1598, who claimed Mauritius for the Netherlands, that the documented history of the Mascarenes began (MOREE 1998; CHEKE & HUME 2008). The endemic fauna was sketchily described or illustrated in ships' logs and journals, which became the source material for popular articles and books and, along with collected specimens, enabled monographs such as that by STRICKLAND & MELVILLE (1848) on the dodo *Raphus cucullatus* (LINNAEUS, 1766) to be produced. STRICKLAND and MELVILLE based their osteological analysis on the surviving remnants of a dodo once exhibited at the Ashmolean Museum in Oxford, and a dodo foot preserved in the British Museum in London (HUME *et al.* 2006). For the next two centuries, the islands' ecosystems were irreversibly destroyed due to anthropogenic activities, which resulted in the extinction of the majority of endemic vertebrates (CHEKE & HUME 2008). The discovery of subfossil material in 1786 on Rodrigues (although the first major discovery was not made until 1865), in 1865 on Mauritius and in the late 20th century on Réunion resulted in the description of new avian fossil taxa and also provided some corroboration with species described in early accounts. In gen-

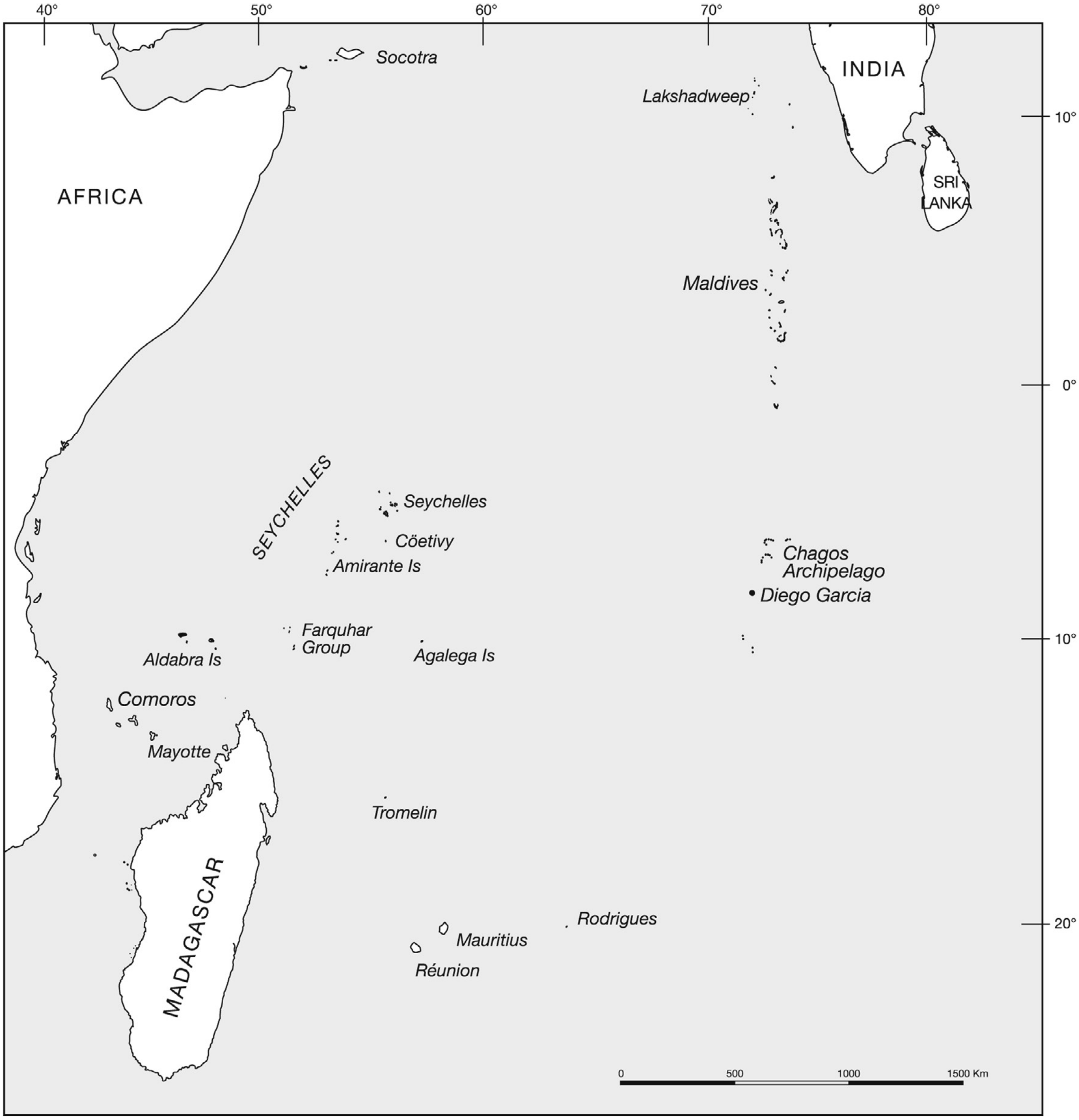

FIGURE 1. Map of the Southwestern Indian Ocean showing the Mascarene Islands of Réunion, Mauritius and Rodrigues. From Cheke & Hume (2008).

eral, only the larger and more distinct avifauna was described from the fossil record, whereas other avian orders, *e.g.*, smaller passerines, were ignored. As a result, determining avian biogeography based on current knowledge of fossil avifaunas is problematic.

This paper provides a synopsis of the pre-human Mascarene avifauna based on recent, more comprehensive studies, using a combination of palaeontological and historical evidence. It addresses the taxonomic problems associated with erroneous identifications and descriptions, and will hopefully provide an important resource for those interested in avian phylogenies and avian biogeography of the region. All taxa considered to be endemic or indigenous to the islands are covered, including extant species, those known from the palaeontological record, and those species known only from contemporary accounts that almost certainly once existed, but have not yet been discovered in the fossil record. But I must emphasise that work is not yet complete. A number of subfossil elements that almost certainly represent further new taxa have been discovered, but the lack of suitable diagnostic specimens and/or suitable comparative material has held back identification. The original Mascarene avifauna must surely have been even more diverse than the results presented here suggest.

Study area

Geology and Physiography: The isolated Mascarene Islands are volcanic in origin, and have never been connected to each other or any other landmass. Réunion (21.0° S, 55.5° E), the most southerly of the islands, lies 665 km east of Madagascar, whereas Mauritius (20.25° S, 57.5° E) is situated 164 km east north-east of Réunion. Rodrigues (19.75° S, 63.5° E) is the most remote, lying 574 km east of Mauritius and approximately 4800 km west of Australia.

Mauritius (Fig. 2) is approximately 60 km long by 40 km wide, with a surface area of 1865 km². As well as being smaller, it is also much lower than Réunion, with Black River Peak being the highest point at 828 m. The broad undulating lava plains of the north rise to a maximum of 152 m above sea level, intersected in the middle of the island by mountains, the rim remnants of a former caldera. Mauritius is surrounded by a reef-fringed lagoon, averaging 0.8 km wide, but on the east coast reaching 5 km, whereas on two short stretches of the west and south coasts, the sea breaks directly onto the cliffs (Cheke & Hume 2008). There are a number of islets within the lagoon; the most biologically important being the northern islets, which are the only places where some endemic reptiles and seabird colonies have managed to survive.

Mauritius emerged around 10 Ma, and was built by three volcanic episodes (Saddul 2002). After a shield-building phase and deposition of the Old Lava Series between 7.6 Ma to 5 Ma, subdued volcanic activity commenced with the formation of a caldera. A new phase of volcanism occurred between 3.5 and 1.7 Ma leading to the formation of the Early Lava Series. A third phase of active volcanism commenced at 0.7 Ma and lasted until 20 Ka, forming the Intermediate and Recent Lava Series (Duncan & Hargreaves 1990; Rijsdijk *et al.* 2009).

Réunion (Fig. 3) is the largest and highest of the Mascarene Islands, being 70 km long by 50 km wide and covering 2,512 km², with over 60 % of the land surface being above 828 m (Nicholls 2006). It has the highest peak in the Indian Ocean, the Piton des Neiges, which rises to over 3,069 m. Its second highest peak at 2,631 m is the Piton de la Fournaise or Le Volcan, an active volcano that is situated to the east of a volcanic hotspot. It is probably the same hotspot that during the past 66 Ma gave rise to the enormous Deccan Traps lava fields in India, the Maldives, the Chagos, the Saya de Malha, Nazareth and St.Brandon (Cargados Carajos) banks (large undersea plateaus), and to Mauritius (Cheke & Hume 2008). The centre of Réunion is divided into massive cirques, each dissected by extremely deep gorges. Around the island, the land shelves steeply into deep water, sometimes under massive sea cliffs. There is virtually no fringing reef and, where coral has developed close inshore, only a narrow lagoon exists.

Réunion is the youngest of the Mascarene Islands and emerged from the surface of the sea approximately 2.8 Ma (McDougall *et al.* 1971). The island comprises two coalesced volcanoes, the Piton des Neiges, which forms two thirds of the island in the northwest, and the Piton de la Fournaise in the southeast (Duncan & Hargreaves 1990). The construction or first phase of the Piton des Neiges includes two main events, the first dating back 2.1 to 0.43 Ma, and the second more explosive phase, which is divided into three events, occurred from 0.35 Ma to less than 30 Ka. The first and second began almost simultaneously around 230 Ka, with the third around 188 Ka. During this time, the Piton de la Fournaise, which began erupting approximately 360 Ka, collapsed several times into the ocean (see Mourer-Chauviré *et al.* 1999 for a detailed summary). The combination of these events may have eliminated the original avifauna.

Rodrigues (Fig. 4) is the smallest of the Mascarene Islands, being 17.7 km long and by 8.45 km wide, with a surface area of 104 km². It has a central ridge with steep, incised valleys extending to the coast, and its highest point, Mont Limon, is just 398 m. The island is surrounded by a vast, submarine platform, of which an area of about twice that of the land surface is occupied by an extensive reef-fringed lagoon (Cheke & Hume

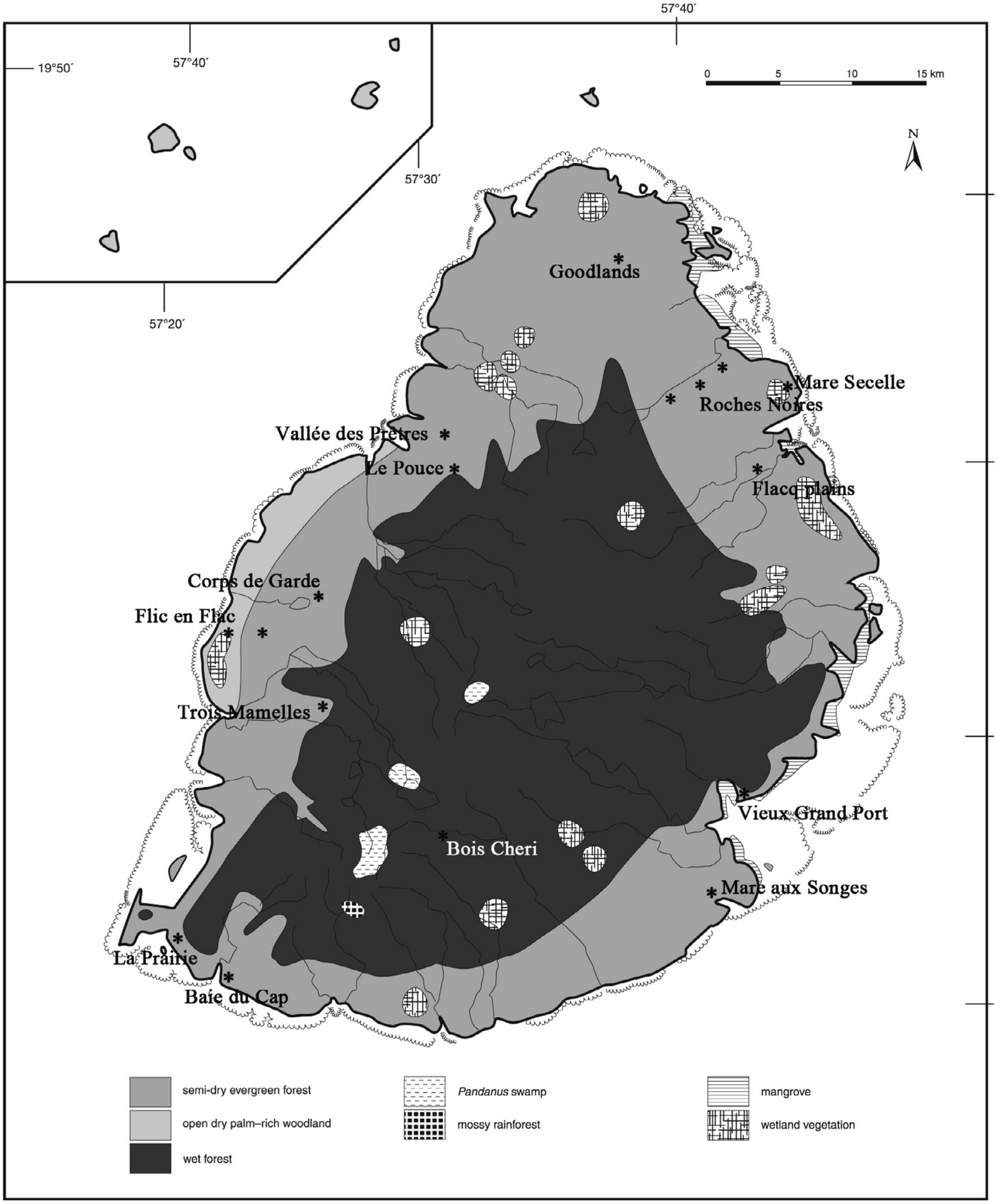

FIGURE 2. Map of Réunion Island showing the original vegetation, and the fossil localities mentioned in the text. From Cheke & Hume (2008).

2008). The lagoon has a number of islets comprising mainly flat calcarenite limestone, though some have basaltic hills, sandbanks or small basalt outcrops. These islets provided refugia for elements of the original fauna decades after their populations had been extirpated on the Rodrigues mainland (Hume 2007, 2011).

Rodrigues has been dated at 1.5Ma (McDougall *et al.* 1965), which would make it the youngest of the Mascarene Islands, but this is not supported by geomorphology and the degree of endemism (Cheke & Hume 2008). More recent work suggests an age similar to that of Mauritius (Giorgi & Borchellini 1998). Although Rod-

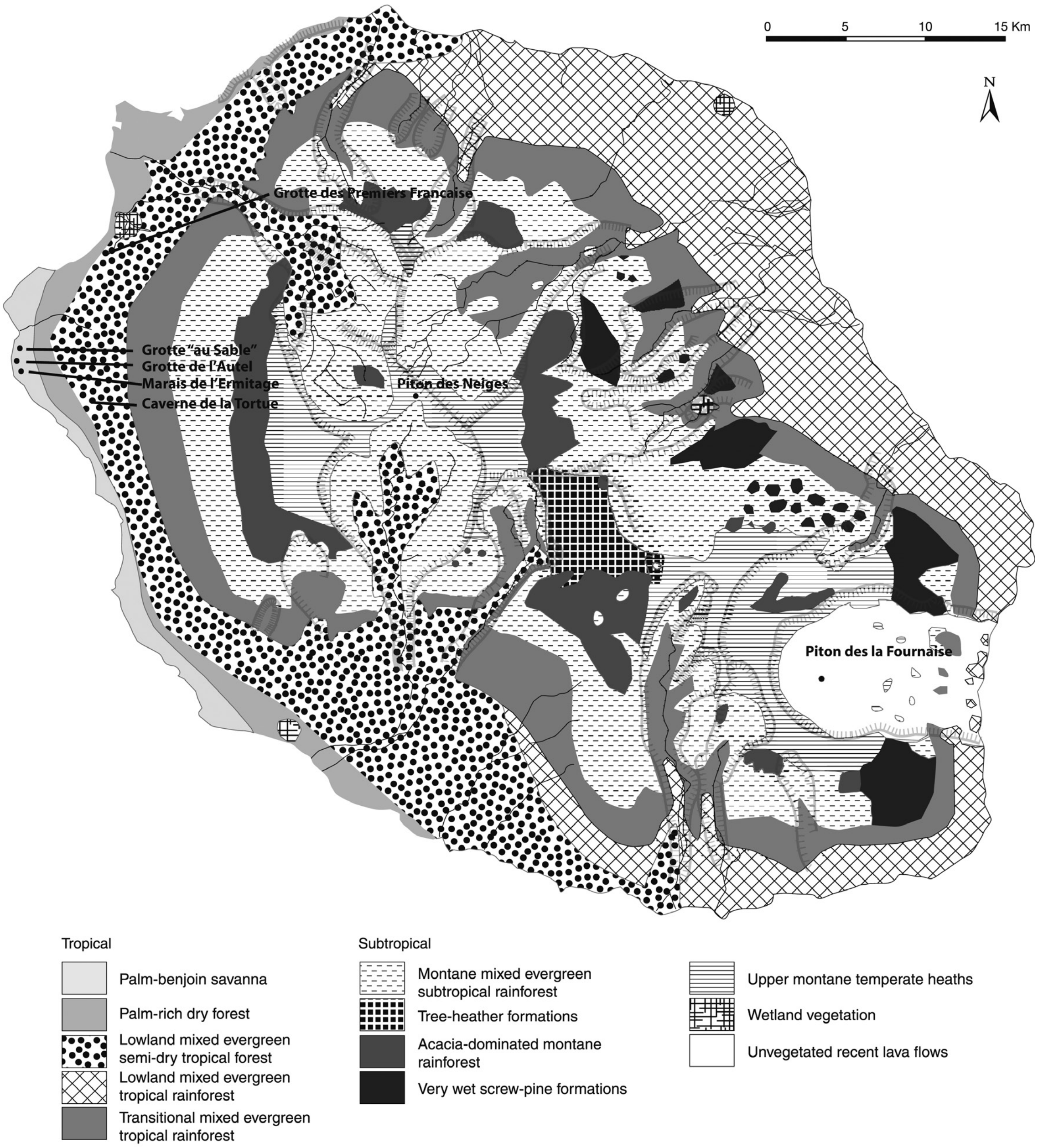

FIGURE 3. Map of Mauritius showing the original vegetation and the fossil localities mentioned in the text. From Cheke & Hume (2008).

rigues is mainly composed of basaltic lavas, it has a large limestone plateau (calcarenite) on the southwest coast called the Plaine Corail, which was formed from the accumulation of wind-blown coral sand. Montaggioni (1973) thought that formation occurred around 80 Ka during the last glacial, however, current consensus suggests that they form during interglacial periods, and not glacial, so date determination remains unknown.

Climate: The Mascarenes lie within the south-easterly trade winds, but during the austral summer months (January, February, March) tropical cyclones and depressions associated with the seasonal movement of the ITCZ (Inter Tropical Convergence Zone) have a marked effect on the islands. Rainfall is seasonal, with a dry season from May through to October under the influence of the cool and dry easterly trade winds, with a wetter, warmer season from November

FIGURE 4. Map of Rodrigues Island showing the fossil localities mentioned in the text. From Cheke & Hume (2008).

to April, when the ITCZ is in its southernmost position (Senapathi *et al.* 2010). Depending on relief and slope orientation to prevailing winds, mean annual rainfall on Mauritius varies from 800 mm in the western coastal lowlands and 1400 mm in the eastern coastal lowlands to 4000 mm in the uplands (Proag 1995). Mean annual temperature is 22°C (Mauritius Meteorological Services 2012). On Réunion, the central massifs create a rain shadow, which exposes the east of the island to prevailing easterly winds creating wet and cloudy conditions most days of the year (Cheke & Hume 2008). Réunion is one of the wettest places on earth, averaging 6–7 m of rainfall per year on the wettest coast to 10–12 m inland (Soler 2000). The coastal leeward area in the west is very dry with average rainfall of 540 mm per year. Mean annual temperature is 23°C on the coast, but the temperatures drop progressively inland and upslope. Rodrigues is the driest of the islands, with rainfall averaging from 800 mm on the Plaine Corail in the coastal southwest to > 1,600 mm in the central-west uplands (Cheke & Hume 2008). Mean summer temperature is 25.9 °C and mean winter temperature is 22.3 °C (Mauritius Meteorological Services 2012).

History of palaeontological research

The first fossil material discovered on Mauritius was found in a marshy deposit known as the Mare aux Songes in the southeast of the island in 1865. Harry Higginson, a railway engineer who was working on the Midlands stretch of the Mauritius railway, noticed that labourers were stock-piling bones while digging peat from the marsh. The embankment of the Midlands stretch ran close to the northern edge of the Mare aux Songes. Higginson informed George Clark, a diocesan teacher in Mahebourg, who had been searching for 20 years for fossil remains on Mauritius (Clark 1866; Hume *et al.* 2009). Clark had a copy of the aforementioned dodo monograph by Strickland & Melville (1848), and from the illustrations he was able to identify dodo remains (Hume *et al.* 2009). Clark obtained permission to work the site, and sent consignments of dodo material to Richard Owen, Superintendent of Natural History Departments at the British Museum, who formally described the dodo's anatomy (Owen 1866a). Due to Clark's monopolisation of the Mare aux Songes and his overriding interest in selling dodo bones for monetary gain, almost no other vertebrate species were collected (Hume *et al.* 2009). Owen received a parrot mandible in one of the dodo consignments, and this was the only fossil bird species described during this time (Owen 1866b; Hume *et al.* 2009).

A second more thorough excavation of the Mare aux Songes was organized under the guidance of Théodor Sauzier in 1879, from which six new fossil bird species were described (Newton & Gadow 1893), but few contextual details were obtained. In the early years of the 20th century, Paul Carié, whose family owned the estate containing the Mare aux Songes, sent more bird material to Paris (Hume 2005), and further very minor excavations took place up to the 1930s; however, no more new bird species were described. The Mare aux Songes was infilled with dolomite gravels and boulders in the 1940s, in an effort to prevent the spread of malaria (Hume *et al.* 2009), after which the site was all but forgotten.

In 2005, the fossil deposit was reinvestigated by a Dutch team researching human-induced changes to the environment. In June the following year, an interdisciplinary team including geologists, geophysicists, palaeobotanists, palaeontologists, and geneticists began a major excavation, which has continued annually until 2011 (Rijsdijk *et al.* 2009; Rijsdijk *et al.* 2011). The Mare aux Songes contains an integrated vertebrate Konzentrat-Lagerstätten, with a high diversity of macrofossils, including seeds, branches, leaves, insects, snails and even fungi, and microfossils (pollen, diatoms, ostracods), buried in a matrix of organic material.

Elsewhere on Mauritius, Etienne Thirioux, an amateur naturalist, excavated cave and boulder-field deposits around Le Pouce Mountain, and lava caves at Pailles, Roches Noires and the Vallée des Prêtres in the late 1890s and early 1900s (Hume 2005), but the exact locations were not specified (but see below). Thirioux collected thousands of bird skeletal specimens including an almost complete, associated Mauritius Red Rail *Aphanapteryx bonasia* (Sélys-Longchamps, 1848) and a dodo. Other cave deposits were discovered in 2007, 2008 and 2009 by myself and colleagues at Plaine des Roches, Vieux Grand Port and La Prairie (Janoo 2005; Hume 2007, 2011), including another associated but badly degraded dodo at Bois Cheri, in the central highlands (Middleton & Hume in press).

No fossil history existed for Réunion Island prior to 1974, when Bertrand Kervazo excavated cave deposits at Grotte des Premiers Française about 1.5 km southwest from St. Paul, from which three new fossil species were described (Kervazo 1979; Cowles 1994). During the 1980s, four other fossil localities were discovered, the Grotte de l'Autel; Grotte "au Sable" (sic) and Caverne de la Tortue cave sites, and the coastal swamp, the Marais de l'Ermitage, all on the northwestern side of Réunion (Mourer-Chauviré & Moutou 1987; Mourer-Chauviré *et al.* 1999).

Although the first Rodrigues subfossil solitaire *Pezophaps solitaria* (Gmelin, 1788) material had been collected in 1786 from caves on the Plaine Corail, the specimens were not described until 1848 (Strickland & Melville 1848). Gmelin (1788) had based his description on the solitaire account of Buffon (1766), and not from any physical evidence. Major excavations of the caves began in the late 1860s and early 1870s (Günther & Newton 1879; Hume *et al.* 2009). Cowles (1987) visited the Plaine Corail as part of the British Ornithologists' Union expedition in 1974, and mentioned, but did not describe, two potentially new fossil species. I searched all previously excavated caves and collected numerous subfossil remains from undisturbed caves over a 10 year period commencing in 2000, from which one new species has been described (Hume 2011) and at least three more await description.

FIGURE 5a. The Mare aux Songes photographed by the author in 2007.

FIGURE 5b. Detail of the Mare aux Songes fossil layer, Unit D. A tarsometatarsus of a dodo *Raphus cucullatus* (centre) is surrounded by the remains of giant tortoises *Cylindraspis* sp. The matrix is made up of seeds, leaves and other plant debris. Photograph courtesy of Ranjith Jayasena (Amsterdam).

The fossil deposits

Mauritius

Mare aux Songes — The Mare aux Songes is situated in southeast Mauritius, approximately 0.5 km from the coast (Figs 2, 5a), and was created by the collapse of a large lava tube system. It comprises four sub-basins separated by rock thresholds, and sub-basins I, II and III are bordered by <15 m rock cliffs. Sub-basins 0, I and II contain (or contained) subfossil material; all recent excavations took place in sub-basin I. The basaltic base rock of sub-basin I is situated 8–10 m below sea level, and is overlain by ~8 m thick sedimentary succession. The succession is divided into five distinct sedimentary units. The bedrock is overlaid by ~1 m of grey clay with very low concentrations of organic material (Unit A), covered by ~6 m of fine to medium carbonate sands with some infiltration of organic matter (Unit B). Above this lies a ~100 mm thick calcareous gyttja (Unit C), which is overlaid by a ~500 mm thick fossiliferous layer (Unit D). The matrix of Unit D is made up of woody material, nuts and seeds, all interspersed with amorphous peat, and contain 99 % of all fossil material (Fig. 5b). This layer is capped by introduced dolomite boulders and gravel (Unit E) (Rijsdijk *et al.* 2009). Sub-basin 0 is now destroyed and sub-basin II is completely infilled with Unit E. Sub-basin III has the same sedimentological units as sub-basin I, but these vary in thickness. Comparatively few subfossil remains are present, however. 14C dating and sedimentological analysis has shown that 4000 Ka the marsh was a fresh water lake that acted as an oasis in an otherwise dry environment (Rijsdijk *et al.* 2009; Rijsdijk *et al.* 2011; Meijer *et al.* 2012).

Le Pouce Mountain — The exact localities where Thirioux was collecting on Le Pouce Mountain (Fig.2) cannot now be determined. A survey by the author, Owen Griffiths and Greg Middleton in 2007 discovered a previously excavated large rock overhang in boulder scree at 350 m in Le Pouce valley, beneath Snail Rock (Hume 2011). As no one else is known to have worked in this area, this overhang might be one of Thirioux's original collecting sites.

Plaine des Roches — Subfossil remains of dodo have been found in the extensive lava tube systems at Plaine des Roches (Janoo 2005). In general, the cave sediments are thin or non-existent, the majority of which are covered with collapsed cave debris. The material is poorly preserved, but appears to represent a natural accumulation. There are numerous large or small openings (pit-fall traps) in the roofs of the caves (Fig. 6), into which the native fauna fell and was unable to get out.

Vallée des Prêtres — A number of Thirioux fossil specimens were supposedly collected in the Vallée des Prêtres, but it is uncertain if this was the true area of provenance. Some specimens have Vallée des Prêtres locality data written on the museum labels, yet they were collected from the Mare aux Songes (pers. obs). The Vallée des Prêtres is situated on the west flank of Le Pouce

Mountain, above and to the north of the capital, Port Louis (Fig. 2). It is steep-sided and arid, and sparsely covered with introduced trees and shrubs. I have not located any caves or large boulder overhangs in the valley, but there is a substantial amount of boulder scree. It is possible that Thirioux collected fossil material from sediment deposits amongst the rocks.

Kanaka Cave, *Bois Cheri* — The discovery of a complete, but badly degraded dodo (Dodo Fred) (Fig. 7) in Kanaka cave, Bois Cheri, in the highlands of Mauritius (Fig. 2) resulted in much media interest (Middleton & Hume In press). The basaltic cave was infilled with roof collapse debris and was extremely humid. Sediments included massive clay bedding interspersed with <5 mm rock fragments, and fine clays and silts. The dodo specimen was partially exposed on bare rock, with the bulk of the skeleton collapsed into a small crevice. This confirmed that dodos once occurred in the highlands as well as the lowlands.

Vieux Grand Port — Near the site of the Dutch fort at Vieux Grand Port (Fig. 2) is a small limestone outcrop, which has a number of small caves. The Dutch used some of these caves for shelter, as purpose-built animal corrals have been constructed inside. The caves are dry, and fining upwards silts reach a depth of up to 300 mm in the deeper recesses. Well preserved subfossil remains have been found buried at depths of 100 mm, including the type specimen of *Nesoenas cicur* Hume, 2011.

La Prairie — La Prairie is a limestone plain on the southwest coast (Fig. 2), which contains a number of caves. Some are permanently filled with water. The sediments comprise silts intermixed with roof collapse debris and can reach depths of 500 mm. The caves contain the remains of native birds and reptiles, and the deposits are particularly rich in *Pteropus* fruit bat remains.

Baie du Cap — Janoo (2005) and his colleagues discovered probable human-predated dodo remains in cliff caves at Baie du Cap (Fig. 2), on the south-west side of Mauritius. A single phalange supposedly exhibits knife marks, but the specimen needs analysis under SEM (Scanning Electron Microscope) to confirm this.

A number of additional fossil localities have been discovered on Mauritius containing the remains of giant tortoises *Cylindraspis* sp. (Austin & Arnold 2001; Bour 1984; Florens 2002), but bird remains are rare or absent in these. They include cave and boulder overhangs at Ile aux Aigrettes, Les Quatre Cocos, Flacq, 'Mt. Zaco'(west of Brise Fer Mountain), Palma, Camp de Masque, Trois Mamelles and Corps de Garde Mountain. Marsh deposits include Mare du Puit; La Mare La Chaux; Mare Sèche; and Riche Mare. Subfossil tortoise remains were also found in sand dunes at Flic en Flac (Florens 2002), but the area has now been completely developed.

FIGURE 6. Palaeontologist, Lorna Steel, beneath a roof opening in Twilight Caverne, Plaine des Roches, Mauritius.

Réunion

This is a summary only; for a complete review see Kervazo (1979); Cowles (1994); Mourer-Chauviré & Moutou (1987); & Mourer-Chauviré *et al.* (1999).

Marais de l'Ermitage — The Marais de l'Ermitage is the only swamp/marsh fossil deposit on Réunion (Figs 3 and 8). The surface sediments comprise an 800 mm thick organic soil (peat?) layer, which is virtually fossil-free. This overlies a 300–400 mm fossil-rich horizon

FIGURE 7. The associated, but badly degraded remains of dodo *Raphus cucullatus* (Dodo Fred) in Kanaka cave, Bois Cheri. Photograph courtesy of Greg Middleton (Hobart).

FIGURE 8. Avian palaeontologist, Cécile Mourer-Chauviré (centre) (UCBL), Sonia Ribes (left) (MHNRUN), Roger Bour (right) (MNHN), and co-workers excavating the Marais de l'Ermitage, Réunion. Photo courtesy of Roger Bour (MNHN).

intermixed with basaltic rocks and coral, resting on marine sediment made up of coralline sands, coral fragments and marine molluscs (Mourer-Chauviré *et al.* 1999). The fossil layer is dominated by giant tortoise *Cylindraspis indica* (Schneider, 1783), with comparatively rare bird and bat remains. The depositional setting of the Marais de l'Ermitage is somewhat similar to that of the Mare aux Songes on Mauritius. Unfortunately, a substantial part of the swamp has now been developed, and the remaining area is also at risk of destruction.

Caverne de la Tortue — This is in the only lava tube system on Réunion, and is situated around 250 m above sea level (Fig. 3). Entrance to the cave is via a roof opening, which drops 5 m to the cave floor. Most subfossil remains were found around the entrance, and were extremely fragile. They included the type, probably associated individual of Réunion rail, *Dryolimnas augusti* Mourer-Chauviré *et al.* (1999).

Grotte des Premiers Française (Grand Caverne) — This large cave was first excavated by Kervazo (1979), and subsequently by Mourer-Chauviré *et al.* (1999) (Fig. 3). It is a prehuman deposit and dominated by two species of shearwater *Puffinus* sp. Discoveries include the type of *Alopochen kervazoi* (Cowles, 1994), and a left distal femur fragment of *Fregilupus varius* (Boddaert, 1783), the only known subfossil passerine bone so far discovered on Réunion.

Grotte de l'Autel — This small cave (Fig. 3) was completely excavated in 1980 and contained a number of subfossils, including a humerus of the Réunion pink pigeon, *Nesoenas duboisi* Rothschild, 1907a, one of only two known, and numerous remains of the Réunion ibis, *Threskiornis solitarius* (Sélys-Longchamps, 1848).

Grotte "au Sable" — This is another small cave (Fig. 3), in which subfossil remains are dominated by *Puffinus* shearwaters (Mourer-Chauviré *et al.* 1999). The deposits included some introduced species, so was contemporary with the first settlers on the island.

Caverne à Cotte — Jouanin & Gill (1967) examined a cave system at 1800 m in elevation, overlooking the Rivière des Remparts, and discovered a smaller chamber about 10 m from the main cave. They discovered cranial and post cranial remains of *Pterodroma baraui* in the sediments. No other details are given.

Rodrigues

There are large numbers of caves and small fissures on the Plaine Corail (Figs 4 and 9), many of which contained subfossil remains. Here I describe only those cave localities that have contributed significantly to our knowledge of the pre-human Mascarene avifauna.

Canyon Tiyel — Canyon Tiyel was probably created by roof collapse of an extensive cave system on the Plaine Corail (Fig. 10). The canyon has a 30+ m high rock face at the northwest end,

FIGURE 9. Cave expert, Greg Middleton (Hobart), entering an unexplored cave on the Plaine Corail. Note the dense covering of introduced, invasive *Lantana* scrub, which now makes locating new caves extremely difficult.

FIGURE 10. Canyon Tiyel looking south. Caves are located at the base of the canyon walls and along the top ridges of the canyon.

which tapers off to approximately 10 m at the southern end, and a number of caves are situated at the base or on top of the canyon walls. The basal sediments are at least 10 m in depth and have been accumulating since the Pleistocene (Burney *et al.* in prep.). The sediments are poor in pollen and subfossil remains.

Caverne Poule Rouge — This cave has proved to be the most palaeontologically productive in recent years (Fig. 11). The cave sediments range from 850 mm in the centre of the cave to <10 mm at the extremities, with the majority of specimens found on or in the uppermost sediments. I discovered a complete, associated male solitaire in 2005, partially buried in flow stone (Fig.12). Other skeletal material retrieved from the site includes the type of *Alectroenas payandeei* Hume, 2011, and remarkably preserved tortoise scutes (outer horny covering), which still retain the original blackish colouration.

Caverne Gastonia — Caverne Gastonia (Fig. 13) is a pit-fall cave with a unique, small pool at the furthest point from the entrance. The pool water is so lime ($CaCO_3$) saturated that precipitated lime flakes form on the water surface, before gently sinking and settling into three underwater mounds. Subfossil remains are partially buried in flowstone throughout the caves, but most loose specimens were found on the surface or buried up to a depth of <200 mm beneath the entrance.

Caverne Tortue — This cave has deep sediment deposits which have slumped away from the entrance, which contained disarticulated elements of many native birds. The rest of the cave has sediments averaging <100 mm in depth, except in a few deep recesses.

Caverne l'Affouche — Caverne l'Affouche has proved extremely productive. It is a deep, wide cave with heavy roof collapse forming a steep scree slope within. Rich fossil deposits

FIGURE 11. Lorna Steel (NHMUK) entering a chamber in Caverne Poule Rouge.

FIGURE 12. A complete, associated solitaire *Pezophaps solitaria*, partly buried in flow stone in Caverne Poule Rouge. Photograph courtesy of Lorna Steel (NHMUK).

occur between boulders and overhangs. Finds include an associated solitaire, a probable new passerine, and numerous disarticulated specimens of native birds.

Caverne Dora — Caverne Dora is situated at the southern end of Canyon Tiyel, and contains a series of narrow corridors and small caves. Excavation at the entrance (Fig. 14) unearthed remains of various birds, including owls, herons (Fig. 15) and hundreds of endemic reptile elements. The site entrance may have been utilised by the Rodrigues lizard owl *Mascarenotus murivorus* Milne-Edwards, 1874. One of the owl elements found in this deposit was used for 14C dating (see below).

Caverne Solitaire — Caverne Solitaire is the only cave I have studied that has a distinct sedimentological unit, compared with the general uniform sediment deposits seen in other Rodrigues caves. Beneath a rock overhang lies a ~300 mm thick unit made up of coarse, angular >50 mm cave debris in a matrix of reddish silt/clay. Embedded in the matrix are pieces of wood and individual bird elements, including shearwater *Puffinus* sp. This unit probably represents a flash flood during a severe cyclonic event, when surface debris and bird bones were washed into the cave.

Caverne Bambara — Three large and connecting caves make up the Bambara series. The largest (Bambara I) is open at both ends and it has been used as a shelter for farm stock. Bambara II and Bambara III are more interesting as the cave floors have not been trampled. Sediments reach a depth of 300 mm in places, and excavations of the caves have resulted in the collection of a large number of subfossil remains, including a partially associated Rodrigues turtle dove *Nesoenas rodericana* (Milne-Edwards, 1874) (Hume 2011).

Grand Caverne — This is the largest cave in the Plaine Corail area, and has been used extensively for livestock housing; thus the cave floor is heavily trampled. A large pit is still present in the centre of the cave, which may have been one of the 1874 Transit of Venus excavation sites. Despite the effects of long-term domestic animal occupation, a number of subfossil bird remains have been found in small side chambers, and in undisturbed sediments at the edges of the cave walls.

Anse Mourouk — Mourouk is a coastal dune site, situated in south-central Rodrigues. A complete femur of *Pezophaps solitaria* was recovered during the excavation of a whale skeleton by the author and colleagues in 2007. This is the first subfossil bird bone found on Rodrigues outside of the Plaine Corail.

Age of the fossil deposits

14C dating of dodo, tortoise *Cylindraspis* sp, wood and seeds from the Mare aux Songes on Mauritius suggest an extremely narrow time window for fossil accumulation, with a calibrated age range of ca 4235 to 4100 cal. yr BP (averaged 14C age of 4200 yr BP for date of deposition) (Rijsdijk *et al.* 2011). This contrasts with two

FIGURE 13. Entering Caverne Gastonia through the roof opening. Most of the subfossil remains were found directly beneath the entrance. Photograph courtesy of Lorna Steel (NHMUK).

FIGURE 14. Excavation of Caverne Dora showing Square A. Note the almost uniform and featureless sediments, common to most cave deposits on the Plaine Corail.

museum specimens of *Cylindraspis* sp. obtained by Günther *c.* 1870, which yielded significantly younger radiocarbon ages, between ca 1260 and 1830 BP (Burleigh & Arnold 1986).

On Réunion, radiocarbon dates obtained for bones of *Cylindraspis indica* (Schneider, 1783) from the Marais de L'Ermitage give dates ranging 915 ± 120 BP (interval in real years after calibration 883–1273 AD) and 1755 ± 40 BP (interval in real years after calibration 186–391 AD), and those of introduced *Sus scrofa* Linnaeus, 1758 associated with *C. indica* 365 ± 35 BP (interval in real years after calibration 1458–1633 AD) (Mourer-Chauviré *et al.* 1999).

Two 14C dates have been obtained from Rodrigues. One taken at 10 m from basal sediments in Canyon Tiyel gave a date of 8490 ± 40 BP (interval in real years after calibration 9540–9460 BP) (Burney *et al.* in prep.). Another 14C date taken from a partial humerus of the extinct Rodrigues lizard-owl *Mascarenotus murivorus* (Milne-Edwards, 1874), excavated from sediment at a depth of 65–75 mm in Caverne Dora, dated to 2850 ± 30 BP (interval in real years after calibration 3060–2870 BP (Burney *et al.* in prep.). The latter dating is indicative of extremely slow sediment depositional rates within the caves themselves.

Palaeovegetation

While we have a comparatively good idea of the original macrofauna on the Mascarenes, the composition of the palaeo-vegetation is more difficult to determine. This is particularly true in the most devastated parts of the islands, *i.e.*, in the coastal and lowland areas, which were probably the prime habitat of many of the endemic vertebrates including the dodo. As these habitats were drier and more open, they were more accessible to humans and vulnerable to fire; hence they were the first areas to be destroyed. Mauritius and Réunion have a wetter windward side on the east side, with a drier zone on the leeward side in the west. Early accounts report that on all three islands, dense canopy forests occurred down to the coast on the windward side, with perhaps a more open, palm-rich forest on the lee (Cheke & Hume 2008). Réunion is a high island with much of its vegetation above 800 m, comprising montane wet forest, heath and upland bogs. As a result, it has the best surviving habitat. Rodrigues was completely forested according to Leguat (1708), being especially dense in the lowland valleys, whereas Pingré (Nagepen 2004) recorded that the forest was thick but stunted on the Plaine Corail; most of the island is now deforested

Recent excavations at the Mare aux Songes have proved invaluable in determining the original composition of lowland forest on Mauritius (Rijsdijk *et al.* 2009). The marsh is situated in a lowland coastal area on the windward side of Mauritius, but receives an average rainfall below 1200 mm, the same average as on the dry, coastal leeward side (Longman 2007).

FIGURE 15. A sternum of the Rodrigues night heron *Nycticorax megalocephalus* on surface sediments in Caverne Dora.

The Mare aux Songes contained forest components from marsh, dry and wet forest zones. The most common species in the deposit is the wet forest tree, tambalacoque *Sideroxylon grandiflorum* (Sapotaceae), which is endangered and confined to mountain forests today. Other wet forest genera include *Canarium* (Burseraceae), *Eugenia* (Myrtaceae), *Elaeocarpus* (Elaeocarpaceae), *Diospyrus* (Ebenaceae) and the endemic palm genus *Dictyosperma* (Arecaceae). Dry forest genera comprise *Foetidia* (Lecythidaceae), lowland species of *Sideroxylon* (Sapotaceae), *Stadmania* (Sapindaceae) and two species of the palm genus *Latania* (Arecaceae), one now extinct (Florens pers. comm.). *Cassine* (Celastraceae) occurs in both wet and dry forest zones. At least four species of screw pines *Pandanus* (Pandanaceae) have also been identified from the deposit, including dry, wet and upland marsh species, indicating that they were once an important component of the lowland coastal forests.

Species accounts (see Tables 1 and 2)

Taxonomic nomenclature follows Howard and Moore (Dickinson 2003).

Ducks and Geese (Anatidae)

Ducks and geese were mentioned on numerous occasions in early accounts, but almost all provide few descriptive details.

Anas theodori — The Mascarene teal once occurred on Mauritius and Réunion, and was last recorded around 1700 on Mauritius and in 1710 on Réunion (Hume & Walters 2012). Osteological studies of postcranial bones have shown that the two populations were undifferentiated, so the birds were almost certainly capable of flying between the islands (Mourer-Chauviré *et al.* 1999; Cheke & Hume 2008). The Mascarene teal was described from postcranial bones collected from the Mare aux Songes (Newton & Gadow 1893), and more recently from postcranial material collected in the Marais de I'Ermitage swamp on Réunion, and are most similar to the Austral teal *Anas gibberifrons* (Müller, 1842) (Mourer-Chauviré *et al.* 1999). Cowles (1994) referred a fragmentary cranium from the Mare aux Songes to *A. theodori*, which differs from that of any other *Anas*.

Alopochen mauritianus — The Mauritian sheldgoose was mentioned in 1681 as 'inhabiting the woods and dry ponds' (Cheke 1987; Young *et al.* 1997), which suggests that it was probably becoming terrestrial. They were last reported in *c.* 1700, so presumably died out shortly after. The Mauritian sheldgoose was described from a partial pelvis and complete carpometacarpus excavated from the Mare aux Songes. Recently, a tarsometatarsus, the first known, was collected there in 2006 (Rijsdijk *et al.* 2009). Furthermore, I have identified a radius, which was erroneously referred to *Nycticorax mauritianus* by Newton & Gadow (1893), as also belonging to *Alopochen*. Mascarene geese are derived from the Egyptian goose *Alopochen aegyptiacus* (Linnaeus, 1766), and the available elements of *A. mauritianus* are smaller than *A. aegyptiacus*.

Alopochen kervazoi — The Réunion sheldgoose was discovered in a number of cave deposits and also in Marais de l'Ermitage swamp. It had disappeared by the end of the 17th century due to over-hunting. *A. kervazoi* differs from *A. aegyptiacus* in having a more robust tarsus and a short, deep bill (Cowles 1994; Mourer-Chauviré *et al.* 1999).

Aythya sp. — Bernardin (1687) and Boucher (1710) both mention 'sarcelles et canards' in Réunion, thereby identifying two species from their observations. Mourer-Chauviré *et al.* (1999) found two carpometacarpi of an *Aythya* sp. in the Marais de l'Ermitage, a genus present on Madagascar, Southeast Asia and Australia, as well as *Anas theodori*. The Madagascar pochard *Aythya innotata* Salvadori, 1894 is most similar

FIGURE 16. A reconstruction of the Mare aux Songes, Mauritius around 4 Kya. Every species depicted here, including the flora, has been found as a fossil in the marsh deposits. Of the vertebrates, only the echo parakeet *Psittacula echo*, pink pigeon *Nesoenas mayeri* and Mauritius kestrel *Falco punctatus* survive today. Illustration by the author.

to the Réunion *Aythya* species, so it may well have been this species or something closely related to it that once occurred on Réunion. Nothing more is known about it.

Stout-legged duck — A single femur discovered in 2009 in Caverne Poule Rouge, Rodrigues, is referable to a small duck, approximately the size of *Anas bernieri* (Hartlaub, 1860). No endemic anatids are known from Rodrigues, but an account by Bouwer (reprinted in Moree 2001), sailing with the fleet under Wolfert Harmenszoon in 1601, stated that he landed on Rodrigues and collected some wild geese (Hume 2003). The bone is robust with a and comparatively lateromedially compressed at the proximal end. More material is needed before any further diagnoses can be made.

Petrels and Shearwaters (Procellariidae)

It is difficult to ascertain the former diversity and abundance of petrels on the Mascarenes. Early accounts report large breeding colonies of various species, particularly on the islets around Mauritius and Rodrigues, but there must have been a number of local extinctions. Furthermore, some very distinct but enigmatic species are known from just a few sightings and even fewer specimens.

Pseudobulweria atterima — The Mascarene Black Petrel is critically endangered, rarely seen and its breeding areas, thought to be confined to Reunion, have only recently been discovered (Tatayah *et al.* 2011). A single specimen has been collected on Mauritius (*ibid*). Bourne (1968) described and figured subfossil remains of a petrel from Rodrigues cave deposits, ascribing them

FIGURE 17. A reconstruction of Canyon Tiyel, Rodrigues around 1 Kya. Every species depicted here has been found as a fossil in the cave deposits. Of the vertebrates, only the two small passerines, the Rodrigues fody *Foudia flavicans* and Rodrigues warbler *Acrocephalus rodericana*, and Rodrigues fruit bat *Pteropus rodricensis* survive today. Illustration by the author.

to *Pseudobulweria atterima*. This was in error as my re-examination of the material shows that the elements are too large and they differ in other characters. Cowles (1987: p. 93) mentioned, but did not describe, the same material, referring it to *Pterodroma*. On Rodrigues in 2008, I found numerous cranial and post-cranial petrel remains, which represent a new, but now almost certainly extinct taxon. It is larger than any petrel known in the region.

Pterodroma arminjoniana — An unidentified species of *Pterodroma*, which bred on Round Island off the north coast of Mauritius, was only recently identified as Trinidae Petrel (Brown & Jordan 2009). It may have only colonised the island since the early 1900s (Vinson 1976). Numerous recent skeletal remains can be found on Round Island, but the species is unknown in the fossil record.

Pterodroma baraui — Barau's petrel is an elusive, endangered species that breeds at high elevations on Réunion (Pinet *et al.* 2009). Cheke (1987) noted that he found a small breeding colony of Barau's petrel on Rodrigues in 1974, but subsequent searches failed to find them. Subfossil remains have been collected from Caverne à Cotte, a cave situated at 1800 m in elevation on Réunion (Jouanin & Gill 1967).

Puffinus iherminieri — Two widespread *Puffinus* shearwaters once bred on Mauritius and Réunion. Audubon's shearwater is no longer resident on Mauritius, but still breeds on Réunion. Subfossil remains of this shearwater are common in Réunion cave deposits, including numerous juvenile specimens (Mourer-Chauviré *et al.* 1999).

Puffinus pacificus — The wedge-tailed shearwater breeds only on a single islet off Réunion, but it is abundant in cave deposits on the mainland. It is still common on Mauritius (Staub 1976), and I discovered skeletal remains in boulder scree below Le Pouce Mountain, and an associated individual in a cave at La Prairie. On Rodrigues, it bred on Ile aux Fregate (Staub 1973, 1976), but my survey of this islet in 2005 failed to locate any birds; feral cats were abundant, and may have exterminated the population. Subfossil remains of this petrel are rare on Rodrigues, but specimens were collected in 1874 , all held at the NHMUK, from unspecified caves on the Plaine Corail.

Grebes (Podicipedidae)

No species of grebe is known to have inhabited the Mascarenes. The supposed extinct species *Podiceps gadowi* Hachisuka, 1953 is based on a mis-identified bone of a whimbrel *Numenius phaeopus* Linnaeus, 1758 (Cowles 1987; see wader accounts below).

Flamingos (Phoenicopteridae)

Phoenicopterus ruber — During the early years of human occupation, greater flamingos were a resident breeding species on Mauritius and Réunion, with stragglers occasionally reaching Rodrigues (Carié 1930; Cheke 1987). Flamingos originally numbered in their thousands and were still considered common during the mid 18th century, but were systematically hunted for food. They were extirpated, or had dispersed from Mauritius by *c*. 1770 and from Réunion by *c*. 1730 (Cheke & Hume 2008). Subfossil remains have been recovered from the Mare aux Songes, Mauritius (Newton & Gadow 1893), and Marais de l'Ermitage, Réunion (Mourer-Chauviré *et al.* 1999), including juvenile specimens.

An enigmatic and hypothetical species, the *Géant*, has created a wealth of literary debate, which is really not deserved. The existence of *Géant* is based entirely on the account of Leguat (1708), who described a bird the height of a man, with a goose-sized body, long neck and legs, and goose-like but pointed bill. He observed a number of them on Mauritius, but saw it only once on Rodrigues. The *Géant* was subsequently described as a valid taxon, *Leguatia gigantia* Schlegel, 1866, and placed in Rallidae, a proposal ardently supported by Rothschild (1907a), Hachisuka (1953) and North-Coombes (1983). However, Leguat also mentions a rose-coloured underwing, which is an important diagnostic character. No rail is known to have any red under the wing (Olson 1977), but flamingos certainly do. With no evidence to the contrary, it seems almost certain that Leguat had observed a flamingo.

Ibises (Threskiornithidae)

Threskiornis solitaries — Ibis of the genus *Threskiornis* occur only on Madagascar and Aldabra in the Indian Ocean, and another species occurred historically on Réunion (Mourer-Chauviré & Moutou 1987; Mourer-Chauviré *et al.* 1995a, b, 1999). It was called the solitaire by the local inhabitants. The solitaire declined once humans settled on the island, gradually retreating into the remote mountain tops as the island became more populated (Cheke 1987; Hume & Walters 2012). The last account to refer to them was in 1708, so they must have died out shortly afterwards (Hume & Walters 2012). Subfossil remains have been found in the Marais de l'Ermitage, Grotte des Premiers Française and Grotte de l'Autel (Mourer-Chauviré *et al.* 1999). It was a derivative of either the sacred ibis *T. aethiopicus* (Latham, 1790), which occurs on Madagascar and Aldabra, or possibly straw-necked ibis *T. spinicollis* (Jameson, 1835) from Australia, Indonesia and New Guinea (*ibid*).

More speculation and misinterpretation has been made about a white dodo on Réunion than any other Mascarene bird, save the dodo of Mauritius (Hume & Cheke 2004). Reports were made during the 17th and early 18th century of a large white bird that could be caught easily and lived alone in the mountains (Mourer-Chauviré *et al.* 1999). These descriptions, which are certainly referable to the solitaire (Mourer-Chauviré *et al.* 1999), were subsequently associated with some white dodo paintings by two Dutch artists, Pieter Holsteyn II and Pieter Withoos (Newton 1869), which elevated the Réunion white dodo *Raphus solitarius* Sélys-Longchamps, 1848 into the realms of scientific credibility (Hume & Cheke 2004). However, no dodo fossil remains have been found on Réunion, whereas the discovery of subfossil remains of an ibis confirmed the solitaire's threskiornithid relationships (Mourer-Chauviré *et al.* 1999), a bird that better corresponds with the descriptions in early accounts.

TABLE 1. Systematic list of Mascarene bird species mentioned in the text including extant species, recently extinct species known from museum skins, and those known from subfossil remains only. Key: * = Misidentified; † = extinct; E = endemic; Ind = indigenous; V = vagrant; F = fossil; S = museum skin.

Common name	**Original Latin name & authority**	**Current Latin name**	**Mauritius**	**Réunion**	**Rodrigues**
Mauritius sheldgoose	*Sarkidiornis mauritianus* Newton & Gadow, 1893	*Alopochen mauritianus*	†FE	–	–
Réunion sheldgoose	*Mascarenachen kervazoi* Cowles, 1994	*Alopochen kervazoi*	–	†FE	–
Mascarene teal	*Anas theodori* Newton & Gadow, 1893	*Anas theodori*	†FE	†FE	–
Réunion pochard	*Aythya* sp. (see Mourer-Chauviré et al. 1999)	*Aythya* sp.	–	†FE	–
Barau's petrel	*Pterodroma baraui* Jouanin, 1964	*Pterodroma baraui*	–	E	†E
Trinidade petrel	*Aestrelata arminjoniana* Gigioli & Salvadori, 1869	*Pterodroma arminjoniana*	Ind	–	–
Mascarene black petrel	*Procellaria atterima* Bonaparte, 1857	*Pseudobulweria atterima*	EV	E	?
Audubon's shearwater	*Puffinus iherminieri* Lesson, 1839	*Puffinus iherminieri*	FInd	FInd	–
Wedge-tailed shearwater	*Puffinus pacificus* Gmelin, 1789	*Puffinus pacificus*	FInd	Find	FInd
Greater flamingo	*Phoenicopterus ruber* Linnaeus, 1758	*Phoenicopterus ruber*	†FInd	†FInd	†V
Réunion ibis or solitaire	*Apterornis solitarius* Sélys-Longchamps, 1848	*Threskiornis solitarius*	–	†FE	–
Mauritius night heron	*Butorides mauritianus* Newton & Gadow, 1893	*Nycticorax mauritianus*	†FE	–	–
Réunion night heron	*Ardea duboisi* Rothschild, 1907a	*Nycticorax duboisi*	–	†FE	–
Rodrigues night heron	*Ardea megalocephalus* Milne-Edwards, 1874	*Nycticorax megalocephalus*	–	–	†FE
Green-backed heron	*Butorides striatus* Linnaeus, 1758	*Butorides striatus ssp.*	†?F		†?F
Javan green-backed heron	*Butorides striatus javanicus* Horsfield, 1821	*Butorides striatus javanicus*	Ind	Ind	Ind
Dimorphic egret	*Egretta dimorpha* Hartert, 1914	*Egretta dimorpha*	†FInd	†Ind	–
Red-tailed tropic bird	*Phaethon rubricauda* Boddaert, 1783	*Phaethon rubricauda*	Ind	Ind	Ind
White-tailed tropic bird	*Phaethon lepturus* Daudin, 1802	*Phaethon lepturus*	Ind	Ind	FInd
Greater frigate-bird	*Fregata minor* Gmelin, 1789	*Fregata minor*	IndV	IndV	IndV
Lesser frigate-bird	*Fregata ariel* Gray, 1845	*Fregata ariel*	IndV	IndV	IndV
Red-footed booby	*Sula sula* Linnaeus, 1766	*Sula sula*	Ind	–	Ind
Masked booby	*Sula dactylatra* Lesson, 1831	*Sula dactylatra*	Ind	Ind	–
Abbott's booby	*Sula abbotti* Ridgway, 1893	*Papasula abbottii*	†E	–	†E
Mauritius darter	**Plotus nanus* Newton & Gadow, 1893	*Phalacrocorax* (*Microcarbo*) *africanus*	–	–	–
Reed cormorant	*Phalacrocorax africanus* Gmelin, 1789	*Phalacrocorax* (*Microcarbo*) *africanus*	†FE?	†E?	–

TABLE 1. (continued).

Common name	Original Latin name & authority	Current Latin name	Mauritius	Réunion	Rodrigues
Mauritius kestrel	*Falco punctatus* Temminck, 1821	*Falco punctatus*	FE	–	–
Réunion kestrel	*Falco duboisi* Cowles, 1994	*Falco duboisi*	–	†FE	–
Réunion harrier	*Circus maillardi* Verreaux, 1862	*Circus maillardi*	†FE	E	–
Réunion rail	*Dryolimnas augusti* Mourer-Chauviré, Bour, Ribes & Moutou, 1999	*Dryolimnas augusti*	–	†FE	–
Mauritius or Sauzier's wood rail		*Dryolimnas sp.*	†FE	–	–
Mauritius red rail	*Apterornis bonasia* Sélys-Longchamps, 1848	*Aphanapteryx bonasia*	†FE	–	–
Rodrigues rail	*Erythromachus leguati* Milne-Edwards 1874	*Erythromachus leguati*	–	–	†FE
Common moorhen	*Gallinula chloropus* Linnaeus, 1758	*Gallinula chloropus*	Ind	Ind	–
Mascarene Coot	*Fulica newtoni* Milne-Edwards, 1867b	*Fulica newtoni*	†FE	†FE	–
Madagascar button-quail	*Tetrao nigricollis* Gmelin, 1789	*Turnix nigricollis*	–	Ind?	–
Whimbrel	*Numenius phaeopus* Linnaeus, 1758	*Numenius phaeopus*	FInd	FInd	Ind
Mauritius grebe	**Podiceps gadowi* Hachisuka, 1953	*Numenius phaeopus*	–	–	–
Curlew	*Numenius arquata* Linnaeus, 1758	*Numenius arquata*	Ind	Ind	Ind
Dodo	*Didus ineptus* Linnaeus, 1766	*Raphus cucullatus*	†FSE	–	–
Rodrigues solitaire	*Didus solitarius* Gmelin, 1788	*Pezophaps solitaria*	–	–	†FE
Mauritian wood pigeon	*Columba thiriouxi* Hume, 2011	*Columba thiriouxi*	†FE	–	–
Mauritius pink pigeon	*Columba mayeri* Prévost & Knip, 1843	*Nesoenas mayeri*	FE	–	–
Réunion pink pigeon	*Nesoenas duboisi* Rothschild, 1907a	*Nesoenas duboisi*	–	†FE	–
Mauritius turtle dove	*Nesoenas cicur* Hume, 2011	*Nesoenas cicur*	†FE	–	–
Réunion turtle dove	*Streptopelia picturata* Temminck, 1813	*Nesoenas aff. picturata*	–	†FE?	–
Rodrigues turtle dove	'*Columba*' *rodericana* (Milne-Edwards, 1874)	*Nesoenas rodericana*	–	–	†FE
Mauritius Blue Pigeon	*Columba nitidissima* Scopoli, 1786	*Alectroenas nitidissima*	†FSE	–	–
Rodrigues blue pigeon	*Alectroenas payandeei* Hume, 2011	*Alectroenas payandeei*	–	–	†FE
Mascarene parrot	*Psittacus mascarinus* Linnaeus, 1771	*Mascarinus mascarinus*	–	†FSE	–
Broad-billed parrot or raven parrot	*Psittacus mauritianus* Owen, 1866b	*Lophopsittacus mauritianus*	†FE	–	–
Rodrigues parrot	*Psittacus rodericanus* Milne-Edwards, 1867a	*Necropsittacus rodericanus*	–	–	†FE
Thirioux's grey parrot	*Lophopsittacus bensoni* Holyoak, 1973	*Psittacula bensoni*	†FE	–	–

TABLE 1. (continued).

Common name	Original Latin name & authority	Current Latin name	Mauritius	Réunion	Rodrigues
Echo parakeet	*Palaeornis echo* Newton & Newton, 1876	*Psittacula echo*	FE	–	–
Rodrigues parakeet	*Palaeornis exsul* Newton, 1872	*Psittacula exsul*	–	–	†FSE
Commerson's lizard-owl	*Strix sauzieri* Newton & Gadow, 1893	*Mascarenotus sauzieri*	†FE	–	–
Gruchet's or Réunion lizard-owl	*Mascarenotus grucheti* Mourer-Chauviré, Bour, Moutou & Ribes, 1994	*Mascarenotus grucheti*	–	†FE	–
Rodrigues lizard-owl	*Strix* (*Athene*) *murivora* Milne-Edwards, 1874	*Mascarenotus murivorus*	–	–	†FE
Mascarene swiftlet	*Hirundo francica* Gmelin, 1879	*Collocalia francica*	Ind	Ind	–
Mauritius cuckoo-shrike	*Oxynotus typicus* Hartlaub, 1865	*Coracina typica*	FE	–	–
Réunion cuckoo-shrike	*Oxynotus newtoni* Pollen, 1866	*Coracina newtoni*	–	E	–
Mascarene flycatcher	*Muscicapa bourbonnensis* Statius Müller,1776	*Terpsiphone bourbonnensis*	E	E	–
Mascarene swallow	*Hirundo borbonica* Gmelin, 1789	*Phedina borbonica borbonica*	Ind	Ind	IndV
Mauritius bulbul or merle	*Hypsipetes olivaceus* Jardine & Selby, 1835	*Hypsipetes olivaceus*	FE	–	–
Réunion bulbul or merle	*Turdus borbonicus* Forster, 1781	*Hypsipetes borbonicus*	–	E	–
Rodrigues bulbul		*Hypsipetes* sp.	–	–	†FE
Rodrigues warbler	*Drymoeca rodericanus* Newton, 1865	*Bebrornis* (*Acrocephalus*) *rodericanus*	–	–	FE
Mauritius olive white-eye	*Zosterops chloronothos* Vieillot, 1817	*Zosterops chloronothos*	FE	–	–
Réunion olive white-eye	*Certhia olivaceus* Linnaeus, 1766	*Zosterops olivaceus*	–	E	–
Mauritius grey white-eye	*Motacilla borbonica* Forster, 1781 (see http://www.zoonomen.net)	*Zosterops borbonicus*	FE	–	–
Réunion grey white-eye	*Motacilla mauritianus* Gmelin, 1789	*Zosterops mauritianus*	–	E	–
Réunion crested starling or huppe	*Upupa varia* Boddaert, 1783	*Fregilupus varius*	–	†FSE	–
Mauritius starling		Sturnidae	†FE	–	–
Rodrigues starling	*Necropsar rodericanus* Günther & Newton, 1879	*Necropsar rodericanus*	–	–	†FE
Réunion stonechat	*Muscicapa tectes* Gmelin, 1789	*Saxicola tectes*	–	E	–
Mauritius fody	*Emberiza rubra* Gmelin, 1789	*Foudia rubra*	FE	–	–
Réunion fody	*Foudia delloni* Cheke & Hume, 2008	*Foudia delloni*	–	E	–
Rodrigues fody	*Foudia flavicans* Newton, 1865	*Foudia flavicans*	–	–	FE

Herons and Egrets (Ardeidae)

Early travelers to the Mascarenes mentioned a number of herons, but the accounts are extremely vague and it is very difficult to interpret the descriptions. Subfossil remains confirm that three endemic species once inhabited the islands (Rothschild 1907a, b; Cheke 1987); however, Newton & Gadow (1893) mention six species of heron, all collected from the Mare aux Songes. My analysis of these latter specimens shows that only three were correctly identified as herons (see below); whereas three are not herons at all (see *Phalacrocorax africanus*, *Alopochen mauritianus* and *Circus maillardi*).

Nycticorax mauritianus — The genus *Nycticorax* (night herons) gave rise to three endemic Mascarene species, all now extinct. Leguat (1708) mentioned 'flights of bitterns' in 1693 on Mauritius, which were probably referable to the Mauritian night heron, *N. mauritianus*, and it is generally assumed that the birds disappeared shortly after this date (Cheke & Hume 2008; Hume & Walters 2012). The Mauritian night heron has often been cited as being flightless, but this was certainly not the case. Although the tarsometatarsus is robust and indicative of a more terrestrial mode of life, a humerus collected from the Mare aux Songes in 1865, but erroneously attributed to great white egret, *Ardea alba* Linnaeus, 1758 by Newton & Gadow (1893), is morphologically more similar to *Nycticorax* and equivalent in size of that of any volant *Nycticorax* species (Hume unpubl. data).

Nycticorax duboisi — Dubois (1674) gave the best account of a night heron from Réunion, a species now confirmed by skeletal remains (Cowles 1994), but appears to have described a juvenile (Cheke 1987; Mourer-Chauviré *et al.* 1999). Night herons were not mentioned again after Dubois's account (Hume & Walters 2012). This was the largest Mascarene species, and like the Mauritian bird, it showed no reduction in wing elements (Mourer-Chauviré *et al.* 1999).

Nycticorax megalocephalus — The Rodrigues night heron was a robust species, with a stout, straight bill and robust legs (Cowles 1987). It was described by Tafforet in 1725–26 as a species reluctant to fly (Hume & Walters 2012). The skeletal morphology confirms that this species was evolving towards flightlessness, but it was still capable of flight. During the Transit of Venus expedition in 1761–3, the astronomer Alexandre-Gui Abbe Pingré made a detailed survey of the Rodrigues fauna (Nagapen 2004), noting that the herons had by this time disappeared. An incomplete associated individual, which included the cranium and jaws, was discovered in Caverne Poule Rouge in 2006 (Hume unpubl. data).

Butorides striatus — Green-backed herons are resident on all of the Mascarene Islands. They are considered to be of the Javan race, *B. s. javanicus* (Ripley 1969), and thought to be a recent colonist to the islands (Cheke & Hume 2008). However, I have identified subfossil remains from Mare aux Songes deposits on Mauritius, and I collected subfossil remains from Caverne Dora on the Plaine Corail, Rodrigues. *Buterides striatus* is a complex group, which not only has a large number of subspecies, but also exhibits extensive individual variation. It is possible that the Mascarenes may once have had an endemic species or subspecies of green-backed heron, but further work is needed before any conclusions can be made.

Egretta dimorpha — The dimorphic egret is common on Madagascar and vagrant to other Indian Ocean Islands (Sinclair & Langrand 2004), and once occurred on Mauritius and Réunion (Cheke & Hume 2008). West-Zanen (1648) mentioned them in 1602 on Mauritius, whilst Dubois (1674) and Feuilley (1705) described them on Réunion. Dimorphic egrets appear to have disappeared sometime during the 18th century. Newton & Gadow (1893) attributed a tarsometatarsus collected at the Mare aux Songes as belonging to *'Ardea ardesiaca'*, but I found that it is referable to *E. dimorpha*, this being the only known subfossil element of this species.

Tropicbirds (Phaethontidae)

Phaethon rubricauda — The red-tailed tropic bird remains fairly common on Mauritius (Sinclair & Langrand 2004), breeding on Round Island off the north coast. It is a rare vagrant to Réunion (Probst 1997) and, although scarce, still inhabits the islets within the lagoon surrounding Rodrigues, and was reported to have bred on the cliffs of Cascade Victoire in 1967 (Staub 1973; 1976). No subfossil remains of *P. rubricauda* have yet been identified on the Mascarenes.

Phaethon lepturus — The white-tailed tropic bird is widely distributed throughout the Mascarenes, and it is the most abundant subfossil bird species found in cave deposits on Rodrigues (Hume 2005); adults, juveniles and eggs are equally represented. After a period of decline on Rodrigues, it is now recovering in numbers, and live birds and occasional fresh corpses are encountered in and around the cave sites.

Frigate-birds (Fregatidae)

Fregata minor/*Fregata ariel* — Frigate-birds have a wide Indo-Pacific distribution and occur on oceanic islands throughout the Indian Ocean (Sinclair & Langrand 2004). Both species are rare vagrants to Réunion (Barré *et al.* 1996). Two species are thought to have once bred on Mauritius and Rodrigues, the greater frigate-bird, *Fregata minor*, and the lesser frigate-bird, *F. ariel* (Cheke 1987). On Mauritius, they were once resident breeders, and a frigate-bird is shown in an engraving depicting Dutch activities ashore in 1598 (Het Tvveede Boeck 1601). Both species had all but disappeared by the 1850s; the last confirmed sightings were on Round Island, Mauritius (E. Newton 1861; Cheke 1987). On Rodrigues, frigates occurred on many of the islets within the lagoon; Pingré reported them as common (Cheke 2001; Nagapen 2004), but it appears that they only bred on Ile aux Fregate (Cheke 1987). Frigate-birds had probably ceased to breed on Rodrigues by *c*. 1850 and were considered rare in 1916 (Bertuchi 1923). They do, however, turn up as rare vagrants within the Mascarenes (Cheke 1987). Probably due to their tree-top nesting preferences and extremely fragile and lightweight skeleton, no subfossil remains of frigate-birds have been discovered in the Mascarenes.

Gannets and boobies (Sulidae)

Sula sula — The red-footed booby occurs year-round on Mauritius but probably never bred there (Cheke 1987, 2001). They do not occur on Réunion (Probst 1997). The islets off Rodrigues, particularly Ile aux Fregate, once harboured large colonies of boobies, and at least one species, dark phase red-footed booby, *Sula sula*, was a resident breeder (Cheke 2001). The population is now extirpated, being last reported in 1916 (Bertuchi 1923; Cheke 1987, 2001). No *S. sula* bones have yet been identified in the Mascarenes.

Sula dactylatra — The masked booby is vagrant to Réunion and still breeds on Serpent Island off Mauritius, the only known breeding site in the Mascarenes (Staub 1976; Cheke 2001), but being a ground nesting bird it is vulnerable to disturbance. As yet, no subfossil remains of this species have been found in the Mascarenes.

Papasula abbotti — Abbott's booby is now confined to Christmas Island, Indian Ocean, the only known breeding population, but colonies also once occurred on Assumption Island and on the Mascarenes. It is also a rare vagrant to the Pacific (Pratt *et al.* 2009). Abbott's booby was mentioned by a number of observers on Rodrigues during the 18th century (Bourne 1976; Cheke 1987, 2001), but was last recorded in 1761 by Pingré (Cheke & Hume 2008). Bourne (1976) confirmed the presence of Abbott's booby on Mauritius from a complete humerus and ulna, collected in the Mare aux Songes. I discovered a proximal humerus, which was mis-identified as solitaire *Pezophaps solitaria*, from Rodrigues cave deposits. Comparison of the Mare aux Songes and Rodrigues specimens with Christmas Island birds indicates that the Mascarene population is distinct. This may also be the case with the Assumption birds (Hume unpubl. data).

Cormorants (Phalacrocoracidae)

Phalacrocorax (*Microcarbo*) *africanus* — Cormorants were reported on Réunion during the early years of settlement; Dubois (1674) and Feuilley (1705) in particular gave good descriptions. They were encountered on the lakes, and when young were considered good to eat (Hume & Walters 2012). They were not recorded again however and presumably died out in the early 18th century. Although not mentioned in early accounts, cormorant subfossil remains have been excavated from the Mare aux Songes. Olson (1975) referred them to the reed cormorant *Phalacrocorax africanus*, a wide ranging African species that is represented on Madagascar by the race *pictilis* Bangs, 1918. However, my analysis of the specimens indicates that it was a smaller taxon, and may represent a new, but extinct subspecies (Hume & Walters 2012). By contrast, an ulna collected from the Mare aux Songes and erroneously referred to *Ardea alba* Linnaeus, 1758 (Newton & Gadow 1893), is most similar to *P. africanus pictilis* (Hume unpubl. data).

Darters and Anhingas (Anhingidae)

Subfossil remains obtained from the Mare aux Songes were described as an endemic anhinga, *Plotus nanus* (Newton & Gadow, 1893), related to the Madagascar species *A. rufa* Daudin, 1802. Olson (1975) re-examined the material and concluded that it was in fact referable to the African Reed Cormorant *Phalacrocorax* (*Microcarbo*) *africanus* (see below).

Hawks and Falcons (Accipitridae)

Birds of prey have populated many island groups throughout the Indian Ocean and far-ranging migrants regularly visit the Mascarenes (Sinclair & Langrand 2004). Two genera are certainly known from Réunion and Mauritius, *Circus* and *Falco*, while a possible third genus remains indeterminate (Mourer-Chauviré *et al.* 1999).

Falco punctatus — The Mauritius kestrel was once considered the most endangered bird in the world, with numbers down to six birds in 1974 (Jones 1987). Due to intensive captive breeding and conservation efforts, by 2005 numbers increased to an estimated 800–1000 individuals (Jones in Cheke & Hume 2008), but this estimate was prematurely optimistic. The population has dropped to <400 individuals and continues to decline (Cade 2008). A few subfossil elements have been collected from both the Mare aux Songes and from caves beneath Le Pouce Mountain.

Falco duboisi — A morphologically distinct species of kestrel, *F. duboisi*, once inhabited Réunion, and was described from subfossil material collected in 1974 (Cowles 1994). In 1671–2 it was reported to *'do harm to the fowls of the inhabitants and the game of the island'* by Dubois (1674) and was persecuted accordingly, but this was its only record from life, so the date of its extinction is unknown (Hume & Walters 2012). The Mauritius kestrel has short, rounded wings, which is indicative of a forest inhabitant (Jones 1987), whereas the Réunion kestrel was more similar to the Eurasian kestrel complex, which are open habitat specialists (Mourer-Chauviré *et al.* 1999).

Circus maillardi — Two species of *Circus* harrier have been described from the Mascarenes. However, that described from subfossil material on Mauritius as *Circus alphonsi* Newton & Gadow, 1893, has been shown by Mourer-Chauviré *et al.* (2004) to be conspecific with the Réunion Harrier, *C. maillardi*, which is extant but endangered on Réunion. On Mauritius, the species is known from subfossil remains collected from the Mare aux Songes and cave deposits around Le Pouce Mountain (Newton & Gadow 1893; Rijsdijk *et al.* 2009), including an ulna formerly attributed to *Nycticorax mauritianus* that I have shown is referable to *C. maillardi*; it is also briefly mentioned in the account of Cornelis Matelieff de Jonge in 1606 (Barnwell 1948).

TABLE 2. List of species that almost certainly once existed, but lack supporting fossil evidence. This category of 'hypothetical' taxa is restricted to Réunion, primarily due to the paucity of subfossil remains of certain avian orders on that island.

Common name	Original Latin name & authority	Current Latin name	Mauritius	Réunion	Rodrigues
Emerillon		*Falco*? sp.	–	X	–
Oiseaux bleu	*Cyanornis coerulescens* Sélys-Longchamps, 1848	*Cyanornis* (*Porphyrio*) *coerulescens*	–	X	–
Réunion blue pigeon		*Alectroenas* sp.	–	X	–
Réunion ring-necked parakeet	*Psittacus eques* Boddaert, 1783	*Psittacula eques*	–	X	–
Réunion grey parrot		*Psittacula* aff. *bensoni*	–	X	–
Réunion red and green parrot	'*Necropsittacus*' *borbonicus* Rothschild, 1907b	Genus indeterminate	–	X	–

No Réunion subfossil material is known. Why the Réunion population has survived, whereas the Mauritius birds disappeared in the early years of human settlement, remains unclear.

Small falcon — Réunion. An enigmatic species called an 'Emerillon (=merlin)' was described by Dubois (1674) as 'although small, do not fail to carry away chickens and eat them' (Mourer-Chauviré *et al.* 1999). Cheke (1987) suggested that this description was referable to *Falco duboisi*, but kestrels had already been mentioned in Dubois's account. The Emerillon may have been a migratory *Falco* species or an endemic small hawk that is now extinct.

Rails and coots (Rallidae)

Rails have colonised almost every oceanic island archipelago throughout the world. At least five genera formerly occurred on the Mascarenes, and two of these, the Mauritius red rail *Aphanapteryx bonasia*, and Rodrigues rail *Erythromachus leguati*, must have been isolated for some time; their relationships with other rails are now difficult to determine (Olson 1977; Livezey 1998, 2003). A sixth genus, *Gallinula*, which still occurs on Mauritius and Réunion, may have been a recent arrival (Cheke & Hume 2008).

Aphanapteryx bonasia — The monotypic genus *Aphanapteryx* is characterised by hair-like plumage, a long de-curved bill, vestigial wings and strong, robust legs. The Mauritius red rail, *A. bonasia*, appears to have been an opportunist omnivore and was able to survive two centuries of anthropogenic changes (Hume & Walters 2012). However, the introduction of cats in the late 17th century proved disastrous, and the rails were not seen again after 1693 (Cheke & Hume 2008). The Mauritius red rail was originally described from illustrations and accounts (Sélys-Longchamps 1848), but the discovery of subfossil remains from the Mare aux Songes allowed Milne-Edwards (1868) to correctly assign it to the Rallidae. Subfossil remains have also been collected in a number of widespread cave localities, which includes a complete associated individual collected by Thirioux somewhere around Le Pouce Mountain and a partially associated individual from a cave near Vieux Grand Port in the southeast.

Erythromachus leguati — The Rodrigues rail is sufficiently distinct from *A. bonasia* in a number of characteristics to warrant generic separation (Olson 1977; Mourer-Chauviré *et al.* 1999; Hume & Walters 2012). It was reported to be common in 1691–3 (Leguat 1708) and in 1725–6 by Tafforet (Hume & Walters 2012), but Pingré in 1761 (Hume & Walters 2012) stated that the species was by then extinct. A large series of subfossil remains collected by colleagues and I in caves on the Plaine Corail exhibit a great size variation, almost certainly due to sexual dimorphism. An incomplete but associated individual, which includes a complete skull and jaws, was collected in Caverne Poule Rouge in 2005.

Dryolimnas augusti — The volant nominate white-throated rail *Dryolimnas cuvieri* Pucheran, 1845 is widely distributed in Madagascar, where it is reasonably common (Sinclair & Langrand 2004). Interestingly, the type, a gravid female collected on Mauritius (Pucheran 1845), may have been a vagrant. There are two closely related subspecies, the flightless Aldabran rail, *D. c. aldabranus* (Günther, 1879), from Aldabra atoll, which holds the distinction of being the last surviving Indian Ocean flightless bird, and the recently extinct Assumption Island rail, *D. c. abbotti* Ridgway, 1894, which had reduced flying capabilities. A second species, only tentatively placed in *Dryolimnas*, has recently been described from fossil remains collected in the Caverne de la Tortue, Réunion (Mourer-Chauviré *et al.* 1999). This Réunion rail *D. augusti* was morphologically similar, although larger, than the Aldabran species and was probably also flightless. Dubois (1674) mentioned a 'wood rail' in his list of species, and this is almost certainly referable to the Réunion rail (Mourer-Chauviré *et al.* 1999).

Dryolimnas sp. — Mauritius. Cowles (1987) identified *Dryolimnas* material collected from the Mare aux Songes, which had previously been ascribed to the common moorhen *Gallinula chloropus* Linnaeus, 1758 (Newton & Gadow 1893). However, he referred the material to nominate *D. cuvieri.* I identified more *Dryolimnas* material from a collection made by Thirioux in caves around Le Pouce Mountain, which shows that an endemic, flightless *Dryolimnas* once occurred on Mauritius.

Cyanornis (*Porphyrio*) *coerulescens* — The most enigmatic of all Mascarene rails is the 'Oiseau bleu,' a bird that once occurred on the Plaine des Cafres, Réunion. They were mentioned on a number of occasions by trustworthy observers and last reported around the middle of the 18th century (Cheke & Hume 2008). Their colour was described as blue with red beak and legs (*e.g.*, Dubois 1674), and they were considered good game and, although able to fly, could easily be caught and killed with sticks (Cheke & Hume 2008). No subfossil remains have yet been found to resolve their affinities, but the oiseau bleu is generally considered to represent a large *Porphyrio* gallinule (Hume & Walters 2012), a genus which occurs on Madagascar (Sinclair & Langrand 2004). No subfossil remains are known from the rich Mare aux Songes deposits or from the Thirioux montane collections, which suggest that Mauritius lacked suitable habitat for this taxon.

Gallinula chloropus — The common moorhen is found on a number of western Indian Ocean islands, including Mauritius and Réunion (Sinclair & Langrand 2004). The Mascarene populations are generally treated as part of *G. c. pyrrhorrhoa* A. Newton, 1861, that also occurs on Madagascar and the Comoro Islands, and appear to be of recent origin (Cheke & Hume 2008). No subfossil remains of *Gallinula* have been identified on the Mascarenes.

Fulica newtoni — A coot of the genus *Fulica* was once found on Mauritius and Réunion. Despite some suggestions that *F. newtoni* was flightless, there is no reduction in the pectoral elements. Furthermore, the birds from Mauritius and Réunion are undifferentiated, indicating that the species was clearly able to fly between the islands (Mourer-Chauviré *et al.* 1999; Cheke & Hume 2008). Both populations had disappeared by the end of the 17th century (Hume & Walters 2012). *F. newtoni* was described from subfossil remains from the Mare aux Songes (Milne-Edwards 1867), and skeletal elements were collected by Kervazo in the Grotte des Premiers Française on Réunion (Cowles 1994).

Button-Quails (Turnicidae)

It appears that there was once an indigenous population of button-quails on Réunion, which were mentioned in a number of accounts, but appeared to have died out around the 1670s (Cheke 1987). It is very likely that these button-quails were *Turnix nigricollis* (Gmelin, 1789), a native of Madagascar. Madagascar button-quails were introduced around 1714 on Réunion and possibly during the 1830s on Mauritius (Cheke & Hume 2008); they still occur on Mauritius and Réunion today (Sinclair & Langrand 2004). No subfossil remains have been found on Réunion, whereas a few post-cranial elements were collected by Thirioux around Le Pouce Mountain.

Waders (Scolopacidae)

A number of waders are regular migrants to the Mascarenes, but only two are identifiable from early accounts and only one from the fossil record.

Numenius phaeopus — The whimbrel is a common migrant to the Mascarenes, and appears to have been regularly hunted on Mauritius in the past. The only evidence of this species in the fossil record is an ulna collected in the Mare aux Songes, Mauritius, which was originally assigned to a *Podiceps* sp. by Newton & Gadow (1893) and later formally described as *P. gadowi* Hachisuka, 1953. Cowles (1987) re-identified this specimen and correctly assigned it to *Numenius phaeopus*. A tarsometatarsus was also collected in the Grotte des Premiers Française on Réunion (Mourer-Chauviré *et al.* 1999).

Numenius arquata — The curlew is a less frequent migrant to the Mascarenes, and was also regularly hunted in the past. No subfossil remains of this species have yet been identified.

Terns (Stercorariidae)

A number of terns breed on off-shore islands on the Mascarenes, but all are unknown in the fossil record, so they are mentioned here only for completeness. The populations of common noddy *Anous stolidus* (Linnaeus, 1758), lesser noddy *Anous tenuirostris* (Temminck, 1823), sooty tern *Sterna fuscata* (Linnaeus, 1766), bridled tern *Onychoprion anaethetus* (Scopoli, 1786) and fairy tern *Gygis alba* (Sparrman, 1786) were variously mentioned in early accounts as being extremely abundant, especially on Rodrigues (Cheke & Hume 2008), but are now much reduced in numbers.

Pigeons and doves (Columbidae)

Pigeons and doves, including the dodo and solitaire, are mentioned in almost all early accounts that relate to the Mascarene fauna. All describe their inherent tameness and the ease with which they could be caught, but few provide descriptive details. Only one species, *Nesoenas mayeri*, of at least 12 endemic pigeons and doves (Hume 2011), survives today.

Raphus cucullatus — The dodo has been the subject of more debatable literature than any other bird (Hume 2006). It was first mentioned in 1599 and first illustrated in 1600 (Hume 2006), but became extinct sometime between 1662 (Cheke 1987) and 1693 (Hume *et al.* 2004). MtDNA analysis has shown that the dodo and solitaire *Pezophaps solitaria* are monophyletic and have a sister group relationship to the Nicobar pigeon *Caloenas nicobarica* (Pereira *et al.* 2007; Shapiro *et al.* 2002). Almost all of the known subfossil remains were excavated from the Mare aux Songes, but Thirioux collected an associated individual and a partially associated individual from undisclosed caves in the centre of the island. More recently, a complete but badly degraded specimen was excavated at Bois Cheri, in the central uplands (Middleton & Hume In press), and individual elements have been collected from caves at Vieux Grand Port, La Prairie, Baie du Cap and Roches Noires and from a marsh at Flacq (Janoo 2005; Hume *et al.* 2009). According to the fossil evidence, the dodo was once widely distributed around Mauritius, but predominantly confined to the lowlands. This may also represent a bias, as fossil depositional environments are more numerous in the lowlands and the lowland cave and marsh deposits are more conducive to bone preservation (Hume 2005). Juvenile dodo remains are incredibly rare; only one tarsometatarsus collected by Thirioux from an unspecified cave/boulder scree deposit in the valleys around Le Pouce (photographed and now lost (Hume 2006)), and a fragment from a cave at La Prairie have been collected.

Pezophaps solitaria — The solitaire was the closest relative of the dodo and endemic to Rodrigues, but differed markedly in morphology. It was considered to be common when first described (Leguat 1708; Tafforet in Hume & Walters 2012), but had disappeared by the 1760s. The solitaire is known from a femur collected at Anse Mourouk and thousands of skeletal elements, including associated individuals, from caves on the Plaine Corail. It exhibited the greatest sexual dimorphism known in any neognathous bird (Livezey 1993), and both sexes were extremely aggressive when defending their territories (Hume & Steel 2013). However, not a single juvenile specimen has yet been identified.

Columba thiriouxi — A small species of pigeon, tentatively referred to typical *Columba* (Hume 2011), disappeared sometime after 1730 (Hume & Walters 2012). It is known from subfossil cave deposits collected around Le Pouce Mountain and Plain des Roches. The short, broad tarsometatarsus suggests that it was an arboreal species.

Endemic *Nesoenas* pink pigeons were confined to Mauritius and Réunion, whereas *Nesoenas* turtle doves once occurred on all three Mascarene Islands. All but the Mauritius pink pigeon *Nesoenas mayeri* had disappeared during the early 18th century. Introductions of Madagascar turtle doves *Nesoenas picturata* (Temminck, 1813) took place on Mauritius and Réunion after the extinction of the native birds, and present populations of *N. picturata* are all introduced. This Madagascar species differs from the endemic *Nesoenas* turtle doves in a number of osteological details (see Hume 2011), and is almost certainly unknown in the fossil record.

Nesoenas mayeri — The pink pigeon is the only surviving Mascarene columbid and confined to Mauritius. It had been reduced to less than 25 birds in the 1970s, but a successful captive-breeding and re-introduction programme has increased the population to 350+ individuals today (Jones in Cheke & Hume 2008). It is the commonest subfossil species found in cave deposits, but markedly less so in the Mare aux Songes marsh (Hume 2011).

Nesoenas duboisi — The Réunion pink pigeon was described by Rothschild (1907a, b) based on the account of Dubois (1674), the only person to record it in life. Humeri referable to this taxon discovered in Grotte des Premiers Française and Grotte de l'Autel are larger than *N.*

mayeri (Mourer-Chauviré *et al.* 1999), a closely related species.

Nesoenas cicur — The Mauritius turtle dove is known from subfossil remains collected at the Mare aux Songes and cave deposits situated in the valleys of Le Pouce Mountain and at Vieux Grand Port (Hume 2011). It became extinct sometime after 1730. The Mauritius turtle dove had comparatively robust pelvic elements and reduced pectoral elements, so was probably more terrestrial than other *Nesoenas* pigeons.

Nesoenas aff. *picturata* — Two *Nesoenas* subfossil elements collected in the Grotte "au sable" on Réunion (Mourer-Chauviré *et al.* 1999) may be referable to *N. cicur* or a closely related species (Hume 2011).

Nesoenas rodericana — The Rodrigues turtle dove is known from early accounts and from cave deposits collected on the Plaine Corail (Hume 2011). It was a small species, with a distinct sternum, and disappeared between 1726 and 1761, due to rat predation and deforestation (Hume & Walters 2012). Partially associated individuals were discovered in Caverne Bambara II in 2006, and Caverne l'Affouche in 2013.

Alectroenas nitidissima — Despite being persecuted for over two centuries, the Mauritius blue pigeon was still comparatively numerous at the end of the 18th century. However, due to severe deforestation, it had disappeared by 1837 (Hume 2011; Hume & Walters 2012). It is known from three skins, the most recent taken in 1826 (Milne-Edwards & Oustalet 1893), and a few subfossil remains collected from the Mare aux Songes and caves around Le Pouce and Roches Noires (Hume 2011).

Alectroenas sp. — It seems probable that an *Alectroenas* once occurred on Réunion (Hume 2011), as a bird of this description was briefly mentioned by Dubois (1674) and Bontekoe (1650), but no skeletal remains have been found to confirm its affinities.

Alectroenas payandeei — The Rodrigues blue pigeon was never mentioned by any visitors to the island. It is known from a single but distinct tarsometatarsus, collected in Caverne Poule Rouge on the Plaine Corail (Hume 2011).

Parrots (Psittacidae)

It is difficult to determine how many species of parrot once inhabited the Mascarenes (Hume 2007), but at least seven taxa were present on the islands, with a further two awaiting confirmation from the fossil record. Like the columbids, almost every early account mentions them, but few provide any details. They were rapidly hunted to extinction, long before any scientific analysis could take place. All Mascarene parrots are now extinct save the echo parakeet *Psittacula echo* (Newton & Newton, 1876) of Mauritius.

Mascarinus mascarinus — The Mascarene parrot is known from two skins, both collected during the 18th century, and from a few subfossil elements excavated in caves on Réunion (Mourer-Chauviré *et al.* 1999). Dubois (1674) gave a good description of this species in 1671–72 and a few live birds survived the journey to France (Brisson 1760; Mauduyt 1784). The much repeated 1834 date of extinction (Hahn 1834) is unfounded; the Mascarene parrot had almost certainly disappeared by *c.* 1800 (Hume 2007). Analysis of skeletal material and similarities in colouration strongly suggest a direct relationship with southeast Asian Psittaculini parrots (Mourer-Chauviré *et al.* 1999; Hume 2007), but mtDNA analysis, according to Kundu *et al.* (2012), embedded *Mascarinus* within *Coracopsis nigra* (Linnaeus, 1758), the lesser vasa parrot of Madagascar and nearby islands. However, this result has been questioned (Joseph *et al.* 2012).

Necropsittacus rodericanus — The Rodrigues parrot was described as a big-headed, long-tailed bird that frequented the southern islets off Rodrigues, returning to the mainland only to drink water (Hume 2007). Pingré listed *N. rodericanus* as very rare in 1761 and this was the last time it was mentioned (Hume & Walters 2012). Subfossil remains are scarce, although cranial and post-cranial specimens have been recovered from unnamed caves on the Plaine Corail. Colleagues and I discovered a rostrum, humerus, and tibiotarsus in Caverne Tortue in 2008.

Lophopsittacus mauritianus — The raven parrot or broad-billed parrot, which was last recorded in 1673–4, had developed huge jaws for cracking the hard nut shells of palms and other forest trees (Hume 2007, contra Holyoak 1971), and exhibited the greatest sexual dimorphism known in any parrot (Hume 2007). Despite statements to the contrary (*e.g.*, Hachisuka 1953), there is no evidence to suggest that this species was flightless (Hume 2007), but it was probably poorly volant. It is known from numerous subfossil remains from the Mare aux Songes, Mauritius, with a preponderance of mandibles and tibiotarsi (Hume 2005), and also from a few specimens collected in caves around Le Pouce Mountain.

At least two species of *Psittacula* parakeet colonised the Mascarenes. A *Psittacula eupatria* (Linnaeus, 1766) derivative, *P. wardi* (Newton, 1867), once occurred on the Seychelles, with probable derivatives on Mauritius (*P. bensoni*), Réunion (*P.* aff. *bensoni*/ red and green parrot) and possibly Rodrigues (*P. exsul*) (Hume 2007). A second colonisation event involved *P. krameri* (Scopoli, 1769), with derivatives on Mauritius (*P. echo*) and on Réunion (*P. eques*) (Groombridge *et al.* 2004).

Psittacula bensoni — Thirioux's grey parrot was a long-tailed, large-headed species, and a probable derivative of the *Psittacula* '*eupatria*' group (Hume 2007). It was considered to be one of the commonest species on Mauritius during the early 18th century, but had disappeared by *c.* 1760 (Hume 2007; Hume & Walters 2012). Subfossil remains are rare. It is known from cave deposits collected by Thirioux from the valleys around Le Pouce Mountain (Hume 2007) and from a few skeletal specimens from the Mare aux Songes (Rijsdijk *et al.* 2009).

Psittacula aff. *bensoni* — Dubois (1674) and Cossigny (1732–55) mentioned a grey parrot on Réunion, which may have been conspecific with *P. bensoni*. However, no skeletal remains have been found to determine its relationships. It was last recorded in *c.* 1730 (Cheke & Hume 2008).

Psittacula exsul — The Rodrigues parakeet is known from two skins collected in the early 1870s (Newton 1875), just prior to the species becoming extinct. There appear to have been two colour morphs (green and blue), of which only the blue morphs were collected. Subfossil remains are rare, but morphometric analysis and one contemporary description suggest that this species may have been derivative of the *Psittacula 'eupatria'* group (Hume 2007).

Psittacula echo — The echo parakeet, the only surviving psittaciform in the Mascarenes, was described in the 1980s as the world's rarest parrot, with a population of less than a dozen birds (Forshaw 1989). It has now recovered to some 350 mature individuals (Jones in Cheke & Hume 2008). Large numbers of subfossil remains have been excavated in caves around Le Pouce Mountain and Plaine des Roches, including juveniles (Hume 2007), but its remains are rare in the Mare aux Songes deposits.

Psittacula eques — The Réunion parakeet is known only from a number of paintings and accounts (Hume 2007) and, putatively, one skin (Jones 1987; but see Cheke & Hume 2008). Despite the survival of *Psittacula echo* on Mauritius, *P. eques* disappeared early in Réunion's history, being last reported around 1730 (Hume & Walters 2012). Pending confirmation from fossil remains, it may be conspecific with *P. echo*.

Réunion red and green parrot. Genus indeterminate. This enigmatic bird, which was reported only once, has caused much taxonomic confusion. Dubois (1674), whose observations can be trusted, described a green parrot with head, wings and tail the colour of fire. It was formerly described as *'Necropsittacus' borbonicus* Rothschild, 1907b, based on the assumption that it was related to *N. rodericanus* of Rodrigues (Rothschild 1907a), but Rothschild confused the early literature (Hume 2007). It is possible that Dubois was describing an endemic *P. 'eupatria'* species on Réunion. The colouration, apart from the red tail, is typical of *P. eupatria* (Hume 2007).

Owls (Strigidae)

Owls of the genus *Otus* occur on a number of Indian Ocean islands (Fuchs *et al.* 2008) and it is from this genus that the endemic Mascarene genus *Mascarenotus* was derived (Mourer-Chauviré *et al.* 1994). The Mascarene species were characterised by large size and robust, long legs (Newton & Gadow 1893; Mourer-Chauviré *et al.* 1994), presumably adaptations for predation of reptiles and small birds. The Mascarene lizard-owls are known from descriptions, one drawing and a few subfossil remains.

Mascarenotus sauzieri — The Mauritian lizard-owl was a large eared owl with bare tarsi. A drawing by Jossigny, reproduced in Oustalet (1897), is the only known illustration of the genus. One individual was described in detail by Desjardins (1837), the specimen of which was lost during a cyclone in the 1850s (Cheke & Hume 2008), while a few others were reported around the same time (Cheke & Hume 2008). *M. sauzieri* appears to have required large trees for nesting and roosting, and disappeared due to extensive deforestation. Clark (1859) stated that at the time of writing they had become extinct after being formerly plentiful. Thirioux collected subfossil remains from cave deposits around Le Pouce and Plaine des Roches, which includes some partially associated material. I collected a complete pelvis in 2007 in Kanaka Cave, Bois Cheri.

Mascarenotus grucheti — Owls were never reported historically on Réunion, but subfossil remains confirm that a species once occurred there (Mourer-Chauviré *et al.* 1994, 1999). It differed from *M. sauzieri* in having slightly more reduced wing elements (Mourer-Chauviré *et al.* 2006).

Mascarenotus murivorus — The Rodrigues lizard-owl was mentioned by Leguat (1708) and Tafforet (Hume & Walters 2012), the latter stating that the small brown owls fed on lizards and birds and lived almost exclusively in trees. Pingré in 1761 never reported them, so they presumably disappeared sometime between the visits of Tafforet in 1725–26 and Pingré (Hume & Walters 2012). Subfossil remains are rare in caves at the Plaine Corail, which suggests that they were not using these areas for roosting or breeding.

Swifts (Apodidae)

Collocalia francica — The Mascarene swiftlet has decreased in numbers on Mauritius, but it is still common on Réunion (Sinclair & Langrand 2004). Fresh skeletal specimens are comparatively numerous on Mauritius, but no subfossil remains have been identified from either island. Despite its habit of nesting in caves, no subfossil remains have been found in the rich fossil deposits on the Plaine Corail, which suggests that

TABLE 3. List of endemic Mascarene bird species mentioned in the text, with percentages of scientifically described species and undescribed species known from the fossil record. This study has shown that certain families of birds are under-represented in the literature, especially the sea birds and passerines. The high number of undescribed taxa on Réunion is a result of the poor fossil record from that island (see also Table 2). Key: † = extinct; * = species occurs on more than one island.

Family	Endemic species described/ undescribed	% of species undescribed	Mauritius	Réunion	Rodrigues
Anatidae	3/2	66%	2†*	2/1†*	1†
Procellariidae	2/1	50%	–	2	1†
Threskiornithidae	1/0	0%	–	1†	–
Ardeidae	3/0	0%	1†	1†	1†
Sulidae	0/1	100%	1†*	–	1†*
Phalacrocoracidae	0/1	100%	1†	1†	–
Falconidae	3/1	33%	1	1/1†	–
Accipitridae	1/0	0%	1†*	1*	–
Rallidae	4/2	50%	2/1†*	2/1†*	1†
Columbidae	12/3	25%	5(4†)	1/3†	2/0†
Psittacidae	9/2	22%	3(2†)/0	4/2†	2/0†
Strigidae	3/0	0%	1†	1†	1†
Campephagidae	2/0	0%	1	1	–
Monarchidae	1/0	0%	1*	1*	–
Pycnonotidae	2/1	50%	1	1	1†
Sylviidae	1/0	0%	–	–	1
Zosteropidae	4/0	0%	2	2	–
Sturnidae	2/1	50%	1†	1†	1†
Muscicapidae	1/0	0%	–	1	–
Ploceidae	3/0	0%	1	1†	1

swiftlets were absent from Rodrigues.

Passerines

Passerines have been particularly successful at colonising remote oceanic archipelagos; however, establishing their former diversity can be problematic. Passerines were rarely mentioned in the early Mascarene literature and, where passerine fossil remains have been collected, there has been a tendency to ignore them. Here I present a preview of my recent findings; even in this initial period of study, a number of new taxa have been discovered (see also Tables 3 and 4).

Cuckoo shrikes (Campephagidae)

Cuckoo-shrikes are endemic to Mauritius and Réunion, but there is no evidence that *Coracina* ever occurred on Rodrigues.

Coracina typica — The Mauritius cuckoo shrike is widespread on the island, but it is declining in numbers and considered endangered (Sinclair & Langrand 2004). I identified subfossil remains from cave deposits collected by Thirioux around Le Pouce Mountain.

Coracina newtoni — The Réunion cuckoo shrike is critically endangered and restricted to two small plateaus, the Plaine d'Affouches and Plaine des Chicots, in the north-west (Le Corre & Safford 2001). No subfossil remains are known, which is unsurprising considering its montane habitat.

Monarch-flycatchers (Monarchidae)

Terpsiphone bourbonnensis — The Mascarene flycatcher is divided into two subspecies, *T. b. bourbonnensis* (Statius Müller, 1776) on Réunion and *T. b. desolata* (Salomonsen, 1933) on Mauritius. Both populations remain comparatively scarce, but they have a widespread distribution where suitable habitat remains. Flycatchers have not been found in any Mascarene fossil deposit, and the genus is absent from Rodrigues.

Swallows (Hirundinidae):

Phedina borbonica borbonica — The Mascarene swallow is found on Mauritius and Réunion and may have been vagrant to Rodrigues in the passed. It is not known from the fossil record, but it is unlikely that the present status is any different now than in pre-human times (Cheke 1987).

Bulbuls (Pycnonotidae)

Hypsipetes olivaceus — The Mauritian bulbul or merle was considered a delicacy (Staub 1976; Cheke 1987), so it is one of the few passerines that can be identified from the early literature on Mauritius. It is considered endangered today. A number of subfossil remains were collected by Thirioux around the valleys of Le Pouce and caves at the Plaine des Roches.

Hypsipetes borbonicus — The Réunion bulbul was also regularly mentioned due to its edibility (*e.g.*, Dubois 1674). It is widespread on Réunion and considered of least concern, but numbers are declining. No subfossil remains have yet been discovered.

Hypsipetes sp. — Cowles (1987: p. 99) mentioned but did not describe a *Hypsipetes* bulbul collected in 1974 from caves on the Plaine Corail. I have since identified a number of cranial and post-cranial elements discovered in Caverne Poule Rouge, Caverne Bambara II and Caverne Gastonia. A Rodrigues bulbul was never recorded in the early literature, so the reasons for its extinction are unclear.

Old World warblers (Sylviidae)

Acrocephalus rodericanus — The Rodrigues warbler is endemic to Rodrigues, and although presently restricted in range, it once occurred all over the island (Newton 1865). Cranial and post-cranial remains of this species have been collected from Caverne l'Affouche, Caverne Gastonia and Caverne Bambara on the Plaine Corail. There is no present evidence to suggest that *Acrocephalus* ever occurred on Mauritius or Réunion, but a related species occurs on the Seychelles.

White eyes (Zosteropidae)

The white-eyes are successful oceanic island colonists and inhabit numerous islands within the Western Indian Ocean (Sinclair & Langrand

2004); the Mascarenes were almost certainly colonised by *Zosterops* twice in their history (Warren *et al.* 2006), but the genus has never been recorded on Rodrigues.

Zosterops chloronothos — The Mauritius olive white-eye is now rare on Mauritius, and confined to the Black River Gorges mountain range. I identified it from Thirioux' subfossil cave material collected around Le Pouce Mountain and Plaine des Roches in central Mauritius, which shows that it was once more widespread on the island.

Zosterops olivaceus — The Réunion olive white-eye is common and widespread, occurring in the highlands as well as the lowlands. No subfossil remains have yet been discovered.

Zosterops borbonicus — The Réunion grey white-eye is endemic to Réunion (Sinclair & Langrand 2004), where it is widely distributed. Despite this, no subfossil remains have yet been found.

Zosterops mauritianus — The Mauritius grey white-eye is sometimes considered to be a subspecies of *Z. borbonicus*. It is extremely adaptable and it is the commonest surviving native bird. I identified post-cranial subfossil remains from Thirioux' cave deposits collected around Le Pouce Mountain and Plaine des Roches.

Starlings (Sturnidae)

The starlings are gregarious, medium to large-sized birds that inhabit forests and open woodlands (Craig & Feare 2009). Each Mascarene island once harboured an endemic species, two of which were described in early accounts, but only the Réunion species has been preserved as skins. MtDNA analysis has shown that a unique skin, supposedly representing another species of Rodrigues starling *Necropsar leguati* Forbes, 1898, is actually an albinistic trembler from the West Indies (Olson *et al.* 2005). My re-examination of a sternum of a supposed babbler (Timaliidae), mentioned but not described by Cowles (1987: p. 99), is referable to *Necropsar rodericanus*.

Fregilupus varius — The Réunion crested starling or huppe was reported as common until the late 1840s (Cheke & Hume 2008). However, it appeared to have disappeared extremely rapidly, probably as a result of habitat destruction and over-hunting (Hume unpubl. data), with the final records being made in the 1850s (Cheke & Hume 2008). The huppe is characterised by a distinct crest, long, decurved bill and robust pelvic elements. There may have been pronounced sexual dimorphism, the males being larger, with a longer, more decurved bill. MtDNA analysis has shown that *Fregilupus* is distantly related to southeast Asian *Sturnus* starlings (Zuccon *et al.* 2008). At least 20 skins have been preserved in various museums, but a distal femur fragment found in the Grotte des Premiers Française is the only subfossil so far discovered on Réunion (Mourer-Chauviré *et al.* 1999).

Mauritius Starling — I identified a number of cranial and post-cranial bones of a starling from Thirioux' material collected around Le Pouce Mountain and Plane des Roches. This new taxon differs markedly from the other Mascarene starling genera and warrants generic status (Hume in press). Most notable is the long, decurved bill with elongate, well-developed retroarticular processes. This suggests that it was a powerful gaper. The Mauritian starling was not mentioned in the literature, so the reasons for its disappearance are unknown.

Necropsar rodericanus — The Rodrigues starling is known from 19th century subfossil remains, and recently collected material from Caverne Poule Rouge, Caverne Bambara II,

TABLE 4. A total of 57 endemic Mascarene birds have been scientifically described, but another 21, all extinct and known only from the fossil record, await description. The passerines make up 28% of the total number of endemic birds, with at least another 6 undescribed, making them the least described Mascarene order of birds. Key: † = extinct; E = extant; * = *Anas theodori*, *Circus maillardi* and *Fulica newtoni* occurred on both Mauritius and Réunion, but have been included here as part of the total of each island.

Totals	Described/ undescribed	Percent of undescribed species	Mauritius	Réunion	Rodrigues
Total number of Passerines/	16/6	37%	6E/4†	8(2†)/0	3(1†)/2
Total number of endemic birds	57/21	36%	28/8*	32/9*	13/6

Caverne Dora, Caverne Gastonia and Caverne Tortue on the Plaine Corail. It is also known from a unique account. In 1725–26, Tafforet (Hume & Walters 2012) observed birds on the southern islets, where he described their ability to tear turtles (juvenile tortoises?) out of their shells. Pingré in 1761 (Nagapen 2004) did not mention them, so it is likely that they had died out in the intervening years. The Rodrigues starling was slightly smaller than *Fregilupus*, with a straighter, more robust bill and more robust pelvic elements.

Stonechats (Muscicapidae)

Saxicola tectes — The Réunion Stonechat occurs only at higher elevations on Réunion, and is common along forest fringes and on heathland (Sinclair & Langrand 2004). Due to its montane habitat and the lack of high elevation fossil deposits, no subfossil remains of *S. tectes* have been discovered.

Weavers (Ploceidae)

The *Foudia* fodies are endemic to Indian Oceanic islands, including Madagascar, and the Mascarenes once harboured three endemic species, with Madagascan *Foudia madagascariensis* (Linnaeus, 1766) also introduced to all three islands by humans. The Madagascan Fody was originally brought in as a cage bird, becoming established on Mauritius and Réunion in *c.* 1770, and sometime before 1916 on Rodrigues (Cheke 1987; Cheke & Hume 2008)

Foudia rubra — The Mauritius fody is now extremely rare and restricted in range, but is one of the few small passerines mentioned in the early literature (Cheke 1987). I identified cranial and post-cranial subfossil remains from cave deposits collected around le Pouce and Plaine des Roches, indicating that it once had a wide range over Mauritius.

Foudia delloni — The Réunion fody was considered a serious pest when first known in the 1670s (Dubois 1674; Dellon 1685), but disappeared with extreme rapidity shortly after (Hume & Walters 2012). No subfossil remains are known.

Foudia flavicans — The Rodrigues fody had declined to less than 20 birds in the 1960s and was confined to the central plateau (Cheke & Hume 2008), but it is now increasing in numbers and naturally extending its range. I collected post-cranial and cranial subfossil remains from Caverne Gastonia and Caverne l'Affouche.

Passeriformes incertae sedis

Sharp-billed finch — Mauritius. Among the subfossil remains collected by Thirioux is a possibly associated premaxilla and rostrum mandibulae, which represent a new taxon. The bill is long and pointed, and intermediate in size between the undescribed Mauritius starling and *Hypsipetes*. Its generic affinities have not yet been determined.

Broad-billed finch — Mauritius. A fragmentary rostrum mandibulae and a series of post-cranial elements differ from all other Mauritian passerines. They appear to belong to a small species with a broad bill, similar to but larger than *Foudia rubra*, a species found in the same deposits.

Long-legged finch — Mauritius. A distinct tarsometatarsus, much longer and more gracile than any other Mascarene passerine, almost certainly belongs to a new taxon. The osteology suggests that it was a terrestrial species, but its relationships are at present unclear.

Intermediate finch. Rodrigues. A series of post-cranial elements belong to a passerine intermediate in size between the undescribed *Hypsipetes* bulbul and *Foudia flavicans*. Its affinities cannot yet be determined, but it almost certainly represents another now-extinct taxon from Rodrigues.

Discussion

Biogeography

The importance of sea level fluctuations and prevailing wind and sea currents in facilitating avian dispersal and colonisation events within the southwestern Indian Ocean is now being recognised. Indian subcontinental winter Monsoon winds, along with winds from the direction of Australia and Indonesia blow across the Indian Ocean towards the Madagascar region, a route also followed by ocean currents (Cheke & Hume

2008; Warren *et al.* 2010). Numerous sea level low stands of up to 50 m lower than present have been recorded in the last 5 Ma (Miller *et al.* 2005), whereas in the last 650 Ka, some sea level low stands were up to 135 m lower than present, and persisted for up 50 Ka at a time (Warren *et al.* 2010). These events would have greatly increased the land-surface area of the Maldives, Seychelles and Mascarenes, and created subaerial island archipelagos in the Chagos, the Saya de Malha, Nazareth and St.Brandon (Cargados Carajos) banks. This not only reduced distances between islands and continental land masses, but also the inter-island crossings; thus the avifauna could encompass vast stretches of ocean via island-hopping. This may explain why much of the Mascarene avifauna has its origins in Southeast Asia (Warren *et al.* 2010), and not in Madagascar or Africa (Agnarsson & Kuntner 2012), the nearest large landfalls. Although the origins of some Mascarene genera remain unresolved, mtDNA studies have shown that *Psittacula* (Groombridge *et al.* 2004); *Alectroenas* (Gibbs & Penny 2010; Pereira *et al.* 2007; Shapiro *et al.* 2002); *Raphus* and *Pezophaps* (Pereira *et al.* 2007; Shapiro *et al.* 2002); the Mascarene *Zosterops* (Warren *et al.* 2006); *Hypsipetes* (Warren *et al.* 2005) and *Fregilupus* (Zuccon *et al.* 2008) all had their origins in Southeast Asia. Interestingly, the Madagascar endemic starling genus *Hartlaubia* is the closest to the Mascarenes biogeographically, but differs completely in morphology from the Mascarene sturnids. Furthermore, the Seychelles scops owl *Otus insularis* (Tristram, 1880) is more closely related to Southeast Asian *Otus* than to those occurring in Africa (Fuchs *et al.* 2008).

While the origins of some genera remain unresolved, *e.g.*, *Aphanapteryx*, *Eurythromachus*, the founding populations of *Nesoenas*, *Alopochen*, *Threskiornis* and *Saxicola* almost certainly lie within Madagascar, whereas others, *e.g.*, *Foudia*, are Indian Ocean island endemics. *Threskiornis* and *Saxicola* are unknown on Mauritius and Rodrigues, which may have been due to the lack of suitable montane heathland habitat in the case of *Saxicola*, or competitive exclusion. Mauritius and Rodrigues already had a diverse range of terrestrial birds, especially rails, which may have prevented *Threskiornis* from becoming established. Furthermore, Réunion lacks the genera *Raphus*, *Pezophaps*, *Lophopsittacus* or *Necropsittacus* parrots, and *Aphanapteryx* or *Erythromachus* rails. Mourer-Chauviré *et al.* (1999) postulate that these genera may have once occurred on Réunion, but disappeared due to the Piton des Nieges volcanism that occurred between 300 to 188 Ka. Thus the avifauna of Réunion is of comparatively recent origin. Apart from the probably poorly volant or flightless Réunion rail *Dryolimnas augusti*, this may explain why none of the Réunion avifauna that survived into the historic period had evolved complete flightlessness, a characteristic so prevalent with birds on Mauritius and Rodrigues.

There are a number of other perplexing paradoxes. The passerine genera *Zosterops*, *Coracina* and *Tersiphone* appear to have colonised Mauritius and Réunion only, whereas *Acrocephalus* seems to be restricted to Rodrigues. There are also other southwestern Indian Ocean passerine genera, *e.g.*, *Copsychus*, *Nectarinia*, which occur in the Seychelles and Madagascar that are not present on the Mascarenes. Is this a natural distribution, or is there a bias in the fossil record? The *Hypsipetes* bulbuls that occur in the Mascarenes occur only on Mauritius and Réunion today, but the discovery of a fossil *Hypsipetes* species on Rodrigues has shown that each island once had its own species. Likewise, starlings were thought to be restricted to Réunion and Rodrigues, but my recent discovery of a fossil sturnid has revealed that an endemic species also once occurred on Mauritius. Therefore, as the islands have suffered severe anthropogenic changes and the fossil record is far from complete (see Tables 3 and 4), any conclusions based on present avian biogeography must be viewed with caution.

Comparison of the island avifaunas

Documentation left by early vistors to the Mascarene Islands and the fossil record have provided a robust insight into the former avian diversity of the islands. However, this is based in part on how fully the palaeontological record represents the avifauna that was in existence at the time of deposition. Each Mascarene island differs topographically, and although the islands may have shared some genera, the processes of evolution unique to each island resulted in differing speciation events. It appears that once established, much of the Mascarene avifauna became sedentary, with little mobility between islands; the notable exceptions being *Fulica*, *Anas*, *Psittacula* and perhaps *Nesoenas* turtle doves that appeared to have migrated between Mauritius and Réunion (Cheke & Hume 2008; Mourer-Chauviré *et al.* 1999). All of the species mentioned in accounts on Mauritius and Rodrigues have now been correlated to some degree with subfossil remains, whereas the recently discovered and undescribed fossil taxa discussed above were never recorded in life. This is certainly not the case with Réunion. The paucity of fossil remains on Réunion has compounded research problems, and left the affinities of a number of taxa unresolved (see Tables 2, 3 & 4). Cecilé Mourer-Chauviré and her co-workers have done much to rectify this shortfall, yet Réunion remains the poorest island palaeontologically. That a cormorant, a *Porphyrio* rail, three parrots, a pigeon and a fody once occurred on Réunion is beyond doubt, yet they lack physical evidence of any kind. Even extant species such as the Réunion harrier, which is known from the fossil record on Mauritius and all extant passerines, are unknown in the Réunion palaeontological record. This may be the result of a fossil depositional bias, as Réunion has few caves, and only one fossiliferous swamp. Mourer-Chauviré *et al.* (1999) have shown that the Marais de l'Ermitage was subject to hydrological sorting; hence the lack of small bird elements.

Centuries of occupation

The Mascarenes have been subject to severe anthropogenic changes for over four centuries, which unsurprisingly has led to high extinction rates. Human impact on the Mascarenes occurred in approximately five phases:

1. Arab period 1300–1500 — Records of Arab traders on the Mascarenes do not exist, but by inference it can be determined that they were aware of the islands from at least the 13th century (North-Coombes 1994a), or 14th century. As far as known, no attempt at settlement was made, but 14C dates obtained from a black rat *Rattus* aff. *rattus* mandible collected from the Mare aux Songes, and from a rat-predated extinct terrestrial snail, *Tropidophora carinata*, both provide dates of 590 ± 27 BP (interval in real years after calibration 1369–1413 AD) (Hume Unpbl. data). Arab traders had thus inadvertently introduced black rats nearly 200 years before the arrival of the Dutch. Mainland Mauritius once harboured a diverse range of endemic snakes and terrestrial reptiles, including the world's largest skink, but these were never mentioned in the historical literature. Early accounts from Mauritius are notorious for the lack of descriptive information about the smaller birds and reptiles (Cheke & Hume 2008), so there is a strong possibility that they were simply not mentioned, especially if they were inedible or not worthy of eating. However, it is extremely likely and as the fossil record has shown (see passerines above), that components of the herpetological fauna and some passerines disappeared as a direct result of the early introduction of black rats.

2. Portuguese period 1510–1528 — The Portuguese first encountered Réunion in 1510, Mauritius in 1516, and Rodrigues in 1528 (North-Coombes 1994a), but appear to have landed only rarely. The Portuguese fleets were under strict state order not to disclose trading details (Moree 1998), so very few records were made. North-Coombes recorded one landing on Réunion by a Portuguese ship in 1528, after which livestock (probably goats) were released to provide fresh meat on future visits.

3. Dutch period 1598–1710 — The Dutch claimed Mauritius for the Netherlands in 1598 and maintained an almost continuous colony until 1710 (Moree 1998). The busiest shipping period took place from 1601 until 1612, after which the island was only sporadically visited. A fort was built in 1638, but the Dutch abandoned Mauritius in 1658, before re-establishing a colony in 1664. By 1710 the island was no longer considered to be worth maintaining, and was completely abandoned. The European population on Mauritius never numbered more than 50 at any one time, but escaped slaves settled in the interior (Hume 2006). Deforestation was confined to coastal and lowland regions, but the Dutch introduced many non-native species. It was during this period that all large and flightless birds, including the dodo, disappeared.

Two Dutch fleets visited Réunion and left reports, the first led by Adriaen Blok in 1612, and another led by Willem Bontekoe in 1619 (Cheke & Hume 2008), but the Dutch never settled on the island. Bontekoe in particular remarked on the abundance and inherent tameness of the fauna.

A fleet under Admiral Wolphert Harmenszoon sailing in the flagship, *Gelderland*, landed on Rodrigues in 1601 and recorded brief details about the island and its fauna (Moree 2001; Hume 2003), but it was not until the arrival of Francois Leguat in 1691 that detailed faunal descriptions were made (Leguat 1708). Rodrigues was still in a comparatively pristine state during this time, but Leguat noted the presence of large numbers of rats. After two years stay, Leguat left Rodrigues for Mauritius and and made a brief faunal report, in which he mentions that rails, ducks, geese and pigeons had become rare.

4. French period 1642–to present (Réunion); 1715–1810 (Mauritius); 1736–1809 (Rodrigiues) — The French claimed Réunion (Bourbon as it was called from 1649) for France in 1642, and a permanent French colony was established in 1665, numbering up to 200 by 1674 (Cheke & Hume 2008). Dubois (1674) in particular gave a good account of the fauna during the early years of occupation. Réunion remained comparatively pristine at this time, and Dubois in 1671–72 noted the absence of rats. However, this situation was to change drastically. By 1676, rats had reached plague proportions (Cheke & Hume 2008), and combined with over-hunting, by the 1730s all of the endemic non-passerines were extinct. The British took control of the island in 1810, but it was restored to France in 1815 (Leguen 1993). In the following decades, a combination of increasing population, especially after the emancipation of the slave population in 1848, deforestation and over-hunting resulted in the extinction of *Fregilupus varius* (Hume & Walters 2012).

In 1715, the French claimed Mauritius for France, renaming it ‘Isle de France’, and established a permanent colony. Over the next 85 years, hunting and large scale deforestation took place. This resulted in the extinction of almost all of the remaining non-passerines, including the endemic pigeons, *Nesoenas cicur* and *Columba thiriouxi*, and parrot, *Psittacula bensoni* (Hume 2007, 2011).

On Rodrigues in 1725–26, a Réunionese mariner, Julien Tafforet, was sent to report on its suitability for French occupation (North-Coombes 1971). He left a detailed account about the fauna and flora; little had changed since the time of Leguat, but he noted that birds were avoiding the mainland, which was almost certainly due to the presence of rats. Tafforet reported the abundance of giant tortoises *Cylindraspis* sp., which resulted in the establishment of a tortoise-collecting station (North-Coombes 1994b). Although deforestation was negligible at this time, the introduction of cats around 1745 proved catastrophic. Just 16 years later, during the visit in 1761 of Guy Abbé Pingré, who was on Rodrigues to measure the Transit of Venus (Nagapen 2004), a number of bird extinctions had taken place. Pingré noted that the night herons, pigeons, owls, starlings and probably the solitaire had vanished, and that both species of parrot were extremely scarce, *Necropsittacus rodericanus* particularly so. When Philibert Marragon settled on Rodrigues in the 1790s and wrote an account of the fauna (North-Coombes 1971), only the Rodrigues parakeet *Psittacula exsul* and two passerines survived.

5. British period 1810–1968 — The British forcibly took Mauritius and Réunion in 1810 after establishing a military presence on Rodrigues, but returned Réunion to France in 1815 (Toussaint 1972; North-Coombes 1971; Leguen 1993). On Mauritius, deforestation accelerated to make way for sugar cane production, and the remaining areas of mountain forest were exploited (Cheke & Hume 2008). The last Mauritius blue pigeon was taken in 1837 (Hume 2011), and the last Mauritian lizard-owl around the same time, but three non-passerines, the pink pigeon *Nesoenas mayeri*, echo parakeet *Psittacula echo*, and Mauritius kestrel *Falco punctatus* survived in mountain forest in the Black River Gorges.

On Rodrigues, slash and burn agricultural practices and high populations of free-range livestock for export to Mauritius combined to destroy or fragment the last remaining forests. In 1874, a second Transit of Venus expedition organised by the Royal Society arrived on Rodrigues, which included the botanist Isaac Balfour. Balfour (1879: p.302) recorded that ‘The great and tall trees have now almost entirely disappeared, the eternally verdant canopy formed by their boughs no longer exists, and the "little Eden" is now a dry and comparatively barren spot, clothed with a vegetation mainly of social weeds, and destitute of any forest growth save in unfrequented and more inaccessible parts in the recesses of the valleys'. This was also the last time that the Rodrigues parakeet, the only surviving endemic, non-passerine bird, was observed.

This study has shown that the avifauna of the Mascarenes has been subject to extremely high extinction rates over a comparatively small period of time. The wealth of documentation that exists has provided some indication as to why and when these events took place. Without exception, the extinction of all bird species was due to human activity. Direct hunting was more prevalent on Réunion than Mauritius and Rodrigues, whereas habitat destruction, particularly in the lowlands, seriously impacted on all three islands. However, it was the introduction of exotic animals that appears to the primary cause. The principal introductions included: black rats (*c.* 1400 on Mauritius, *c.* 1676 on Réunion, *c.* 1675 on Rodrigues); goats (*c.* 1606 on Mauritius, probably earlier (1528?) on Réunion, *c.* 1730 on Rodrigues); monkeys (*c.* 1606 on Mauritius); pigs (*c.* 1606 on Mauritius, *c.* 1620s on Réunion, *c.* 1790 on Rodrigues); cattle (*c.* 1606 on Mauritius, *c.* 1645 on Réunion, *c.* 1840 on Rodrigues); deer (*c.* 1638 on Mauritius, *c.* 1760 on Réunion, 1860 on Rodrigues); cats (*c.* 1688 on Mauritius/Réunion, *c.* 1745 on Rodrigues); and brown rats *Rattus norvegicus* (*c.* 1730 on Mauritius/Réunion, *c.* 1870 on Rodrigues) (see CHEKE & HUME 2008 for a comprehensive list). Of all the introductions to the Mascarenes, the black rat was by far the worst invasive. This ferocious predator was directly responsible for the extinction or reduction in ranges of the majority of smaller birds, predated the eggs and chicks of the larger terrestrial birds, and competed with all native avifauna for limited food resources.

The fossil record has provided evidence of higher rates of extinction than previously realised, and more species await description. Therefore, caution should be applied when interpreting biogeography within the region. This is particularly pertinent to the fossil record of the smaller avifauna, especially passerines, on which little work has been undertaken, and those species inhabiting the more vulnerable lowland areas.

Acknowledgements

I thank Robert PRYS-JONES (Natural History Museum, UK (NHMUK)), Dave BURNEY (National Tropical Botanical Gardens, Kauai (NTBG)), Jo COOPER (NHMUK), and Lorna STEEL (NHMUK) for suggestions which have greatly improved the manuscript. I thank Owen and Mary Ann GRIFFITHS (Mauritius Bioculture Ltd, François Leguat Ltd), Storrs OLSON (National Museum of Natural History (USNM)), Greg MIDDLETON, Richard PAYENDEE, Pieter FLOORE, Perry MOREE, and all Dutch colleagues who worked at the Mare aux Songes, Mauritius, Lida BURNEY (NTBG), Steve BOURNE, Aurèle ANQUETIL ANDRÉ (François Leguat Museum, Rodrigues (FLMR)), Arnaud MEUNIER (FLMR), Carl JONES (Durrell Wildlife Conservation Trust), Anthony CHEKE, Glyn YOUNG (Durrell Wildlife Conservation Trust), Pierre BRIAL, Jean MICHEL-PROBST, Dave MARTILL (University of Portsmouth), and all staff, past and present, of the Mauritius Wildlife Foundation (MWF) for support and assistance over the years. I thank Carl JONES, Nick ARNOLD (NHMUK) and Jeremy AUSTIN (University of Adelaide) for making available to me Rodrigues subfossil remains collected in 1997. I thank Mike BROOKE (University Museum of Zoology, Cambridge (UMZC)), Matt LOWE (UMZC), Sandra CHAPMAN (NHMUK), Paul SWEET (American Museum of Natural History (AMNH)), Ronan ALLAIN (Muséum national d'Histoire naturelle (MNHN)), Claire SAGNE (MNHN), Jean-François VOISIN (MNHN), René DEKKER (Naturalis–Nationaal Natuurhistorisch Museum (RMNH)), Sonia RIBES (Muséum d'Histoire Naturelle de La Réunion (MHNRUN)) and Andrew KITCHENER (National Museums of Scotland (NMSZ)) for providing me access to museum material in their care. I thank the NHMUK Special Fund for funding my trip to SAPE, Vienna. The National Geographic Research Grant, Percy Sladen Centenary Fund, Dodo Research Foundation, FRA Synthesys, Mauritius Bioculture Ltd, François Leguat Ltd, Gen Foundation, and Frank Chapman Fund supported my field and museum work, which made this research possible. I thank the referees Jo Cooper (NHMUK) and Dave Burney (NTBG) for helpful comments on the manuscript.

I especially thank Cecilé Mourer-Chauviré (Université Claude Bernard Lyon 1 (UCBL)), who has been an inspiration to me over the years, and helped encourage my interest in Mascarene palaeontology.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

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Holocene fossil bird remains from subantarctic Macquarie Island

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Abstract — Holocene fossil bird bones recovered from several sites on subantarctic Macquarie Island, southwest of New Zealand, provide a novel source of information about the island's history. There has been heavy modification through human activities, including the introduction of foreign mammals and a predatory flightless bird, the Weka (*Gallirallus australis*). The extinction of two endemic birds — the Macquarie Island Rail (*Gallirallus macquariensis*) and the Macquarie Island Parakeet (*Cyanoramphus novaezelandiae erythrotis*) — was documented in historic times. Fossils from the island include both these extinct species and provide evidence of a probable third global bird extinction — a teal (*Anas* sp.). Most fossil remains are from King Penguins (*Aptenodytes patagonicus*) and Royal Penguins (*Eudyptes schlegeli*) but several other species of seabird are represented, including one widespread species not previously reported from the island — the Subantarctic Little Shearwater (*Puffinus elegans*). The fossils provide evidence of population declines of some species.

Key words: Macquarie Island, Holocene, bird, fossils

Introduction

The subantarctic islands south of New Zealand are rich in wildlife but most have suffered much modification through human activities. The most southern of these, Macquarie Island, was discovered in 1810 and within 100 years several introduced pests became established, including Cats (*Felis silvestris catus* Linnaeus, 1758), Ship Rats (*Rattus rattus* Linnaeus, 1758), House Mice (*Mus musculus* Linnaeus, 1758), Rabbits (*Oryctolagus cuniculus* Linnaeus, 1758) and Weka (*Gallirallus australis* Sparrman, 1786) (Carrick 1957; Clark & Dingwall 1985; Cumpston 1968; Johnstone 1985; Selkirk *et al.* 1990). This isolated island is about 34 km long and 5.5 km wide, lying about 1,100 km southwest of New Zealand at 54°30′S 158°57′E. The direct exploitation of the penguin populations for oil from the 19th century until 1919 eventually caused an international outcry, with campaigners against the slaughter including the Antarctic explorer Douglas Mawson and the author H.G. Wells (Crowther 1933; Cumpston 1968; McEvey & Vestjens 1974; De La Mare 1990). Today the island is a wildlife sanctuary and boasts a rich fauna of seabirds but before the 20th century this was not well documented. Two endemic land birds, the Macquarie Island Rail (*Gallirallus macquariensis* (Hutton, 1879a)) and the Macquarie Island Parakeet (*Cyanoramphus novaezelandiae erythrotis* (Wagler, 1832)), are known to have become extinct on the island in the late 19th century owing to Cat and Weka predation (Taylor 1979) and numbers of many other species declined as a result of the introduced pests (Brothers 1984; Selkirk *et al.* 1990). Some species (e.g. Blue Petrels (*Halobaena caerulea* (Gmelin, 1789))

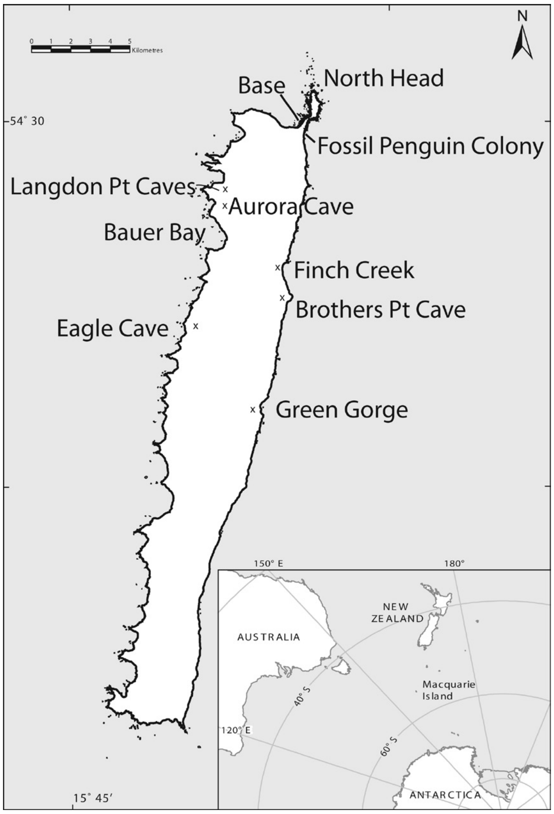

FIGURE 1. Macquarie Island showing location of fossil sites

are now restricted to breeding on offshore stacks (Brothers 1984; Garnett *et al*. 2011).

Holocene fossil bones have been recovered from three of the six subantarctic island groups south of New Zealand: Auckland (Tennyson 2009), Campbell (Holdaway *et al*. 2010) and Macquarie Islands but the information from Macquarie Island has been scattered and not thoroughly reviewed. A. Hamilton found fossil bones in 1894 (Hamilton 1895), as did L.R. Blake and H. Hamilton in 1911–14 (McEvey & Vestjens 1974), but no fossils from these expeditions have been located. A.M. Gwynn's 1949 collections appear to be the earliest Macquarie Island fossil bone collections preserved (Vestjens 1963; McEvey & Vestjens 1974). In the 1950s–1960s several collections were made: K. Keith (1956), A.R. McEvey, W. Whitten and R.A. Falla (1957), W.J.M. Vestjens and I. Pederson (1962) (Vestjens 1963; McEvey & Vestjens 1974) and R. Carrick (?1960s) (this paper). Vestjens (1963) reviewed records of Macquarie Island Rail fossils. An analysis of penguin bones from sites at Finch Creek and Bauer Bay was published by McEvey and Vestjens following field studies carried out by them (McEvey & Vestjens 1974). "*A few bones of species other than penguins*" were collected by McEvey and Whitten but McEvey & Vestjens (1974) did not list them. Colhoun & Goede (1973) collected fragmentary penguin remains in 1972 and G.F. van Tets made further bone collections on the island in 1973 (unpublished and, in 2003, stored in the Australian National Wildlife Collection (ANWC), Canberra). Meredith (1985) examined fossil sites on the island during a three or four day visit and located and examined the previously collected non-penguin fossil collections from Finch Creek held (but unregistered) in the Museum Victoria, Melbourne (MV).

In late 1995, one of us (RPS) found a Subantarctic Little Shearwater (*Puffinus elegans* Giglioli & Salvadori, 1869) bone in the Langdon Point caves, which AJDT later identified. RPS looked for further material during his second visit in 1996-97 in an attempt to better document the pre-human avifauna of the island. We identified the material collected by RPS and re-examined most of the pre-1995 collections of Holocene fossils (but excluded the penguin fossils that had previously been analysed).

Subsequently a few more bones have been collected including a parakeet beak in 2001 (K. Medlock pers. comm.) and more penguin bones, most recently by C. Oosthuizen and B. Arthur (Heupink *et al*. 2012).

Methods

The vast majority of fossil bones on Macquarie Island comprises penguins (Meredith 1985 gave a ratio of penguin to petrel bones in McEvey & Vestjens' collection, held in Melbourne, as 116: 1). As the penguin bones had already been thoroughly analysed, RPS concentrated on collecting non-penguin material; however, a few penguin bones were collected by RPS and these, along with some collected by van Tets, are listed here for completeness. Archaeological sites were not collected from by RPS. The bones collected by RPS were donated to the Museum Victoria and subsequently exchanged with the Museum of

New Zealand Te Papa Tongarewa (NMNZ), where AJDT was able to identify them using comparative material.

We reviewed the identity of most previous Holocene bird remains collected on Macquarie Island by visiting the MV, examining van Tets' collection in ANWC, and borrowing most of the non-penguin bones from MV. Without carbon-dates and knowing the exact stratigraphy of the sites, it was sometimes unclear whether a collected specimen was truly a Holocene fossil or was actually recent — no doubt some sites contain bones of both ages and from those in the grey area in between. This was particularly the case for van Tets' collection but even RPS's collections include species such as Grey Duck (*Anas superciliosa* Gmelin, 1789), which may have colonised Macquarie during the 20th century (Carrick 1957; but see Norman 1987). Our list reflects our interpretation of the taphonomy of the bones. To increase the sample size of measurements of Chestnut Teal (*Anas castanea* (Eyton, 1838)) crania, extra specimens were measured in museums in Frankfurt (SMF) and Tring (NHM) in 2012. We have not examined fossils found by others since 1997. Anatomical terms follow Baumel & Witmer (1993). Bird taxonomy follows Gill *et al*. (2010), except for the Macquarie Island Rail which follows Tennyson & Martinson (2007).

Abbreviations

alar phal = alar phalange, cf. = similar to and probably, cmc = carpometacarpus, coll = collected, cor = coracoid, fem = femur, fib = fibula, frag = fragment, hum = humerus, L = left, MNI = minimum number of individuals, ped phal = pedal phalanx, R = right, rad = radius, pel = pelvis, scap = scapula, tbt = tibiotarsus, tmt = tarsometatarsus, uln = ulna.

Results

Fossil remains of birds found at Macquarie Island listed by site and taxonomically, including only a summary of penguin finds.

Aurora Cave

Teal(?) (*Anas* sp.) — MNI = 1: 1 partial skull, coll: 5 Jan 1962, Vestjens, Australian National Antarctic Research Expeditions (ANARE) Zoology Number M62/B/48, MV collection unnumbered. On 15 Nov 1978, H. King identified this specimen as "*Anas* ?*giberifrons*[sic]" [= Grey Teal *A. gracilis* Buller, 1869] and Meredith (1985) confirmed it as an *Anas*. We compared this cranial fragment with skulls of other ducks (Tab. 1).

The overall shape of the skull is similar to that of other *Anas* but it has a relatively larger prominentia cerebellaris and the interorbital width most closely matches the skulls of the Chestnut Teal and Brown Teal (*Anas chlorotis* Gray, 1845) (Tab. 1). The interorbital width is greater than that of the flightless Auckland Island Teal (*Anas aucklandica* (Gray, 1849)) and Campbell Island Teal (*Anas nesiotis* (Fleming, 1935)), slightly broader than that of Grey Teal (*Anas gracilis*), and narrower than that of Mallard (*Anas platy-*

TABLE 1. Measurements (mm) of minimum dorsal interorbital bone width of *Anas* species. All recent specimens were from the NMNZ collection, apart from *Anas castanea* SMF 4578, SMF 10575, NHM S/1966.51.5, NHM S/1966.51.10 & NHM S/2002.35.2.

Species	Mean (range)	Sample size
Grey Teal *Anas gracilis*	7.0 (5.8–8.1)	10
Chestnut Teal *Anas castanea*	8.1 (7.2–9.0)	7
Brown Teal *Anas chlorotis*	8.8 (7.7–10.2)	10
Auckland Island Teal *Anas aucklandica*	5.9 (5.4–6.7)	12
Campbell Island Teal *Anas nesiotis*	5.5 (5.1–6.3)	6
Macquarie Island specimen	8.4	1
Mallard *Anas platyrhynchos*	9.8 (8.7–10.8)	13
Grey Duck *Anas superciliosa*	9.3 (6.9–10.7)	13

rhynchos Linnaeus, 1758). It is narrower than that of a Grey Duck (although within the width range of this species) but overall has a much smaller cranium.

"Wandering Albatross" (*Diomedea exulans* Linnaeus, 1758) — MNI = 8: pel, coll: 13 Apr 1962, Vestjens, ANARE M62/B/118, MV B12147; L hum, coll: 30 Jul 1962, Vestjens, ANARE M62/B/119, MV B12148; skull, 2L3R cor, coll: 5 Jan 1962, Vestjens, ANARE M62/B/41, MV B12149; sternum, coll: 13 Apr 1962, Vestjens, ANARE M62/B/120, MV B12150; 5 furcula, MV B31651; 3L5R hum, 3L uln, 1 R rad, coll: 12 Apr 1956, Keith, MV B31703; skull, 20 vertebrae, 4L4Rscap, 7L8Rtbt, 1L1R cmc, 2L2Rfem, 1Ltmt, coll: 14 Apr 1956, Keith, MV B31705. "Aurora Point" is the locality recorded for MV B11860 and "NT of Aurora Point" is the locality recorded for MV B31703 but we have assumed that both these specimens are from Aurora Cave. Although MV B31651 has little collection information, we have assumed that it is part of the Aurora Cave 1956 Keith collection. MNI is based on the 8 right tbt (MV B31705).

In 1949 Gwynn found a midden of bones ("*almost exclusively... young wandering albatrosses*", that he believed were of human origin, in a cave about half a mile north of Aurora Point (Gillham 1967: 101). In 1956 "*parts of at least seventy birds were collected from it, but it still appeared to be full in 1960, when part of it had disappeared under a recent rock fall*" (Gillham 1967: 101). In 1957, after recently returning from Macquarie, Carrick noted that the "Wandering Albatross" would have been "*an easy source of winter food*" for sealers and shipwrecked mariners and that a "*collection of skeletons*" had been recently found in a west coast cave (Carrick 1957). We presume that this "west coast" cave is Aurora Cave. A collection of 48 skulls and mandibles of albatrosses collected by R. Carrick from a "sealers' midden" in "196?" (ANWC reg. nos. 5438-5468, van Tets' nos. PROS1087-1117) was thrown out from the ANWC collection in the 1990s when van Tets' disordered collections were partly sorted and reorganised following his death (J. Wombey pers. comm. 2003). Carrick & Ingham (1970) reported a "recent discovery of over 100 ["Wandering Albatross"] skulls in caves inhabited by sealers or castaways", which presumably refers to Keith's and/or Carrick's collections. Although some 1956 collections made by Keith remain at MV, it is possible that the material thrown out from ANWC was actually much of the 1956 collection. We have not located an unpublished 1956 manuscript by Keith that contains further details about these collections (see De La Mare & Kerry 1994).

Lengths of the "Wandering Albatross" crania, humeri, tibiotarsi and tarsometatarsi in the MV collection were measured for comparison with modern skeletons of Antipodean Albatross in NMNZ (Tab. 2). The Macquarie skull measurements are larger than those of Antipodean Albatrosses but the post-cranial bones, although averaging larger, are all within the range of those of Antipodean Albatrosses. This suggests that some of the fossils represent the Wandering Albatross, which is a larger species (see Marchant & Higgins 1990), and that some may represent Antipodean Albatrosses, but we lacked

TABLE 2. Summary of measurements (mm) of maximum bone lengths of fossil Macquarie Island "Wandering Albatross" specimens and modern Antipodean Albatross specimens, showing mean ± 1 s.d., n = sample size, range. Macquarie Island specimens: Museum Victoria B12148, B12149, B31703, B31705; each element was assumed to be from a different individual, except in one case (right tibiotarsus B31705) which was excluded from the analysis because identical lengths were obtained for 2 left tibiotarsi. Antipodean Albatross specimens: Museum of New Zealand Te Papa Tongarewa NMNZ 606-S, 19352, 24673a, 24674a, 24973, 24979, 25130, 25131, 25132, 25210, 25211, 25212, 25213, 25214, 25215, 25628a, 25629a, 25630a, 25631, 26744, 26885, 27007, 27008, 27188, 28654a.

	Macquarie Island	***Diomedea antipodensis***
Crania	247, 261, n = 2	227.0 ± 8.86, n = 24, 213–2442
Humeri	408.6 ± 13.19, n = 9, 378–422	398.2 ± 14.32, n = 23, 376–427
Tibiotarsi	232.4 ± 7.83, n = 14, 220–242	225.3 ± 8.37, n = 21, 212–243

comparative measurements of modern Wandering Albatross skeletons.

Macquarie Island Rail (*Gallirallus macquariensis* (Hutton, 1879a)) — Vestjens (1963) noted that the remains of several Macquarie Island Rails had been found in this cave: a mandible (by Keith in 1956), a skull (by Falla in Dec 1957, but subsequently lost), 3 skulls (by Vestjens on 5 Jan 1962; MV B31658–31660).

General observations — Meredith (1985) noted "*abundant remains of seabirds eaten by the past human occupants of this cave*" and "*more recent material, presumably collected by cats... in small amounts*". He specifically noted the presence of "Wandering Albatross", White-headed Petrel (*Pterodroma lessonii* (Garnot, 1826)), Blue Petrel, Grey Petrel (*Procellaria cinerea* (Gmelin, 1789)), Sooty Shearwater (*Puffinus griseus* (Gmelin, 1789)) and Subantarctic Skua (*Catharacta skua lonnbergi* (Mathews, 1912)). However, "*due to the historic nature of these deposits*" Meredith "*left them as little disturbed as possible*", but noted that "*they are so extensive*" that they warranted further investigation. Two complete Southern(?) Giant Petrel (*Macronectes ?giganteus* (Gmelin, 1789)) mandibles were sketched and measured (141 & 144 mm long) (but not collected) by RPS on 21 Jan 1997. RPS also noted about 50 partial skulls of "Wandering Albatrosses" but owing to its archaeological nature he left this site undisturbed also.

Bauer Bay Site F

coll: RPS on 10, 12, 15, 20 Nov, 2, 9, 10 Dec 1996, 15 Jan 1996, 23 Apr 1996

Grey Duck — MNI = 1: hum 1, 1 uln, 1 rad, 2 cmc, 1 fem, 2 tbt, 1 fib, NMNZ S.44619, S.44646.

Giant Petrel (*Macronectes* sp.) — MNI = 1: 1 tmt, 1? feather, NMNZ S.44630, S.44644.

White-headed Petrel — MNI = 1: 1 hum, 1 uln, 1 cmc, 1 fem, NMNZ S.44620, S.44633.

Blue Petrel — MNI = 5: 8 hum, 3 uln, 1 rad, 1 cmc, 1 fem, 2 tbt, 1 tmt, NMNZ S.44615, S.44626, S.44637, S.44641, S.44648.

Antarctic Prion (*Pachyptila desolata* (Gmelin, 1789)) — MNI = 4: 6 hum, 7 uln, 3 rad, 5 cmc, 1 tbt, NMNZ S.44614, S.44625, S.44636, S.44647.

Short-tailed Shearwater (*Puffinus tenuirostris* (Temminck, 1836)) — MNI = 1: 1 hum, 1 uln, 1 cmc, NMNZ S.44618, S.44623, S.44632.

Subantarctic Little Shearwater — MNI = 1: 1 tbt, 1 tmt, NMNZ S.44635.

Diving petrel (*Pelecanoides* spp.) — MNI = 4: 5 hum, 1 rad, 1 cmc, 1 tmt, NMNZ S.44616, S.44629, S.44640, S.44645.

Macquarie Island Rail — MNI = 2: 2 tbt, NMNZ S.44624.

Subantarctic Skua — MNI = 2: 1 hum, 2 uln, 2 rad, 1 alar phal, 2 tmt, NMNZ S.44617, S.44622, S.44634.

Macquarie Island Parakeet — MNI = 1: 1 rectrix, NMNZ S.44639.

General observations — Between Oct and Dec 1962, Vestjens made the first collections of bones at this site, which was described in detail by McEvey & Vestjens (1974). King Penguin (*Aptenodytes patagonicus* Miller, 1778) bones were more common than those of Royal Penguins (*Eudyptes schlegeli* Finsch, 1876), and bones from here were dated at 3,980 ± 140 years B.P. (McEvey & Vestjens 1974). In Nov 1972, Colhoun & Goede (1973) collected additional fragments of King Penguin bones at Bauer Bay. In 1996 RPS collected only fragmentary penguin remains here including: Eastern Rockhopper Penguin (*Eudyptes filholi* Hutton, 1879b) (MNI = 1: 1 quadrate, 1 scap, 1 fem; NMNZ S.44627, S.44638, S.44643) and Royal Penguin (MNI = 1: 1 mandible; NMNZ S.44628). Recent radiocarbon dating of eight King Penguin bones from this location (including bones collected by McEvey and more recently by Oosthuizen and Arthur) revealed them to average 7,927 (range 6,834-8,429) years old (Heupink *et al*. 2012). Meredith

(1985) located six of the seven sites (sites A-G) recorded by McEvey & Vestjens (1974) at Bauer Bay and found abundant King Penguin bones but he did not find site F where RPS collected bones.

Bauer Bay, Strata FS (DD are collector numbers)

Teal(?) (*Anas* sp.) — MN1 = 1: 1 pel, MV collection unnumbered. This fragmentary pelvis resembles that of a Brown Teal in that it appears to have a broad fused dorsal surface to the synsacrum. It is smaller than that of Mallards and Grey Ducks which suggests that it may be from a teal.

Grey-headed(?) Albatross (*Thalassarche* cf. *chrysostoma* (Forster, 1785)) — MNI = 1: ped phal, DD16, MV collection unnumbered.

White-headed Petrel — MNI = 1: 1 fem, DD16, MV collection unnumbered.

Blue Petrel — MNI = 1: 1 hum, 1 rad, DD16, MV collection unnumbered.

Antarctic Prion — MNI = 1: 1 cor, DD3, MV collection unnumbered.

Sooty Shearwater — MNI = 1: 1 uln (possibly large *Pterodroma*),1 cmc, 1 alar phal, 1 ped phal, all DD16, MV collection unnumbered.

Subantarctic Little Shearwater — MNI = 3: 1 skull (DD1), 1 sternum (DD15), 3 cor (DD2, DD4, DD5), 1 hum (DD16), 1 uln (DD16), 2 pel (DD11, DD12 & DD13 are parts of the same pel), 1 tbt (DD16), MV collection unnumbered.

Diving petrel — MNI = 1: 1 rad, 1 fem, both DD16, MV collection unnumbered.

General observations — Meredith (1985) identified bones of Blue Petrel and Antarctic Prion in site "F5#DD16" and those of White-headed Petrel, a "*Pterodroma sp. medium size, (mollis?)*", Antarctic Prion, juvenile Sooty Shearwater, ?Fluttering Shearwater (*Puffinus gavia* Forster, 1844) and Common(?) Diving petrel ("*Pelecanoides* prob. *urinatrix*") in site "F5#DD3" ("F5" appears to be a misreading of "FS"). Meredith's (1991) reference to the presence of bones of "*Pterodroma lessonii, juvenile Puffinus prob. griseus, and a small Puffinus similar to Puffinus gavia but too poorly represented to be confidently identified*" is based on his 1985 article. We believe that Meredith's "*Puffinis gavia*" bones are those of Subantarctic Little Shearwaters because they are too small for those of Fluttering Shearwaters. Also the preserved humerus has a flattened shaft characteristic of several *Puffinus* spp. but unlike the humeri of *Pterodroma* petrels. We did not identify any medium-sized *Pterodroma* bones among these specimens.

Brothers Point Caves

Antarctic Prion — MNI = 1: 1 hum, coll: 1 Nov 1996, RPS, NMNZ S.44612.

General observations — Meredith (1985) first brought attention to the potential for bird bones to be found in a group of caves just south of Brothers Point, near Finch Creek. In one cave he found "*a variety of petrel, skua and penguin bones, but all appeared to be recent in origin, their presence due to the use of these caves by cats*". In another cave which he was not able to fully explore he found "*abundant material of the Dove [= Antarctic] Prion Pachyptila desolata... but...no evidence of cat activity*". A parakeet beak and some other bird bones were collected in these caves on 7 Dec 2001 by G. Hedley and deposited in the Tasmanian Museum & Art Gallery, Hobart (registration number of beak B4678) (K. Medlock pers. comm. 2012; G. Hedley pers. comm. 2013). Photos of other bones collected in 2001 (G. Hedley pers. comm. 2013) include a few post-cranial Macquarie Island Rail bones and possibly some duck bones. Clearly a full investigation of these caves and collections made in them is needed.

Eagle Cave

Meredith (1985) noted that this cave may be worth excavating for bones but did not visit it due to lack of time. Although he noted that it had been "*well picked over in the past*", we have not located any collections of bones from this site. Vestjens (1963) reported that he found part of a cranium of the Macquarie Island Rail in this cave on 16 Jan 1962 (MV B31661).

Finch Creek

McEvey & Vestjens (1974) provided a detailed history and description of this site. Blake recorded probable penguin bones and may have collected some in 1911-14. Gwynn collected some bones in 1949, which were deposited in the MV. On 13, 17 and 18 Dec 1957, McEvey and Whitten studied this site and collected further bones, including "*a few bones of species other than penguins*". Vestjens spent all of 1962 on the island and, with Pederson, made further collections of the bones here. The majority of bones from this site are Royal Penguin, a sample of which were dated at 6,100 ± 120 years B.P. Meredith (1985) found all of McEvey & Vestjens' sites at Finch Creek and identified a few Royal Penguin bones. RPS did not investigate this site. We have not located the non-penguin bones that were apparently collected but they may be listed here under Bauer Bay as this collection is poorly labelled.

Green Gorge

In Nov 1972, Colhoun & Goede (1973) collected fragmentary King Penguin bones from an uplifted marine terrace at this site.

Isthmus at base of North Head

In 1894, A. Hamilton (1895) found bones representing a large former King Penguin rookery and two skulls "*of a very large species of albatross*" (presumably "Wandering") at this site. Along with some crew members, the skulls were subsequently swept overboard from the ship and lost on Hamilton's return journey to New Zealand. In 1911, H. Hamilton found "masses" of King Penguin bones here (McEvey & Vestjens 1974). This is now near the site of the main ANARE base station and the beach where the deposit is exposed on the eastern coast is named Fossil Beach. van Tets collected only penguin bones at "Base Camp" on 1 Dec 1973: King Penguin (4L1R cor, 5 fib, 1 partial pel, 1 distal R fem, 12 L16R tbt, 6 tmt, all were juvenile except one R tbt; all van Tets no. SPHS30, ANWC collection unnumbered). Recently at least 20 King Penguin bones were collected by Oosthuizen and Arthur from the Landing Beach on the Isthmus for DNA analysis; radiocarbon dating of seven of these bones revealed them to average 1,002 (range 816-1,134) years old (Heupink *et al*. 2012).

Langdon Point Caves

Subantarctic Little Shearwater — MNI = 1: 1 tmt, coll: late 1995, RPS, NMNZ S.44610.

General observations — Meredith (1985) was correct in predicting that a bone deposit may have occurred in caves here, although he did not find it himself. RPS found a significant natural deposit of bones here in late 1995 but as most appeared to be recent, he collected only one.

North Head (presumed to be north of the ANARE base station)

Macquarie Island Shag (*Leucocarbo purpurascens* (Brandt, 1837)) — MNI = 1: alar phal, 3 ped phal, coll: 30 Nov to 3 Dec 1973 by van Tets, ANWC collection unnumbered.

General observations — van Tets also collected a small number of penguin bones at this time: Eastern Rockhopper Penguin (1 ped phal, ANWC collection unnumbered), Royal Penguin (1 L cor, van Tets no. SPHS30, ANWC collection unnumbered; 1 ped phal, van Tets no. SPHS36, ANWC collection unnumbered).

Plateau between Bauer Bay and Finch Creeks

White-headed Petrel — MNI = 1: hum 1, uln 1, coll: 20 Nov 1996, RPS, NMNZ S.44613.

Discussion

The human impacts on the bird fauna of Macquarie Island have been both colourful and devastating; however, with the exception of up to four extinct taxa, most species found in fossil sites on the island still breed there. Fossils provide evidence of reduced distributions of some species. McEvey & Vestjens (1974) noted that fossil bones suggested that "*colonies of King Penguins at Macquarie were either more numerous than, or differently situated from those mentioned in the recorded history of this species*" and that the "*fossil remains of [King and Royal Penguins] provide evidence of former colonies that do not now exist, in certain localities*". Colhoun & Goede (1973) suggested that King Penguins "*were formerly distributed on most beaches*" on the island.

Almost all species known to currently or formerly breed on the island are now known from fossil sites, with our study reporting the first fossils of Grey Duck, Eastern Rockhopper Penguin, Grey-headed(?) Albatross, Southern(?) Giant Petrel, Short-tailed Shearwater, Subantarctic Little Shearwater, Macquarie Island Shag and Macquarie Island Parakeet (Tab. 3). Breeding species that should be present with larger samples of fossils but not yet identified are: Gentoo Penguin (*Pygoscelis papua* (Forster, 1781)), Light-mantled Sooty Albatross (*Phoebetria palpebrata* (Forster, 1785)), Northern Giant Petrel (*Macronectes halli* Mathews, 1912), Southern Black-backed Gull (*Larus dominicanus* Lichtenstein, 1823) and Antarctic Tern (*Sterna vittata* Gmelin, 1789) (Selkirk *et al.* 1990; Copson & Brothers 2008). The Soft-plumaged Petrel (*Pterodroma mollis* (Gould, 1844)), which has only just colonised Macquarie (Fullagar *et al.* 1986; Holdaway *et al.* 2001; Copson & Brothers 2008; Garnett *et al.* 2011), was not identified from fossil material, despite Meredith's listing of "*Pterodroma* sp. medium size, (*mollis*?)". He did not detail to which specimens he was referring, however, we suspect that these bones were of the Subantarctic Little Shearwater, as some bones of this species are similar in size to those of Soft-Plumaged Petrel but differ in shape. Similarly, Black-browed Albatrosses (*Thalassarche melanophris* (Temminck, 1828)) and Cape Petrels (*Daption capense* (Linnaeus, 1758)) are probably also recent colonists of Macquarie Island (Carrick 1957; MacKenzie 1968; Tennyson *et al.* 1998; Copson & Brothers 2008), and so these species would not be expected in fossil deposits.

A significant find of this study is the probable presence of an extinct teal on Macquarie Island. This small duck is represented by a fragmentary skull and pelvis — unfortunately the bones are too damaged to identify the species represented with certainty using morphological criteria. Some 19th century authors suggested that there was a teal resident on Macquarie Island (e.g. see Scott 1883; Falla 1937: 19). On the basis of morphology and measurements, we favour the idea that the bones represent an extinct endemic species. Endemic flightless teals are found on the two nearest subantarctic islands — Auckland and Campbell — so an endemic teal on Macquarie might be expected. Norman (1987) concluded

TABLE 3. List of species recorded in fossil sites on Macquarie Island. *no specimens preserved in museum collections, **new fossil records for Macquarie Island.

Teal(?) (*Anas* sp.)
Grey Duck (*Anas superciliosa*)**
King Penguin (*Aptenodytes patagonicus*)
Eastern Rockhopper Penguin (*Eudyptes filholi*)**
Royal Penguin (*Eudyptes schlegeli*)
"Wandering Albatross" (*Diomedea exulans/antipodensis*)
Grey-headed(?) Albatross (*Thalassarche* cf. *chrysostoma*)**
Southern(?) Giant Petrel (*Macronectes* ?*giganteus*)**
White-headed Petrel (*Pterodroma lessonii*)
Blue Petrel (*Halobaena caerulea*)
Antarctic Prion (*Pachyptila desolata*)
Grey Petrel (*Procellaria cinerea*)*
Sooty Shearwater (*Puffinus griseus*)
Short-tailed Shearwater (*Puffinus tenuirostris*)**
Subantarctic Little Shearwater (*Puffinus elegans*)**
Diving petrel (*Pelecanoides urinatrix exsul/georgicus*)
Macquarie Island Shag (*Leucocarbo purpurascens*)**
Macquarie Island Rail (*Gallirallus macquariensis*)
Subantarctic Skua (*Catharacta skua lonnbergi*)
Macquarie Island Parakeet (*Cyanoramphus novaezelandiae erythrotis*)**

that all early "teal" records related to the Grey Teal. However, the only confirmed records of Grey Teal on the island relate to vagrants (Copson & Brothers 2008). An 1822 reference reporting "*Widgeons (called Tussock fowl by the sealers as they lived among the tussock and did not fly)*" as well as "*teal (from the lagoons on top of the island)*" (Cumpston 1968: 51) may well refer to a locally breeding teal (Tennyson & Martinson 2007: 80). Finds of more complete bones of this duck should quickly resolve the question.

Another important finding of this study is the presence of 13 Subantarctic Little Shearwater bones in fossil sites. These bones come from three sites and suggest that this species may have formerly bred. The Subantarctic Little Shearwater currently breeds in the New Zealand region at the Chatham and Antipodes Islands and, further afield, on islands in the Tristan and Gough groups in the South Atlantic (Marchant & Higgins 1990), so a former breeding colony on Macquarie would not be surprising. Falla (1937) correctly commented that the island "*compares unfavourably with many other subantarctic islands in regard to the number of petrel species found breeding there*" and that the "*possibility of some of the smaller ones having been previously exterminated by dogs, cats, rats, or wekas must...be considered*". If Subantarctic Little Shearwaters did breed on Macquarie, it is likely that the species was exterminated in the late 19th century by Cats and Weka, at the same time that the rail and parakeet were wiped out. Holocene Subantarctic Little Shearwater bones are also found in dune deposits on Enderby Island, Auckland Islands, but breeding has also never been detected on that island group (Tennyson 2009), so another possibility is that the seas around Auckland and Macquarie Islands are (or were) part of the normal at-sea range of Subantarctic Little Shearwaters and predatory skuas caught them and regurgitated their remains onshore. The Subantarctic Little Shearwater is considered a "*very rare vagrant*" at Macquarie Island today (Selkirk *et al*. 1990). The previous tentative identification of small shearwater bones as being from Fluttering Shearwaters is most unlikely because the Macquarie bones are too small and the island is well outside the normal range of this species. There is only one record of a Fluttering Shearwater on Macquarie Island (a mummy found by K.G. Simpson in 1965, ANWC 10602, pers. obs.). Otherwise the most southerly records of a Fluttering Shearwater, and the similar Hutton's Shearwater (*Puffinus huttoni* Mathews, 1912), are nearly 1,000 km to the northeast at The Snares in the 19th century and even these records are doubtful (Miskelly *et al*. 2001; Tennyson *et al*. submitted manuscript).

The bones of a Short-tailed Shearwater from Bauer Bay site F appear to be from one individual, which was presumably a vagrant. This species has never been found breeding on Macquarie Island but it has been found as a vagrant on the island several times since 1960 (Jones 1980; Brothers 1984; Copson & Brothers 2008; RPS found the remains of five individuals in 1996), and it regularly ranges south to Antarctic waters (Kerry *et al*. 1983).

Both birds previously known to have become extinct on Macquarie Island (the endemic rail and parakeet) have now been found in fossil sites. The Macquarie Island Parakeet previously occurred "*in great numbers round the shore*" (Scott 1883) and was recorded alive between 1810 and 1890, with 21 specimens being collected for museums (Taylor 1979; Scofield 2005; RPS unpublished data). The tail feather found in 1996 and the beak found in 2001 are the first fossil records of this species.

We are aware of the following fossil Macquarie Island Rail bones having been found: one mandible in Aurora Cave in 1956, one complete skull in Aurora Cave in 1957, three skulls in Aurora Cave in 1962, one skull in Eagle Cave in 1962 (Vestjens 1963), two tibiotarsi in Bauer Bay in 1996 and some post-cranial bones in Brothers Point Cave in 2001 (reported here). This rail became extinct about 1890 and is represented by only three surviving skin specimens (Tennyson & Martinson 2007) — one in Otago Museum (AV740, AJDT pers. obs.) and two in the Natural History Museum, England (NHM 1881.12.27.1 & NHM 1881.12.27.2) (Buller 1905; Oliver 1955; Vestjens 1963; AJDT pers. obs.). When Joseph Burton left Macquarie Island in 1900, he apparently left behind a collection of prepared bird skins, including "*four or five landrails of a kind of which no Museum in Europe possesses a specimen, except Rothschild, and he* *only one*" (Cumpston 1968: 206–210). Although some specimens from this collection were salvaged for the British Museum (now the Natural History Museum) in 1902 (Cumpston 1968: 209-210), apparently the rails were not among them. The holotype is the Otago Museum specimen. It was described in October 1879, being collected "*last March by a sealing expedition, and... presented to the Otago Museum by Messers. Elder and Co.*" when the species was "*common on the south part of the island*" (Hutton 1879a). The two Natural History Museum specimens were sent by George Grey to P.L. Slater "*some twenty years ago or more*" before 1902 (Buller 1905). Oliver (1955) speculated that these were collected by the same collector who obtained the Otago bird. Additionally, the Otago Museum specimen includes a sternum, ribs and pectoral elements (Hutton 1879a; AJDT pers. obs.) and there is a Macquarie Island Rail pelvis labelled "prior to 1894" in the NMNZ collection (reg. no. 15139). The pelvis is well preserved and appears to have been extracted from a whole bird. In the late 1800s, body bones from skinned or mounted specimens were often preserved in the Colonial Museum (now NMNZ) (AJDT pers. obs.). The pelvis has a label "*Rallus macquariensis*" in what appears to be Hutton's handwriting (AJDT pers. obs.). As Hutton described this species based on the Otago specimen which lacks a pelvis, Tennyson & Bartle (2008) concluded that the NMNZ pelvis is part of the holotype specimen.

Given the wealth of fossil bone sites on Macquarie Island, much more research on deposits should be done to elucidate the past bird fauna of the island. Further collecting should reveal whether other species have become extinct in historic times. More bones of the small duck are required to firmly establish its status. Bones of other species, *e.g.*, a *Coenocorypha* snipe and pipit *Anthus* sp., might be expected.

The past status of "Wandering Albatrosses" on the island needs clarification. The current population has built up from just one or two nests in 1911 and results from "considerable immigration" but the source population(s) are unknown (De La Mare & Kerry 1994). There have been suggestions that the smaller darker Antipodean Albatross (*Diomedea antipodensis* Robertson & Warham, 1992) used to occur on Macquarie Island (Smith 1997). Measurements of the Aurora Cave fossil bones indicate that Wandering Albatrosses are represented and Antipodean Albatrosses may be represented. It is unfortunate that the majority of fossil albatross skulls from Macquarie Island were thrown out after about 40 years in a museum collection and, subsequent to our 2003 visit, apparently further van Tets material has been disposed of from ANWC (T. H. Worthy pers. comm. 2012). Wandering Albatrosses breed on Macquarie Island currently and the fossil evidence suggests that they used to historically also. However, the past and current status of Antipodean Albatrosses on the island is less clear as the identity of most fossil albatross bones is uncertain and records of darker-plumaged "Wandering Albatrosses" recorded ashore by Gillham (1967: 104) and Terauds & Stewart (2005) suggest that Antipodean Albatrosses may be more regular than previously documented. It would be valuable to carry out molecular analyses on the fossil bones to expand on a previous study which examined the relationships of the living Macquarie Island Wandering Albatross population (Alderman *et al.* 2005).

Subantarctic Diving Petrels (*P. urinatrix exsul* Salvin, 1896) and South Georgian Diving Petrels (*Pelecanoides georgicus* Murphy & Harper, 1916) have been recorded at Macquarie Island (Bourne 1981; Brothers 1984; Copson & Brothers 2008) but we were unable to assign a species to the fossil material. Seven Subantarctic and eight South Georgian Diving Petrel skeletons (in the NMNZ collection) were measured for comparison with Macquarie Island bones. Some fossil Macquarie diving petrel bones fell within the size range of the larger Subantarctic Diving Petrel, others were within the range of the South Georgian species and others fell between the ranges of both. Therefore, we could not determine whether both species were represented or whether all bones belonged to one species that has a larger size range than is represented in the NMNZ collection. If cranial material was found, this should allow specific identity (Worthy 1998). Similarly, further work on prion (*Pachyptila* spp.) fossils would be valuable as the past breeding status of several prion taxa is unclear (Brothers 1984; Copson & Brothers 2008). Investigating the identity of fossils of these taxa using molecular analyses would be helpful also.

A great deal more systematic excavation and analysis of fossils is required to help illuminate the pre-human bird fauna of Macquarie Island — the identity of large albatrosses and the teal are a priority.

Acknowledgements

Thanks to: Bob GOULD (Tasmania Parks and Wildlife Service) for allowing his permit to be used by RPS to collect the Macquarie Island bones; Rory O'BRIEN (Museum Victoria) for the loan and exchange of bones from Melbourne; Kerri-Anne EDGE (Otago Museum) for providing information on the Macquarie Island Rail type specimen in 1998; John WOMBEY for information on collections in ANWC (Canberra), and to him, Robert PALMER and Terry CHESSER for hosting us there in Dec 2003; Wayne LONGMORE for assisting AJDT at the Museum Victoria in Apr 2007; Gerald MAYR (SMF) for helping AJDT at the Forschungsinstitut Senckenberg Museum, Frankfurt in Jun 2012; Joanne COOPER for assisting AJDT at the Natural History Museum, Tring, in Jul 2012; Karen Roberts (Museum Victoria) for providing registration details of Macquarie Island Rail specimens; Kathryn MEDLOCK (Tasmanian Museum and Art Gallery) and Georgie HEDLEY (New Zealand) for information on the bones found in Brothers Point Caves; and Martin LEWIS and Christine KIDDEY (NMNZ library) for obtaining some of the references. Walter BOLES (Sydney) and Colin MISKELLY (NMNZ) provided helpful comments on the manuscript.

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)

Notes on Pelvic and Hindlimb Myology and Syndesmology of *Emeus crassus* and *Dinornis robustus* (Aves: Dinornithiformes)

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Abstract — *Dinornis robustus* and *Emeus crassus* represent two variants of moa locomotor adaptations, *Dinornis* being more cursorial. Their overall hindlimb anatomy resembles that, inferred for primitive birds. While the hindlimb anatomy and syndesmology of moa resemble that of Tinamiformes and geographically close Apterygiformes and Casuariiformes, the development of *m. iliofemoralis externus* is peculiar to Dinornithiformes and far surpasses the bulk recorded for this muscle in other birds. In addition, moa appear to have a unique insertion of *m. iliofemoralis internus*, although additional observation of mummies would be desirable. On the anterior surface of the femoral shaft, this muscle inserts just distally to the neck where it must have changed its regular function of a weak outward rotator of femur. The attachment of *m. iliofemoralis* on the posterior surface of femur is unusually long and comparable to the structure observed only in Dinornithiformes and *Apteryx*. Terminal tendons of the long digital flexors to the second toe were, at least in *D. robustus*, separated from those to the other foretoes. This feature might indicate that the second toe played a major role in scratching and digging, an activity reported as one of the ways moa obtained their food. Caudal migration of the center of gravity, proposed for moa in comparison to other birds and for *Dinornis* in relation to other moa, does not have anatomical support.

Key words: Dinornithiformes, hind limbs, morphology, syndesmology, locomotion

Introduction

Since the first account (Polack 1838) and the group's formal description in the following year (Owen 1839), moa have been the subject of meticulous scientific study (for an overview, see Worthy & Holdaway 2002). As representatives of the order Dinornithiformes, moa represent the most striking example of insular ratite vicariance (Worthy *et al.* 2005). Despite long standing problems in moa classification due to their high level of morphological variability and unprecedented levels of sexual dimorphism, the latest morphometric and genetic studies support the major division of Dinornithiformes among three families, Emeidae, Dinornithidae and Megalapterygidae (Bunce *et al.* 2009). Bones of the pelvic girdle and its appendages are among the best preserved and their morphology and proportions have traditionally played a major role in the group's taxonomy. In fact, Owen (1879) based his initial classification solely on the basis of the hindlimb bones but he was not always correct. In his earliest paper, Owen (1839) describes morphological features related to the muscular insertions (ridges and reticulate surface) on a fragment of femur, concluding, (p. 170) "… the Struthious bird indicated by the present fragment to have been heavier and more sluggish than the Ostrich; its femur, and probably its whole leg, was shorter and thicker". Many of his later works (collected in Owen 1879), which support the conclusion of sluggishness in the dinornithiforms, contain comments on certain ligamentous and muscular structures of moa hind limbs. “Strongly marked and indented … muscular impressions” on the hindlimb bones of moa were also early noticed by COLENSO (1843). But it was not until 1869, when the description of anatomical features of hind limbs, other than bones, was provided. OWEN (1869) described mummified tendons, sesamoids and integumentary sole-pads of the inner toe of the right foot of *Dinornis robustus* OWEN, 1846, discovered in Manuherikia Valley (South Island). Later, COUGHTREY (1874a, b) described some muscles, tendons, ligaments and integuments of the mummified legs of *Emeus crassus* OWEN, 1846 (femur and tibia), found in Earnscleugh Cave near Alexandra and *D. robustus*, found in the lowlands of the Knobby Range on the South Island. Another mummified foot of *Dinornis (=Megalapteryx) didinus* OWEN, 1883 was described by OWEN (1883b). Besides describing the integument and feathers still attached, OWEN made an important suggestion of how the feet of *Megalapteryx* might have once been used. He wrote (p. 260) “From the osseous structure of the foot, especially the strength and curvature of the ungual phalanges of the digits ii, iii, iv, it was inferred that the hind limbs of the Moas might have been put to the work of uprooting the ferns which, from the unusual proportion of nutritious matter their roots contain, are peculiar to New Zealand, and still afford the material of a favourite bread of the Maoris”.

CRACRAFT (1974, 1976a, b, c) used certain morphological characters and the dependence between the size and shape of hindlimb bones to calculate the groups diversity and position within ratites. He suggested that the unusual degree of diversity in the hindlimb bones was related the prolonged growth period in moas, attaining maximum weight only after their long bones reached maximal length. He also noted that members of the genus *Dinornis* might have been more cursorial, than other moas.

ALEXANDER (1983a, b, 1985) tried to determine the meaning of the unusual proportions of moa hind limbs using allometrical equations developed for flying birds. Dinornithidae fell well into the allometric continuum of flying birds, while members of Emeidae did not. He suggested that this situation in moas was the product of a caudal migration of the center of mass coincident with the reduction of the wings. To keep the feet within the projected center of mass, the moa must have shortened its tarsometatarsus. In contrast, the narrow posterior part of the trunk in living ratites retains the center of the mass in the old position. The structure of *Apteryx* argues against such a hypothesis by having short tarsometatarsi along with a strongly narrowed posterior part of the pelvic girdle. ALEXANDER concluded that although moa were able to run, the absence of terrestrial predators led to the development of the robust graviportal limbs with unusually high optimum factors of safety.

KOOYMAN (1985), in his PhD dissertation on moas and archaeological evidence for moa hunting, provided functional interpretations of osteological hindlimb landmarks, used in the classification of moa. This not only allowed refinement of the existing classification but also led the author to the uncovering of some trends in moa locomotor diversification. *Megalapteryx* was found to be less agile, while members of genus *Dinornis* were the most cursorial and differed from their relatives by the position of their center of gravity. Feet of *Anomalopteryx* might have been better adapted to digging and scratching (KOOYMAN 1991).

Two other moa mummies with hind limbs (*Megalapteryx didinus* and *Anomalopteryx didiformis* OWEN, 1844) were found in 1980s (FORREST 1987; WORTHY 1989), but details of their anatomy have remained undescribed. The same can be said for specimens found in 1884 in the Hector Range (*Pachyornis elephantopus* OWEN, 1856) and in 1894 in the Old Man Range (*Megalapteryx didinus*) (BULLER 1888; ANDERSON 1989).

Here I offer the first detailed restoration of pelvic and hindlimb myology and syndesmology for two species of moa, belonging to two distinct families. I establish the basis for further comparative studies that link functional interpretations and morphological characters in an effort to understand the peculiarities of moa locomotor adaptations.

Material and Methods

I used pelvic and hindlimb bones of two species of moa from the collection of Museum für Naturkunde, Humboldt Universität zu Berlin (MB). An almost complete, mounted skeleton of adult Eastern Moa *Emeus crassus* (MB. Av. 1571) that included a sternum and part of the skull was shipped to Germany by Julius von Haast sometime before 1850. His handwritten labels, referring to *Dinornis casuarinus*, are still preserved but, unfortunately, more detailed records describing the site, where this specimen was found, are missing in Germany and in New Zealand. The "Exchange Book" of Canterbury Museum at Christchurch begins only in 1856. Femora, tibiotarsi and tarsometatarsi of the skeleton are perfectly preserved (only pieces of both cristae cnemiales craniales are slightly abraded, apparently during transportation). Distal halves of both fibulae are missing. Cranial edges of alae preacetabulares and postacetabular portions of both ilia, both ischia and pubes are broken off. Several phalanges are missing, including the third of the third toe and the ungual of the fourth on the right foot; the ungual of the second toe and second, third and fourth (ungual) of the fourth (*Emeus* had normally only four phalanges in the outer toe) on the left foot. The hallux and related metatarsal elements are missing on both limbs.

A skeleton of an adult female of South Island Giant Moa *Dinornis robustus* (MB. Av. 1570, labeled as *Dinornis novaezealandiae*), once mounted, was originally found in Glenmark Swamp near Canterbury. The specimen preserves both alae preacetabulares ilii of the pelvis, both acetabula and the postacetabular part of the right ilium along with right ischium and pubis. As in the skeleton of *Emeus crassus*, the cranial portions of both preacetabular portions of iliac bones are broken off. Cavities in the right femur still contain portions of swampy soil. Surfaces of the femoral head, trochanteric ridge and both condyli are abraded exposing the spongy inner structure. Both tibiotarsi are preserved, showing similar abrasion of protruding surfaces (cristae cnemiales, condyles, caudal edges of proximal articular surfaces). Both fibulae are preserved with only the most distal and thinnest portions missing. The right tarsometatarsus is in particularly good condition, showing only slight traces of abrasion in the hypotarsal and trochlear areas. The foretoes are well preserved; only the ungual phalanx of the right fourth toe is missing and substituted by artificial one. The hallux or hind toe and its metatarsal elements are missing.

Because many of the mounted skeletons from the 19th century are composites, often including material from different taxa, I made sure, that each bone belonged to *E. crassus* or *D. robustus* (Worthy & Holdaway 2002; Worthy, pers. comm.), although not always to the same individuals.

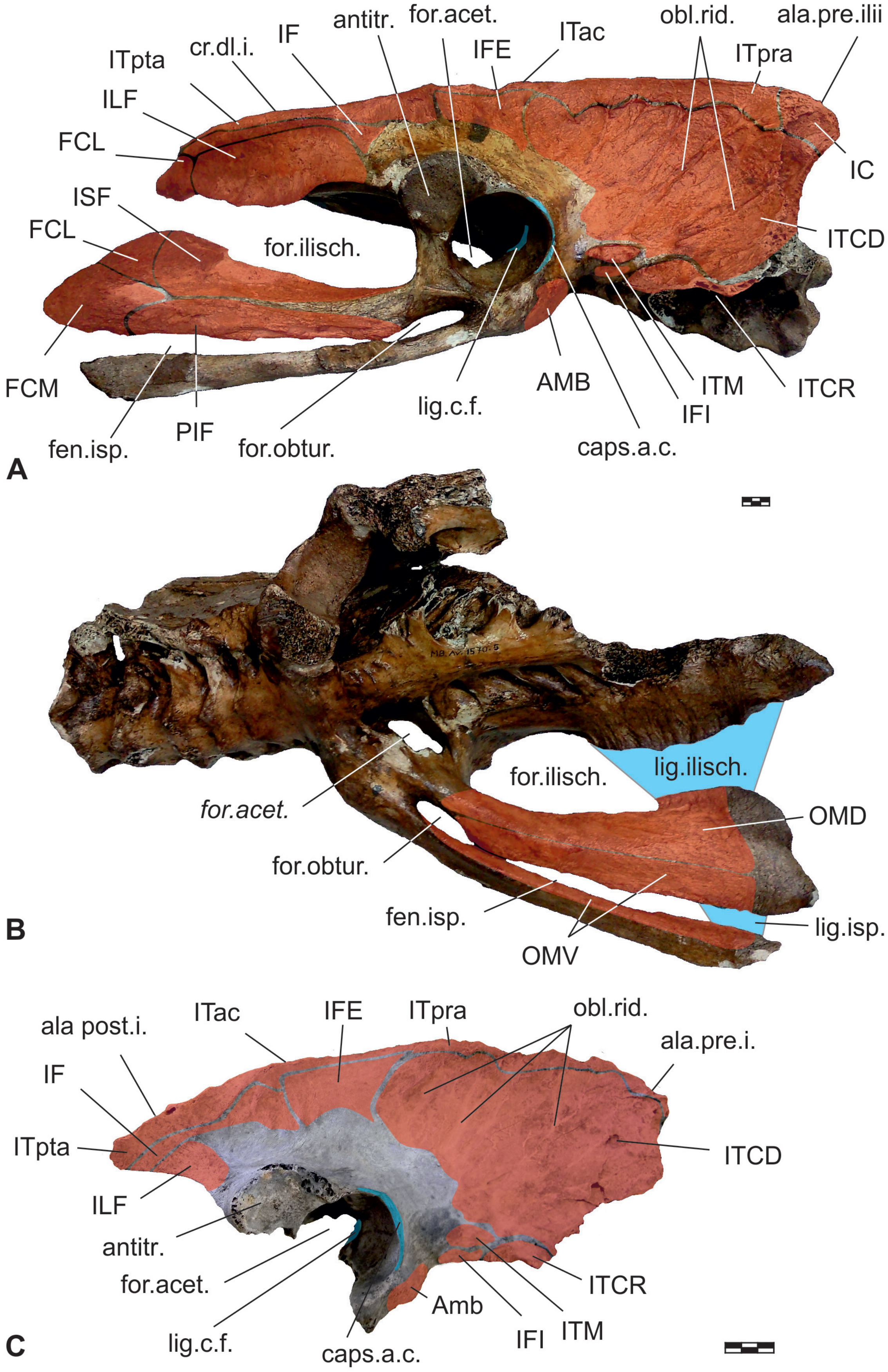
In the reconstruction, I depended on the extensive comparative data on pelvic and hindlimb osteology, myology and syndesmology for Class Aves in Zinoviev (2010). I also followed certain rules of reconstruction, which had been successfully applied in the earlier reconstruction of the hind limbs of *Hesperornis regalis* Marsh, 1872 (Zinoviev 2011). Although members of Casuariiformes are considered the closest living relatives of moa (Johnston 2011), I was extremely cautious in direct extrapolation of morphological characters from extant paleognaths (*Dromaius*, *Casuarius*, *Apteryx*) onto dinornithid material. Besides being graviportal and often attaining great dimensions, moa retained the primitively broad pelvis (Cracraft 1974) with pedomorphically unfused ilia, ischia and pubes. In this way they may have differed from more specialized runners such as *Dromaius* or *Casuarius* and even *Apteryx*. Beautiful lithographs from Owen's papers were also quite instructive for interpreting absent or damaged osteal parts in the material.

Anatomical names follow *Nomina Anatomica Avium* II (Baumel *et al.* 1993) with some changes and additions made by Zinoviev (2010).

Myology and syndesmology

Hip joint

The hip joint belongs to the so called congruent joints in which the articular surfaces of both counterparts match each other closely (Figs 1, 2). The femoral head fits snuggly in the acetabulum, where it is held in place by the well-developed ligamentum capitis femoris. In moa, the origin of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this stout ligament is marked on the cranial rim of the acetabular foramen by a concavity with osseal papillae which gradually fades towards the ventral rim of the opening, blending there clearly with the membrana acetabuli. The insertion of the ligament is in a fovea lig. capitis near the top of the femoral head. In our specimen of *E. crassus* the insertion of lig. capitis femoris was slightly moved proximally from the apex capitis, thus making it protrude and giving to entire head the conical appearance. In contrast, the femoral head of *D. robustus* was perfectly round with a more typical, centered fovea lig. capitis. The functional significance of this variation is obscure and, perhaps, non-existent, since in some specimens of *E. crassus* the femoral head is reported to be as rounded as in *Dinornis* (Kooyman 1991). Lig. capitis femoris and the articular cartilage that retained their flexibility were recorded for a specimen of a femoral head from *Dinornis* (Allis 1864).

The hip joint in birds is not limited to the acetabular region. It extends onto adjacent trochanteric surface of the femur, which rests on the antitrochanter of the ilium. This trochanter-antitrochanter complex produces the habitual, somewhat horizontal position of femur. The proposed position of the femur contrasts with some earlier reconstructions but is consistent with the structure of all extant birds with the exception of penguins and some specialized foot-propelled divers. A proposed difference for the position of the center of gravity that distinguishes the Dinornithidae and other moas from other birds (Alexander 1983a; Kooyman 1985, 1991) is thus not supported by the position of the femur. The femur is not close to vertical (Alexander 1983a).

The origin of capsula articularis coxae is well-defined on the cranial and dorsal surfaces of the elevated acetabular rim. There is an area of tendinous attachment on the cranial surface of the proximal femoral shaft distal to the femoral head and medial to the crista trochanteris. This area is round and slightly excavated in *Dinornis* and longitudinally extended and deeply excavated in *E. crassus.* Although the area appears to be the place of insertion for the lig. iliofemoralis (Zinoviev 2010), the absence of an equally strong origin of this ligament on the ilium suggests an alternate explanation; it is possible that m. iliofemoralis internus (Owen 1858) or m. femorotibialis internus (Kooyman 1991) have inserted here.

Pelvic muscles

For the description of pelvic muscles (Figs 1, 2, 4) I used the sequence reconstructed for *Hesperornis* (Zinoviev 2011). The deepest muscles, which control the movements in the hip joint, usually leave the clearest traces on the bones. This is especially true for the group mm. iliotrochanterici, which resist supination (outward rotation) of the femur caused by the action of the femoral retractors (Zinoviev & Dzerzhinsky 2000). These muscles traditionally extend across the entire surface of ala preacetabularis ilii, leaving definite traces of their fleshy and tendinous origins.

***Mm. iliotrochanterici* —** In both species studied here, there are pronounced traces of muscular and tendinous origin of mm. iliotrochanterici on

FIGURE 1. Pelves of moa, showing attachments of muscles and ligaments: **A**, **B**, *Dinornis robustus* (MG. Av. 1570), lateral and ventrolateral views; **C**, *Emeus crassus* (MB. Av. 1571), lateral view. Origins and insertions of muscles are filled with red and those of ligaments with blue. Muscular attachments of pubis are not shown due to the compete erosion of its surface.
Abbreviations: ala post. i., ala postacetabularis ilii; ala pre. i., ala preacetabularis ilii; AMB, m. ambiens; antitr., antitrochanter; caps. a. c., capsula articularis coxae; cr.dl.i., crista dorsolateralis ilii; FCL, m. flexor cruris lateralis; FCM, m. flexor cruris medialis; fen. isp., fenestra ischiopubica; for. acet., foramen acetabuli; for. ilisch., foramen ilioischiadicum; for. obtur., foramen obturatum; IC, m. iliotibialis cranialis; IF, m. iliofibularis; IFE, m. iliofemoralis externus; IFI, m. iliofemoralis internus; ILF, m. iliofemoralis; ISF, m. ischiofemoralis; ITac, m. iliotibialis lateralis pars acetabularis; ITCD, m. iliotrochantericus caudalis; ITCR, m. iliotrochantericus cranialis; ITM, m. iliotrochantericus medius; ITpra, m. iliotibialis lateralis pars preacetabularis; ITpta, m. iliotibialis lateralis pars postacetabularis; lig. c. f., lig. capitis femoris; lig. ilisch., lig. ilioischiadicum; lig. isp., lig. ischiopubicum; obl. rid., oblique ridges; OMD, m. obturatorius medialis pars dorsalis; OMV, m. obturatorius medialis pars ventralis; PIF, mm. puboischiofemorales.

ala preacetabularis ilii (Figs 1A, C; 2A, B, D, E). Unfortunately, both specimens lack the fragile cranial edges and, consequently, I am unable to reconstruct the cranialmost parts of the muscle group. However, the preserved surface of ala preacetabularis ilii shows the beginning of the most powerful of the iliotrochanterici – m. iliotrochantericus caudalis. Its origin covers almost the entire surface of ala preacetabularis ilii extending from its cranial part approximately to the line passing vertically through the middle of the acetabular opening. The structure of this muscle must have been as complex, as it is in the large living ratites (Sudilovskaya 1931; Zinoviev, 2006). The short muscular fibers of m. iliotrochantericus caudalis started from the preacetabular portion of the ilium but also originated from a number of aponeuroses. Origins of these aponeuroses on ala preacetabularis ilii are marked by prominent oblique ridges. Muscle fibers ended on a number of intramuscular aponeuroses, contributing to a large aponeurosis on the lateral surface of the muscle. This aponeurosis gave rise to a stout terminal tendon, which inserted into the crescent-like rugosity on the craniolateral surface of the greater trochanter, proximal to the insertion of m. iliotrochantericus medius. The area craniad to this insertion is smooth and variable in different species of moa (Kooyman 1991) and was covered by a sheet of cartilage that facilitated sliding of the terminal tendon of m. iliotrochantericus caudalis over the crista trochanteris (Zinoviev 2010). The large and powerful belly of m. iliotrochantericus caudalis covered the smaller bellies of mm. iliotrochanterici cranialis et medius. The fleshy origin of m. iliotrochantericus medius is marked on the lateral surface of ala preacetabularis ilii by an oval rugose area between the beginning of m. iliotrochantericus caudalis and m. iliotrochantericus cranialis. In many birds this muscle fuses with the more powerful m. iliotrochantericus cranialis (Zinoviev 2010). The presence of a separate medial iliotrochanteric muscle in moas is also marked by its well-defined place of insertion on the rugose area between the insertions of m. iliotrochantericus caudalis and m. iliotrochantericus cranialis. The insertion of m. iliotrochantericus cranialis on the craniolateral surface of the femoral shaft is also marked by rugosity. A shallow saddle-shaped area marks the passage of the terminal tendon of this muscle over the distal part of crista trochanteris. The origin of m. iliotrochantericus cranialis, like that of m. iliotrochantericus caudalis, is a combination of muscular and tendinous attachments. The area of origin is from the ventral rim of ala preacetabularis ilii and the adjacent area of its lateral surface just below the origins of other iliotrochanterici. Remains of terminal tendons of mm. iliotrochanterici caudalis et cranialis were reported by Coughtrey (1874a).

Comparison — As in other large cursorial birds, mm. iliotrochanterici of moa are well developed with a complex structure and bear the closest topological resemblance to those of *Dromaius* and *Apteryx* of Ratitae (McGowan 1979; Patak & Baldwin 1998). However, the position of mm. iliotrochanterici in moa is typical of most of birds and can be considered primitive (Zinoviev 2010). Mm. iliotrochanterici of other ratites, such as *Rhea* and *Struthio*, show features of specialization (Gangl *et al*. 2004; Zinoviev 2006; Picasso 2010).

***M. iliofemoralis internus* —** The presence of a minute m iliofemoralis internus (Figs 1A, C; 2A, C, E) is marked by a rugosity on the lateral surface of ala preacetabularis ilii just caudal to the origin of m. iliotrochantericus cranialis and craniad to that of m. ambiens. This muscle is weak and parallel-fibered in birds, other than *Struthio*, and inserts on the ventromedial surface of femoral shaft often leaving no trace of its insertion. In *E. crassus*, a slight tuberosity in the corresponding area is likely the point of insertion for this muscle. However, an oval tuberosity (deeply excavated in *E. crassus*) on the craniomedial surface of the femoral shaft, just distal to the *caput femoris*, could also be a candidate for the point of insertion (Owen 1858). Coughtrey (1874a) found several fibers still attached to this area and followed Owen in attributing them to m. iliofemoralis internus. Such an unusual insertion for the internal iliofemoral muscle poses a problem of interpretation. Although generally weak and sometimes absent in birds, this muscle in its regular position turns the femur outwards, thus regulating movements in hip joint (Zinoviev 2007). In the position, proposed by Owen (1858), it would be an extremely ineffective inward rotator of the femur, compared to the much more powerful mm. iliotrochanterici.

Comparison — M. iliofemoralis internus is quite uniformly weak in the majority of birds. Among ratites it is generally weaker in Casuariiformes but strongly developed with shift in the point of origin in *Struthio*. None of the recent or extinct birds show a comparable shift of the insertion of this muscle (Zinoviev 2010, 2011).

***M. iliofemoralis externus* —** The origin and insertion of a strong m. iliofemoralis externus (Figs 1A, C; 2D) are well marked in moa. Like m. iliotrochantericus caudalis it had fleshy and tendinous origin (multipinnate) on ala preacetabularis ilii just caudal to the origin of the aforementioned muscle. The extent of the caudal expansion of this muscle is limited by the beginning of crista dorsolateralis ilii. The insertion of this muscle on the femoral trochanter is among the most prominent. An extensive, slightly oblique scar is situated between insertion of mm. iliotrochanterici and that of m. ischiofemoralis. On its way to the insertion, a strong and broad tendon of m. iliofemoralis externus must have crossed underlying terminal tendons of m. iliotrochantericus caudalis and m. obturatorius medialis. The remains of this tendon are described by Coughtrey (1874a).

Comparison — M. iliofemoralis externus is generally a weakly developed femoral abductor in birds, as more powerful protractors and retractors of the femur also abduct it (Zinoviev & Dzerzhinsky 2000). However, in cursorial and, especially, large cursorial birds, it is better developed (Zinoviev 2007, 2010). Among ratites this muscle is stronger in *Apteryx* (Owen, 1849a) and *Dromaius*, the latter having multipinnate m. iliofemoralis externus (Patterson, 1983).

***M. ambiens* —** In *D. robustus* m. ambiens (Fig. 1A, C) arose from a rugose area at the junction of the ilium and the pubis (the pectineal process in moa is not prominent). The rugose area is more expansive on the ilium. The course of the muscle is obscure, since it does not insert on a bone in birds; its terminal tendon fuses with aponeurosis communis fibularis upon crossing the knee joint.

Comparison — Generally vestigial, m. ambiens disappears in a number of perching birds. In cursorial birds it is better developed and associated with locomotion in groups with single limb supported phases (Zinoviev 2007). Ratites show considerable variation in the morphology of this muscle. In *Struthio*, it originates from the center of ala preacetabularis ilii, whereas in others it originates from the pectineal process. It is reportedly absent in Casuariiformes (Garrod 1873; Gadow 1880; Beddard 1898). However, a slip that originates from proc. pectineus and fuses with the tendon of m. femorotibialis medius could be the remnant of m. ambiens. It shows tendencies for similar fusion in Rheiformes (Gadow & Selenka 1891).

***M. obturatorius medialis*[1] —** M. obturatorius medialis is the only muscle in modern birds which originates on the visceral surface of the pelvis (Figs 1B; 2B, D). Traces of its origin in *D. robustus* suggest that it must have had two bellies. The dorsal belly originated aponeurotically from the medial surface of the postacetabular ilium, immediately adjacent to foramen ilioischiadicum as well as from the dorsal half of the ischium facing the foramen. The main bulk of muscular fiber of the dorsal portion undoubtedly arose from membr. ilioischiadica itself. The ventral belly originated from membr. ischiopubica and adjacent surfaces of the ischium and pubis that are tilted towards it. It is difficult to reconstruct the expansion of the bellies caudally, since they have not left definite traces. However, they must have expanded to some extent along the strengthened caudal portions of membr. ilioischiadica and membr. ischiopubica (ligg. ilioischiadicum et ischiopubicum). The terminal tendon passed through foramen obturatum, which was separated from fenestra ischiopubica by the tendinous bridge. It inserted on the lateral surface of the proximal femur just caudal to the insertion of m. iliotrochantericus caudalis. The passage of the terminal tendon along the femur is marked by smooth area that was undoubtedly covered by the thin layer of cartilage. Remains of the terminal tendon are reported by Coughtrey (1874a).

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[1] *M. obturatorius lateralis*, which is always present in birds (Zinoviev 2010), sheathes the terminal tendon of m. obturatorius medialis and must have been present in moa. However, it leaves such faint traces on bones, that its precise reconstruction is not possible.

Comparison — M. obturatorius medialis is quite uniform in birds, sometimes having two heads of origin. It is quite variable in Ratitae; *Struthio* is the only bird, in which part of the muscle starts from lateral surfaces of lamina ischiopubica and adjacent areas of ischium and pubis (Zinoviev 2007). Casuariiformes and Rheiformes also have two heads of this muscle (Gadow 1880; Gadow & Selenka 1891; Patterson 1983; Picasso 2010).

M. ischiofemoralis **—** The deepest muscle of the acetabular pelvis is m. ischiofemoralis (Figs 1A; 2B, D, F). Origins of muscles of the postacetabular pelvis are difficult to reconstruct because they leave only faint traces on the bones. This is also the case for m. ischiofemoralis, the large part of which originates from the lateral surface of membr. ilioischiadica. This membrane was undoubtedly present in moa (see the description of the previous muscle) as indicated by the sharp rims of the ilium and ischium that project towards each other. Only the ventral border of m. ischiofemoralis is detectable on the ischiac bone of *D. robustus.* The muscle's belly started from the dorsal half of the ischium, near the level of the caudal half of foramen obturatum, and extended about two-thirds along that bone. To what extent it expanded over membr. ilioischiadica or perhaps originated on the adjacent area of the postacetabular ilium, as in many modern birds, remains unclear. A strong tendon of this muscle inserted on the lateral side of the femoral shaft on a tuberosity just caudal and distal to the insertion of m. iliofemoralis externus. This area is quite pronounced in *E. crassus* but much fainter in *D. robustus*.

Comparison — M. ischiofemoralis is quite morphologically conservative in birds and moas are not an exception.

M. iliofemoralis and m. caudofemoralis **—** The presence of a well-developed m. iliofemoralis (Figs 1A, C; 2 B, F) is defined by attachment to a ridge, which extends along the caudal border of the femoral shaft from the insertion of m. ischiofemoralis to the proximal point of insertion of pars accessoria m. flexor cruris lateralis. This ridge in *E. crassus* runs very close to that of the medially situated mm. puboischiofemorales, whereas *D. robustus* shows a greater distance between the two ridges. The pelvic origin of m. iliofemoralis should have started somewhere on the ilium between crista iliaca dorsolateralis and membr. ilioischiadica. In life, part of it might also have started on the membrane. There are no definite traces of the presence of m. caudofemoralis in either species of moa examined in this study.

Comparison — Although proceeding from the position of the adjacent muscular bellies, the shape of the belly of m. iliofemoralis in *D. robustus* must have been similar to that of the majority of birds, its extended insertion on the femoral shaft is a rare feature, which was earlier recorded only for *Apteryx australis* (McGowan 1979). The postacetabular portion of the pelvis in *E. crassus* was not available for the study. As for m. caudofemoralis, it might have been altogether absent in moa. The presence of this muscle is usually related to the development of the tail, which it bends sideways. It is absent in Rheiformes and *Dromaius*, vestigial in *Casuarius* (Garrod 1873; Gadow 1880; Pycraft 1900; Patterson 1983; Picasso 2010), but present in *Apteryx* and *Struthio* (Gadow 1880; Owen 1849a; McGowan, 1979).

Mm. puboischiofemorales **—** These major femoral retractors, mm. puboischiofemorales (Figs 1A; 2B, F), are always present in birds and consist of two parts, one superficial or lateral and another deeper or medial. The beginning of the lateral portion is partially detectable on the pelvis of *D. robustus*. It started from the ventral half of the ischium, leaving free only its caudal fifth. The deeper part must have originated ventrally from the same bone and also from the part of membr. ischiopubica. The insertions of the muscles are on the ridge, running along the caudal surface of the femoral shaft medial to the ridge marking the insertion of m. iliofemoralis. The ridge starts from the level of insertion of m. ischiofemoralis and terminates at the distal level of the insertion of pars accessoria m. flexor cruris lateralis.

Comparison — As major femoral retractors, mm. puboischiofemorales are quite uniform in birds, and the moa does not show any deviations from the general plan.

Mm. flexores crures lateralis et medialis — Both flexors of the knee joint and inward rotators of

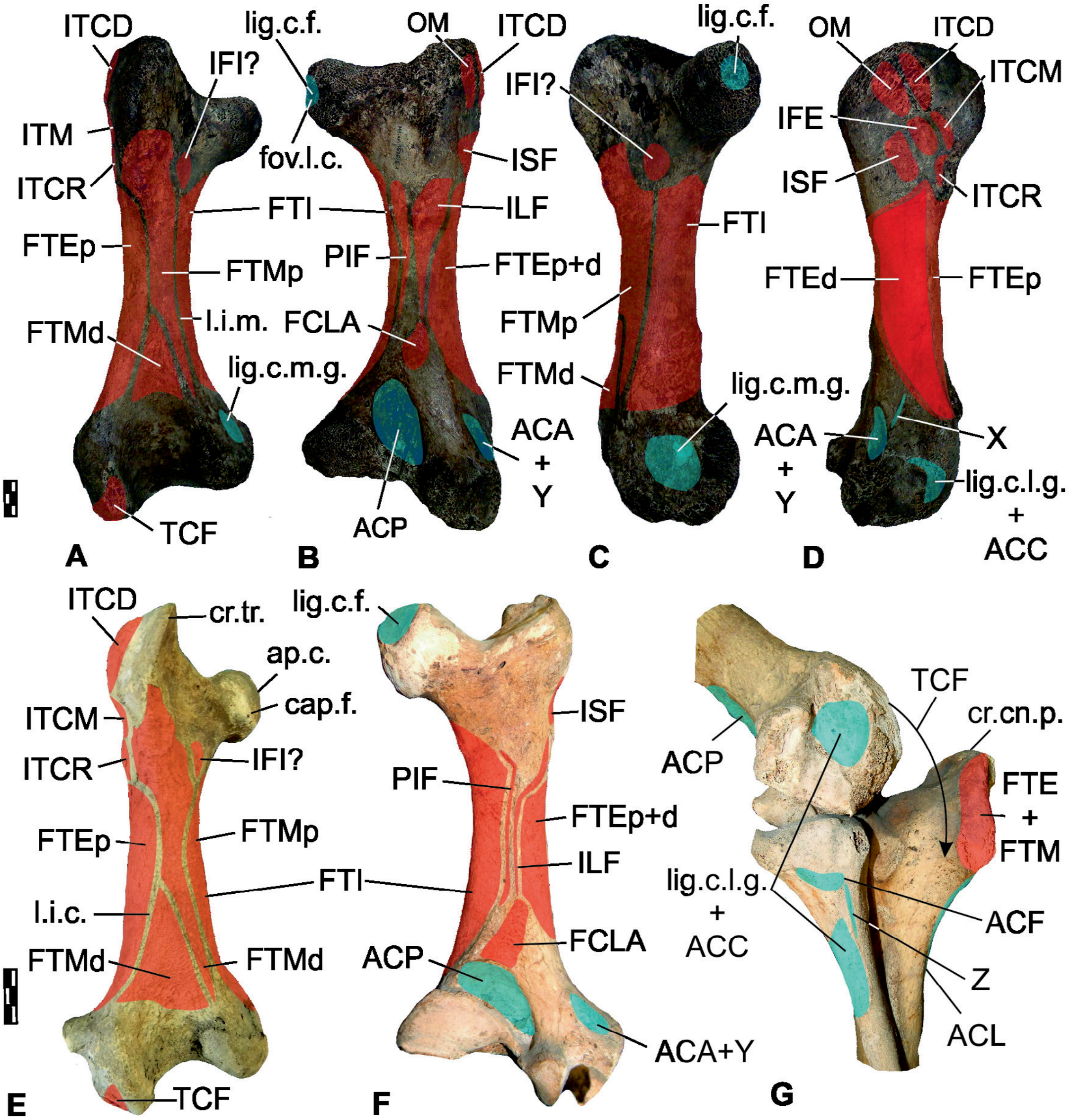

FIGURE 2. Right femora of: **A-D,** *Dinornis robustus* (MG. Av. 1570) cranial, caudal, medial and lateral aspects; **E-F,** *Emeus crassus* (MB. Av. 1571), cranial and caudal aspects, **G**, right knee joint of the same *Emeus* specimen, showing attachments of some muscles and ligaments.

Abbreviations: ACA, apon. communis ansae; ACC, apon. communis collateralis; ACF, apon. communis fibularis; ACP, apon. communis poplitea; ap. c., apex capitis; cap. f., caput femoris; cr. cn. p., crista cnemialis patellaris; cr. tr., crista trochanteris; FCLA, m. flexor cruris lateralis pars accessoria; fov. l. c., fovea lig. capitis; FTE, m. femorotibialis externus; FTEd, m. femorotibialis externus pars distalis; FTEp, m. femorotibialis externus pars proximalis; FTEp+d, m. femorotibialis externus partes proximalis et distalis; FTI, m. femorotibialis internus; FTM, m. femorotibialis medius; FTMd, m. femorotibialis medius pars distalis; FTMp, m. femorotibialis medius pars proximalis; IFI, m. iliofemoralis internus; ILF, m. iliofemoralis; ISF, m. ischiofemoralis; ITCD, m. iliotrochantericus caudalis; ITCR, m. iliotrochantericus cranialis; ITM, m. iliotrochantericus medius; lig. c. f., lig. capitis femoris; lig. c. l. g., lig. collaterale laterale genus; lig. c. m. g., lig. collaterale mediale genus; l. i. c., linea intermuscularis cranialis; l. i. m., linea intermuscularis medialis; OM, m. obturatorius medialis; PIF, mm. puboischiofemorales; TCF, m. tibialis cranialis caput femorale; X, pars proximalis ansae m. iliofibularis; Y pars lateralis ansae m. iliofibularis.

the shank, mm. flexores crures lateralis et medialis, were present in moa (Figs 1A, B; 2B, F). The origin of the lateral one is detectable on the ischium caudal to the origin of m. ischiofemoralis. It might have also originated from the caudal part of the postacetabular ilium and strong ligament, which united ilium and ischium (see above). But these traces are not detectable. The medial muscle started from the apical part of the ischium, ventral to the origin of lateral part and caudal to that of mm. puboischiofemorales. Both bellies ran towards the tibiotarsus to insert on its medial surface at the pronounced, slightly oblique rugosity cranial to the insertion of lig. collaterale mediale genus. Before providing the terminal tendon for the common tibiotarsal insertion, the lateral part gave a rise to an accessory belly whose fleshy part attached to the triangular area proximal to aponeurosis commuis poplitea.

Comparison — Both muscles are well developed in cursorial birds, including ratites. Their origin may migrate onto several tail vertebrae (Rheiformes, Apterygiformes), which is impossible to prove for moa. However, it is almost certain, that the lateral muscle had a tendinous connection with the intermediate head of m. gastrocnemius, which is characteristic for all the Ratitae and a majority of basal birds.

M. iliofibularis **—** Moa exhibit a muscular organization seen in other birds in which m. iliofibularis originates along almost the entire length of postacetabular ilium, just above the origins of m. ischiofemoralis and m. iliofemoralis and below the postacetabular portion of m. iliotibialis lateralis (Figs 1A, C; 4C, D). It gradually tapered distally and a tendon of insertion passed through the tendinous loop (as described in the section on the knee joint, below) to insert on tuberositas m. iliofibularis on the lateral side of the fibula, just distal to the insertion of lig. collaterale laterale genus. The tendinous evidence for this insertion in *D. robustus* is reported by Coughtrey (1874a).

Comparison — This muscle is quite uniformly developed through the entirety of Class Aves, regardless of variation in locomotor habits (Zinoviev 2010).

Mm. iliotibiales lateralis et cranialis **—** The most superficial muscles of the thigh, mm. iliotibiales lateralis et cranialis were extremely well developed in moa. Although the most cranial part of ala preacetabularis ilii is missing in our material, the caudal surface of the origin of m. iliotibialis cranialis is fortunately preserved (Fig. 1A, C). It shows a thick combination of fleshy and tendinous origins but not the aponeurotic type seen in many birds. The preacetabular portion of m. iliotrochantericus lateralis shows a similar origin that extended up to the beginning of m. iliofemoralis externus. The acetabular portion of the muscle had a much thinner origin, providing adequate space for the origin of m. iliofemoralis externus. The beginning of the postacetabular portion was equally thick and extended to a point slightly behind the caudal edge of the antitrochanter. From that point, a much thinner line of origin for the postacetabular portion ran caudally along the rest of crista iliaca dorsolateralis. Both muscles contributed to the formation of the patellar tendon, which inserted on crista cnemialis lateralis and crista cnemialis patellaris. Part of the tendinous insertion of these muscles is reported by Coughtrey (1874a).

Comparison — Well developed mm. iliotibiales are characteristic for cursorial birds and are especially strong in ratites (Zinoviev 2011).

Femoral muscles

The femoral muscle complex of birds (Fig. 2) consists of three major parts, which envelope almost the entire femoral shaft. The primary function of these muscles is to extend of the knee joint. The lateral and medial portions of this complex can also supinate and pronate the crus (Zinoviev 2010). These muscles are especially well developed in cursorial birds.

M. femorotibialis externus **—** Both proximal and distal parts of m. femorotibialis externus were present in *D. robustus* and *E. crassus* (Fig. 2A, B, D-G). They were better defined in the latter species with greater femoral relief. Pars proximalis originated from an area, bordered cranially by crista trochanteris; proximally, by the insertion of m. iliotrochantericus caudalis; proximoventrally, by the insertion of m. iliofemoralis externus and m. ischiofemoralis; and ventrally, by the extended insertion ridge for m. iliofemoralis (see above).

On the cranial surface of the femoral shaft the expansion of pars distalis is restricted by linea intermuscularis cranialis, whose lateral branch goes to the condylus lateralis. Pars distalis was covered by the proximal portion and partially had the same ventral and proximal borders. Its cranial expansion on the lateral side of the femoral shaft was limited by a faint ridge, which starts at the point between the insertions of m. iliofemoralis externus and m. ischiofemoralis and runs along the lateral surface of the femoral shaft to a point slightly beyond the proximal level of the insertion of pars accessoria m. flexorius cruris lateralis. Both, proximal and distal parts contributed to the lateral part of patellar tendon that inserted on the external edge of crista cnemialis lateralis.

Comparison — The development of m. femorotibialis externus in moa is typical for cursorial birds. In ratites the proximal part of the muscle completely covers the distal one, which extends proximally along the femoral shaft (Zinoviev 2010).

M. femorotibialis medius **—** M. femorotibialis medius had the fleshy origin along the entire cranial surface of the femoral shaft (Fig. 2A, C, E, G). It was also divided into proximal and distal parts. The proximal part had a tendinous origin from the tuberosity on the distal portion of crista trochanteris and a fleshy origin from the area between linea intermuscularis cranialis (with a branch to condylus medialis) and linea intermuscularis medialis, dividing the belly of m. femorotibialis medius from that of m. femorotibialis internus. The extent of proximal migration of the m. femorotibialis medius belly between crista trochanteris and caput femoris is not clear. A terminal tendon from the proximal part contributed to the formation of the patellar tendon. The distal part of m. femorotibialis medius had a fleshy origin in a well-defined area between branches of linea intermuscularis cranialis. It was completely covered by the proximal part of mm. femorotibiales lateralis et medius. Muscle fibers of the distal part, most likely, inserted directly to the proximal border of the patella, as in the majority of birds. Some muscular fibers of m. femorotibialis medius were described by Coughtrey (1874a).

Comparison — As for the previous muscle, the development of m. femorotibialis medius in moa is typical for cursorial birds. Ratites show progressive enlargement of the distal part of the muscle, which reaches its maximal development in *Struthio* (Zinoviev 2010).

M. femorotibialis internus **—** The origin of m. femorotibialis internus was confined to the medial and caudomedial surfaces of the femoral shaft (Fig. 2A, C, E, F). Its body was restricted caudally by the ridge of insertion for mm. puboischiofemorales and cranially by linea intermuscularis medialis. The extent to which m. femorotibialis internus expanded proximally is not clear. However, there is an excavated area near the proximal reaches of the muscle that strongly suggests a tendinous origin. Such a structure is unique for Dinornithiformes. If it does not reflect the insertion of m. iliofemoralis internus, the strengthened tendinous part of the other (superficial) head of m. femorotibialis internus might have been solely responsible for this feature. In this suggestion I agree with the interpretation of Kooyman (1991).

Comparison — M. femorotibialis internus generally consists of two bellies (Zinoviev 2010). Ratites show many deviations from the general type by having up two three bellies (Struthioniformes, Rheiformes, Casuariiformes). The unusual rugose pit near the beginning of m. iliofemoralis internus belly might represent a deviations strictly confined to Dinornithiformes.

Knee joint

Due to the migration craniad of the center of gravity in birds, the knee joint has become the major pivot, around which the hind limb moves (Figs 2, 3, 4). Despite the majority of locomotor adaptations, avian knee joint is morphologically conservative, showing striking similarity among the various ecological groups (Zinoviev 2010) and does not differ from the general type, even in highly specialized birds (Zinoviev 2011). Therefore, it seems very likely that the moa, residing well within Neornithes, had a knee joint similar to that of other modern birds. All evidence suggests that this is, in fact, so.

In addition to the relatively feeble joint capsule, the knee of moa was stabilized by a robust set of collateral ligaments. Lig. collaterale laterale genus originated in a deeply excavated

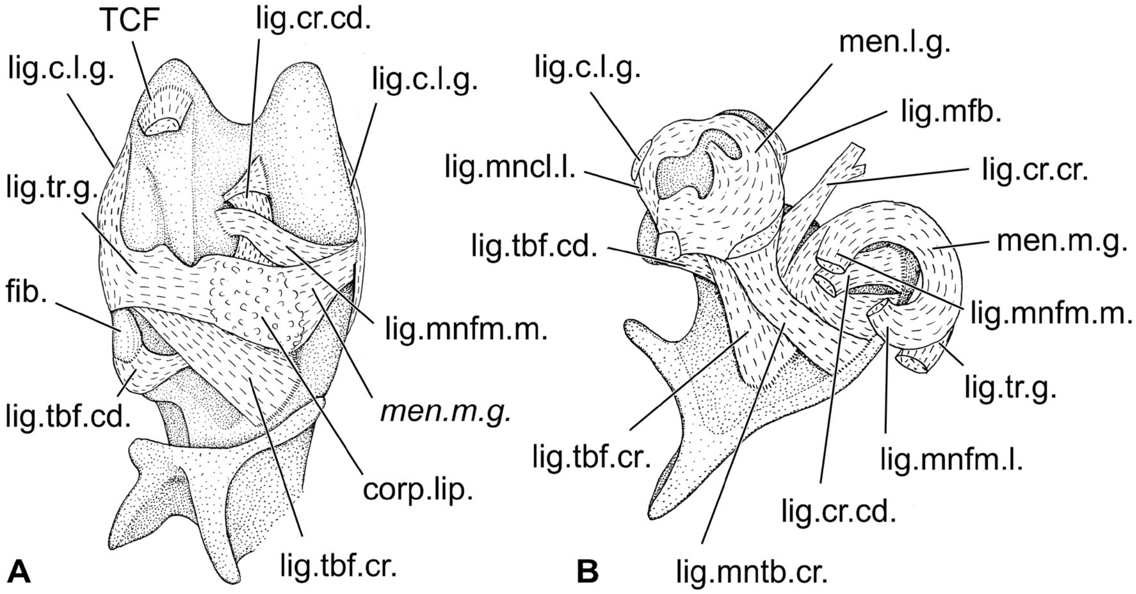

FIGURE 3. Right knee joint of *Dromaius novaehollandiae* (Museum of Natural History of the University of Kansas, without no.) **A**, overflexed, cranial view; **B**, distal articular surface. From Zinoviev (2010) with changes. Abbreviations: corp. lip., corpus liposum; fib., fibula; lig. c. l. g., lig. collaterale laterale genus; lig. cr. cd., lig. cruciatum caudale; lig. cr. cr., lig. cruciatum craniale; lig. mfb., lig. meniscofibulare; lig. mncl. l., lig. menisco-collaterale laterale; lig. mnfm. l, lig. meniscofemorale laterale; lig. mnfm. m., lig. meniscofemorale mediale; lig. mntb. cr., lig. meniscotibiale craniale; lig. tbf. cr., lig. tibiofibulare craniale; lig. tbf. cd., lig. tibiofibulare caudale; lig. tr. g., lig. transversum genus; men. l. g., meniscus lateralis genus; men. m. g., meniscus medialis genus; TCF, m. tibialis cranialis caput femorale.

fossa on the lateral surface of corresponding femoral condyle. Its passage to the place of insertion is marked by a groove on the lateral femoral condyle and a smoothed area on the lateral surface of the fibula. The lateral collateral ligament of the knee was inserted on the lateral surface of the fibular shaft just proximal to the insertion of m. iliofibularis. Lig. collaterale mediale genus started from a less deeply excavated fossa on the medial side of the corresponding femoral condyle. Its passage across the knee joint is marked by a slight depression in condylus femoris medialis. The ligament inserted on the medial surface of the tibiotarsal shaft slightly distal to the insertion of its lateral counterpart. The place of insertion of this ligament was covered by the common tibiotarsal attachment of mm. flexores crures lateralis et medialis. The articular surfaces have been damaged in the mounted skeleton of *E. crassus* and in the previously mounted specimen of *D. robustus* and did not allow us to prepare clear illustrations. However, the position of ligg. cruciata and other ligaments, which held both menisci in place, and ligaments holding the head of fibula against tibiotarsus, closely resembled those of *Dromaius* (Fig. 3).

Muscles of the crus

As noted in an earlier publication (Zinoviev 2011), the reconstruction of the crural muscles is difficult due to the limited space available for their origin on the distal femur and proximal crus (Figs 1, 4–6). This shortage of space and the necessity to retain mobility in the knee joint has resulted in crowding of the origins for crural muscles near the knee. They often share an origin on common aponeuroses rather than originating separately from the bones (Zinoviev 2003a). However, the aponeuroses leave clear traces on the bones and thus can be reconstructed with the high degree of confidence (Zinoviev 2011). Those attached to cnemial crests might have been relatively smaller than in the majority of other birds (a feature, already noted by earlier authors: Owen 1849c) and closely approached proportions seen in *Apteryx* (see Discussion). The following description includes the reconstruction of the ligamentous loop (ansa m. iliofibularis), which is intimately associated with aponeuroses originales (Figs 2, 4).

Aponeuroses originales communes musculorum cruris

Aponeurosis communis ansae (Fig. 2B, F) — originates in all known birds on the lateral femoral epicondyle and is associated with the lateral branch of ansa m. iliofibularis. It was enormously developed in moa. Both of the species studied here and others show a deep elongated or circular fossa at the same location on the lateral femoral epicondyle. The feature was correctly interpreted by KOOYMAN (1991), who associated the fossa with the lateral branch of the loop (Fig. 2D) and with the beginning of the lateral part of m. gastrocnemius. Aponeurosis communis collateralis (Fig. 2D, G) is intimately associated with the beginning of lig. collaterale laterale genus and is detectable in moa. It started from a site near the origin of the mentioned collateral ligament and expanded cranioproximally along the lateral surface of the femoral condyle. The cranial branch of ansa m. iliofibularis (Figs 2G, 4C) left a longitudinal rugosity on the lateral side of the fibular shaft between the fibular head and the beginning of lig. collaterale laterale genus. Aponeurosis communis poplitea (Fig. 2B, F, G) started from the entire popliteal area, in front and slightly mediad to the insertion of accessory part of m. flexor cruris lateralis. The presence of aponeurosis communis fibularis (Figs 2G, 4C) is marked by rugosity on the lateral surface of the fibular head just above the insertion of the cranial branch of the ligamentous loop[2]. Whether it was associated with the terminal tendon of m. ambiens, as in the majority of birds possessing this muscle, or not, is unclear. There are no traces of m. ambiens crossing the knee joint; no such traces have been reported for the preserved patella (OWEN 1883a). The beginning of aponeurosis communis lateralis (Figs 2G, 4A–C) is traceable along the distal portion of crista cnemialis lateralis. In contrast, the beginning of aponeurosis communis dorsalis (Fig. 4A, B) is quite continuous, starting on the cranial cnemial crest and extending down the tibiotarsus well to the beginning of sulcus extensorius. The last, proximal, branch of ansa m. iliofibularis started from the slight depression on the lateral surface of the femoral shaft cranioproximally from the place of beginning of aponeurosis communis ansae (Fig. 2D).

M. popliteus **—** The inward rotator of the crus, m. popliteus (Fig. 4D), is essential in assisting cursorial birds to place the foot accurately under the body's centre of mass (ZINOVIEV 2011). It was well developed in moa and started from a slightly elevated area on the ventral surface of the fibular shaft just distal to the fibular head. The muscle inserted on a rugose area of the ventral tibiotarsus just below facies articularis medialis tibiotarsi.

Comparison — M. popliteus, when present, is quite uniform in birds. It is well developed in ratites. *Apteryx* might be an exception by having a vestigial m. popliteus. It was reported for *Apteryx australis* by OWEN (1849a), but has not been mentioned by the later authors (BEDDARD 1899; MCGOWAN 1979; VANDEN BERGE 1982).

M. plantaris **—** The beginning of m. plantaris is clearly marked in *E. crassus* by the relatively small unevenness on the ventromedial surface of tibiotarsus just below facies articularis medialis (Fig. 4A, D). This part of the tibiotarsus in the specimen of *D. robustus* has unfortunately been eroded. Undoubtedly small in *E. crassus*, it was partially covered near its origin by lig. collaterale mediale genus. The insertion must have been typical to the proximomedial edge of the tibial cartilage. The terminal tendon of this muscle is so feeble in ratites, that it might have not been preserved in the mummy of *D. robustus*, inspected by COUGHTREY (1874b).

Comparison — This muscle is small, vestigial or sometimes absent in Ratitae (ZINOVIEV, 2010).

M. extensor digitorum longus — The common extensor of foretoes had a fleshy origin in moas, arising from the area between cnemial crests (Figs 4A, B, C; 5A; 6A, C, D, E, G, H). Due to the restriction of this area in Dinornithiformes and relatively small size of the cnemial crests, the bulk of the muscle must have been distributed distally along the cranial shaft of the tibiotarsus

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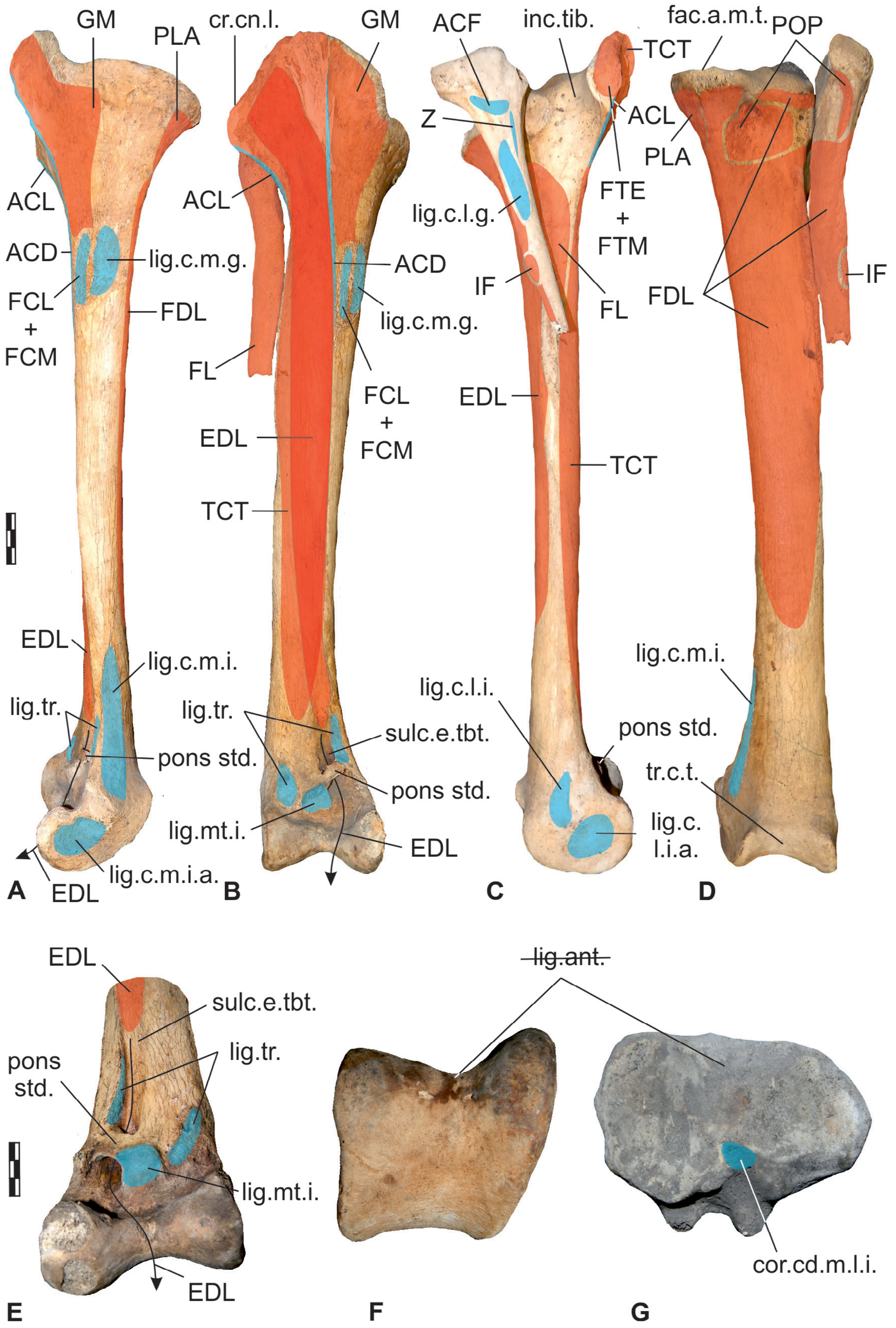
[2] Lig. collaterale laterale genus and aponeurosis communis are often fused at the insertion on fibula, so their division on Fig. 2G is very approximate.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with some of the muscular fibers starting on the lateral surface of aponeurosis communis dorsalis. Other fibers might have started on the cranial surface of fibular shaft, as in Rheiformes (Haughton 1868; Gadow & Selenka 1891). As discussed above, most of the muscles originating along the tibiotarsal shaft do not leave well-defined traces on the bone. Moa are not an exception. Keeping in mind the graviportal nature of New Zealand's feathered giants, I can assume that the belly of this muscle ended near the beginning of sulcus extensorius tibiotarsi, in which only the terminal tendon of the muscle entered. The oval terminal tendon of m. extensor digitorum longus passed under ligamentum transversum together with the terminal tendon of m. tibialis cranialis. The transverse ligament, the presence of which is marked by two corresponding tuberosities, was slightly elevated medially, as in other birds. After emerging from beneath lig. transversum, the terminal tendon of the long extensor of the foretoes passed through canalis extensorius below the ossified pons supratendineus and crossed the intertarsal joint in incisura intercondylaris. The terminal tendon then followed a path medial to the insertion of m. tibialis cranialis and was held in place by retinaculum extensorium tarsometatarsi, which medial insertion lies immediately craniad of the insertion of lig. collaterale mediale intertarsale. After emerging from under the retinaculum, the terminal tendon attained a central position on the dorsal surface of the tarsometatarsus. There are no traces of its passage along the anterior surface of the tarsometatarsus and only the most proximal portion is preserved on the mummy of *D. robustus* studied by Coughtrey (1874b). However, the terminal tendon must have widened before trifurcating near the distal end of tarsometatarsus to send three branches to the foretoes. The pattern of further branching is too complex and variable among birds to be reconstructed with confidence in moa (Zinoviev 2010). The only thing I can be sure of that all three branches inserted to the extensorial tuberosities of the corresponding ungual phalanges.

Comparison — The muscle is quite uniform in birds (Zinoviev 2010). In Casuariiformes and Apterygiformes the branch to the third toe bifurcates. However, that can not be proved for Dinornithiformes. In the majority of Ratitae and some other birds the terminal tendon of m. extensor digitorum longus perforates that of m. tibialis cranialis. The absence of this feature in Dinornithiformes makes them similar to Tinamiformes and Apterygiformes.

***M. tibialis cranialis* —** M. tibialis cranialis is a dorsal flexor of the intertarsal joint and consists of two heads (Figs 2A, E, G; 3A; 4B, C; 5A, E). The femoral head had its tendinous origin in fovea tendineus m. tibialis cranialis on the anterior surface of the lateral condyle of the femur. It passed then through incisura tibialis and merged with the belly of the tibiotarsal head. The tibiotarsal head overlaid m. extensor digitorum longus, originating from facing surfaces of the cnemial crests and of aponeuroses communes lateralis et dorsalis, as well as from the cranial surface of the tibiotarsal shaft. The breadth of the muscle's belly can be traced along the bone to the origin

◀ **FIGURE 4.** Right tibiotarsus and proximal half of fibula of *Emeus crassus* (MB. Av. 1571), **A–D**, medial, cranial, lateral and caudal aspects; left tibiotarsus of Dinornis robustus, **E,** distal fourth, cranial aspect; proximal and distal articular surfaces of right intertarsal joint of *E. crassus*, showing attachments of some muscles and ligaments, **F, G**. ~~Lig. ant~~. illustrates the absence of any traces of lig. intercondylare. Abbreviations: ACD, apon. communis dorsalis; ACF, apon. communis fibularis; ACL, apon. communis lateralis; cor. cd. m. l. i., cornu caudale menisci lateralis intertarsi; cr. cn. l., crista cnemialis lateralis; FCL, m. flexor cruris lateralis; FCM, m. flexor cruris medialis; EDL, m. extensor digitorum longus; fac. a. m. t., facies articularis medialis tibiotarsi; FDL, m. flexor digitorum longus; FL, m. fibularis longus; FTE, m. femorotibialis externus; FTM, m. femorotibialis medius; GM, m. gastrocnemius medialis; IF, m. iliofibularis; inc. tib., incisura tibialis; lig. c. l. g., lig. collaterale laterale genus; lig. c. l. i., lig. collaterale laterale intertarsi; lig. c. l. i. a., lig. collaterale laterale intertarsi accessorium; lig. c. m. g., lig. collaterale mediale genus; lig. c. m. i., lig. collaterale mediale intertarsi; lig. c. m. i. a., lig. collaterale mediale intertarsi accessorium; lig. mt. i., lig. meniscotibiale intertarsi; lig. tr., lig. transversum; PLA, m. plantaris; pons std., pons supratendineus; POP, m. popliteus; sulc. e. tbt., sulcus extensorius tibiotarsi; TCT, m. tibialis cranialis caput tibiotarsale; tr. c. t., trochlea cartilaginis tibialis; Z, pars distalis ansae m. iliofibularis.

of sulcus extensorius tibiotarsi, as in the previous case. The terminal tendon passed superficially to the terminal tendon m. extensor digitorum longus, under lig. transversum tibiotarsi and then, over pons supratendineus. It crossed the intertarsal joint in sulcus intercondylaris tibiotarsi and inserted in the deeply excavated fossa on the cranial surface of the proximal tarsometatarsus. It was not penetrated by the terminal tendon of the long flexor of the foretoes (see above). No such penetration was found by Coughtrey (1874b) on the mummy of *D. robustus*, which preserved only "a tuft of the insertion" of the terminal tendon of m. tibialis cranialis.

Comparison — The muscle is quite uniform in birds and better developed in those, for which the flexion of intertarsal joint is of particular importance (cursorial, raptorial, foot-propelled swimming etc.). As it was mentioned above, the tendon of m. extensor digitorum longus penetrates the terminal tendon of the muscle in some birds. This is characteristic for ratites, except for the Tinamidae and *Apteryx*.

***M. flexor digitorum longus* —** The deepest of avian digital flexors, m. flexor digitorum longus originated on the posterior surfaces of tibiotarsus and fibula (Figs 4C, D; 5B, C, D, F, G, H). Both surfaces of the bone are rough, suggesting the fleshy origin for the muscle. The exact extent of the muscule's belly is impossible to reconstruct as it has not left definite traces of its borders. Nor is their evidence to suggest a third origin of the muscle from the ventral surface of the lateral femoral condyle. The terminal tendon of the muscle crossed the intertarsal join in the tibial cartilage, the presence of which in moa is marked by a well-developed trochlea cartilaginis tibialis. The tibial cartilage is clearly illustrated on the drawing from Coughtrey (1874b). In *D. robustus* the lateral portion of it contained a sesamoid bone. The surface, incorporating similar bone is also seen in *E. crassus*. The terminal tendon travelled along the plantar surface of the tarsometatarsus in a channel deeper than other flexorial tendons. After branching at the base of the toes and going over sesamoid cartilages, reported by Coughtrey only for the second and third toes, the terminal tendon of m. flexor digitorum longus serviced three foretoes with the main slips inserted on tubercula flexorii of the ungual phalanges. Variably arranged additional slips attached to the proximal phalanges. Unfortunately, the description, given by Coughtrey (1874b), is not sufficiently clear to understand the exact arrangement of the branching.

Comparison — The belly of the muscle is quite uniform in birds, the size of it and expansion on the femur are being slightly variable. The pattern of terminal tendon branching is much more variable, being a subject of individual variation (Raikow 1978).

***M. flexor hallucis longus* —** All the Dinornithiformes possessed a hallux, which was, however, much reduced and elevated. It must have been supplied by m. flexor hallucis longus. This muscle is always present in birds even in those that lack a hind toe. The tendinous bridge, vinculum tendineum flexorum, which runs obliquely from the terminal tendon of m. flexor hallucis longus to that of m. flexor digitorum longus, allows the former to assist in the flexion of the foretoes. Upon the disappearance of the hallux and the corresponding tendon of m. flexor hallucis longus, m. flexor hallucis longus becomes an accessory flexor of the foretoes. Being superficial to m. flexor digitorum longus, it has more space to expand. These novel duties explain why m. flexor hallucis longus is not only preserved in birds that lack a hallux, but is sometimes enlarged. Its exact development in moa is impossible to reconstruct, since this muscle is rarely in contact with bone, typically originating from some common aponeuroses (e.g. aponeuroses communes fibularis et poplitea) and from superficial aponeurosis of the deeper belly of the long flexor of the foretoes. As in living ratites, which retained a vestigial hallux (some of Tinamiformes and Apterygiformes), m. flexor hallucis longus of moa should have made a main contribution through the aforementioned tendinous bridge to the terminal tendon of m. flexor digitorum longus, sending a much weaker tendon to the hallux. This is a Type II of the deep plantar tendon configuration (Raikow 1985; Zinoviev 2008).

Comparison — Other members of the Ratitae have quite uniform muscle, which might have two tibial heads (Tinamiformes: Picasso 2010) or additional femoral head (Apterygiformes: Bedd-

ARD, 1899). In *Struthio,* it sends a branch to each of the two remaining foretoes.

***Mm. flexores perforantes et perforati digitorum 2 et 3 and mm. flexores perforati digitorum 2, 3 et 4* —** A cluster of muscles, mm. flexores perforantes et perforati digitorum 2 et 3 and mm. flexores perforati digitorum 2, 3 et 4, provide flexion for individual digital phalanges (Fig. 6B-D, F-H, J-L). As for the previous muscle, the reconstruction of their bellies is impossible for moa, as they mostly start from the common aponeuroses. However, all of them were present in moa. Their passage along the plantar surface of tarsometatarsus in *D. robustus* and some patterns of insertion on the toes are described by COUGHTREY (1874b). Tendons of flexors to the second toe passed through the separate aponeurotic sheath and possessed an individual cartilaginous semi-sesamoid. M. flexor perforatus digiti 2 inserted to the base of the first phalanx, being penetrated by m. flexor perforans et perforatus digiti 2 and by the corresponding branch of m. flexor digitorum longus. The details of their insertion remain unknown due to the absence of the rest of the toe in the mummified foot. However, two rugosities on the plantar surface of the second phalanx of the second toe in both species of moa indicate that m. flexor perforans et perforatus digiti 2 inserted there, being penetrated by the branch of long digital flexor. Tendons of flexors for toes three and four were held by a common aponeurotic sheath. The description, given by COUGHTREY (1874b), does not provide the necessary information to interpret details of branching and insertion of the muscles. However, the osseal material shows, that m. flexor perforatus digiti 3 inserted to the base of the first phalanx of the corresponding toe, being penetrated by other tendons. The same is true for m. flexor perforans et perforatus digiti 3, which penetrated the tendon inserted at the base of the second phalanx. Two pronounced rugose surfaces on the base of the first phalanx of the fourth toe show the insertion of the proximal branches of m. flexor perforatus digiti 4. The insertion of distal branches is variable in avian taxa and can not be reconstructed with confidence.

Comparison — The insertions of mm. flexores perforates et perforate digiti 2 et 3 and mm. perforati digiti 2 et 3 of moa are typical to the majority of birds including the Ratitae (except for Struthio which lacks the second toe). The branching pattern of the terminal tendon of m. flexor perforatus digiti 4 is variable in birds. The direct comparison will be possible only after further studies of mummified feet in moa.

***M. fibularis longus* —** Extensor (along with m. gastrocnemius) of intertarsal joint, m. fibularis longus is better developed in cursorial species. The beginning of this muscle in moa is detectable by the uneven surface on the cranial surface of the fibula (Figs 4B, C; 5F, G). Its points of origin from crista cnemialis lateralis and the fibula itself are difficult to define, as they coincide with the origins of several other muscles. Although the mummy of *D. robustus* did not preserve the insertion of the m. fibularis longus to the proximolateral edge of tibial cartilage, it must have been the point of insertion for the well developed m. fibularis longus as it is in all other cursorial birds (ZINOVIEV 2010). Besides the main insertion, the long fibular muscle has a second tendinous branch leading to the terminal tendon of m. flexor perforatus digiti 3. This muscle, in turn, has a connection to the terminal tendon of m. flexor perforans et perforatus digiti 3 by vinculum tendinum flexorum. This tendinous bridge transmits the power of the large m. fibularis longus to the base of the second phalanx of the third toe, thus preventing overextension during a propulsive push. This vinculum is excellently developed in cursorial birds and would be expected in moa, along with a corresponding branch of m. fibularis longus. In fact, this branch did leave a trace on the lateral surface of the tarsometatarsus as noted, but not interpreted, by OWEN (1874). The trace is a smooth, oblique depression that starts near the level of insertion of m. tibialis cranialis and ends at the middle of the tarsometatarsal shaft. Its passage is fairly clear in *D. robustus* (Fig. 5F, G) but extremely faint in *E. crassus*.

Comparison — The reconstructed details of m. fibularis longus morphology in moa correspond to those of other cursorial birds, including members of the Ratitae.

***M. fibularis brevis* —** The presence and degree of development of an inward rotator of the tarsometatarsus, m. fibularis brevis, is correlated with the degree of rotational freedom in intertarsal joint (Zinoviev 2000, 2011). In moa, strong collateral ligaments, poorly developed menisci, and the absence of lig. anticum indicate highly restricted rotational movement in the intertarsal joint (see below), to the point where I might expect the absence of m. fibularis brevis. In fact, I can detect neither traces of a retinaculum to hold the terminal tendon of this muscle near the distal end of the tibiotarsus (medial to the ligamentum transversum tibiotarsi) nor an insertion on the medial side of the proximal end of the tarsometatarsus. Coughtrey (1874b) did not report the terminal tendon of this muscle on an otherwise well-preserved lateral aspect of the proximal tarsometatarsus of *D. robustu*s and, consequently, the tuberosity, found by Kooyman (1991) on the lateral aspect of pons supratendineus, cannot be associated with a retinaculum m. fibularis brevis.

Comparison — In ratites, m. fibularis brevis is either altogether lost (Struthioniformes, Rheiformes, Casuariiformes) or extremely vestigial (Tinamiformes, Apterygiformes).

***Mm. gastrocnemii* —** Powerful extensors of intertarsal joint, mm. gastrocnemii are well-developed in cursorial birds (Figs 4A, B, 5B–D, F-H). Being the most superficial muscles of the shank, they originate from common aponeuroses shared with deeper muscles (except for the medial part, which originates from the medial surface of cranial cnemial crest and adjacent area of the shank of the tibiotarsus). Thus, their exact morphology can not be reconstructed from skeletal material. Well-developed origins of aponeuroses communes popliteus et collateralis show correspondingly well developed lateral and intermedial parts of m. gastrocnemius. The medial surface of crista cnemialis cranialis is large enough to harbor the origin of powerful medial part of the muscle. All three parts contributed to a common tendon of insertion, which ran superficially to the tibial cartilage, on the plantar surface of the tarsometatarsus, to form the tendinous sheath over the terminal tendons of the long digital flexors. This sheath was found by Coughtrey (1874b) in mummified foot of *D. robustus*. The insertion of it is marked by two wide rugosities running on both sides of the tarsometatarsus, from its proximal end almost to the base of the second and fourth trochleae. This feature is more pronounced in *D. robustus* and much fainter in *E. crassus.* The lateral side of the tendinous sheath is penetrated by the cranial branch of the terminal tendon of m. fibularis longus. The medial side of the sheath passes laterally to the insertion of the first metatarsal element.

Comparison — The composition, degree of development, and the insertion of mm. gastrocnemii in moa are typical for cursorial birds, including ratites.

Intertarsal joint

Avian intertarsal joint chiefly provides flexion-extension movements, being held in place by the capsule of the joint and by a number of ligaments (Figs 4, 5). Traces of strong collateral ligaments are well defined in moa. There were two lateral collateral ligaments. Lig. collaterale laterale intertarsi originated from a tuberosity on the level of the lateral attachment for lig. transversum tibiotarsi. It then crossed the intertarsal joint and attached to the tuberosity on the lateral side of the proximal tarsometatarsus but extended no further than the insertion of m. tibialis cranialis. Lig. collaterale laterale intertarsi accessorium originated from depressio epicondylaris lateralis and inserted on the previously mentioned tuberosity, in front of lig. collaterale laterale intertarsi. There were also two ligaments on the medial side of the intertarsal joint. Lig. collaterale mediale, which was far longer its lateral counterpart. It originated from a deeply imprinted tuberous area that starts on the same level as the beginning of the distinct sulcus extensorius tibiotarsi. Lig. collaterale mediale inserted on the tuberosity on the medial side of the proximal tarsometatarsus, extending slightly behind the level of the medial attachment of retinaculum extensorium tarsometatarsi. Lig. collaterale mediale intertarsi accessorium was much shorter and originated in the depressio epicondylaris medialis. It inserted on the lateral surface of the proximal tarsometatarsus in front of, and much proximally to the previous tendon. As the medial articular surface of tarsometatarsus is more congruent with the corresponding condyle of the tarsometatarsus, it was covered by only by a thin layer of articular cartilage, which

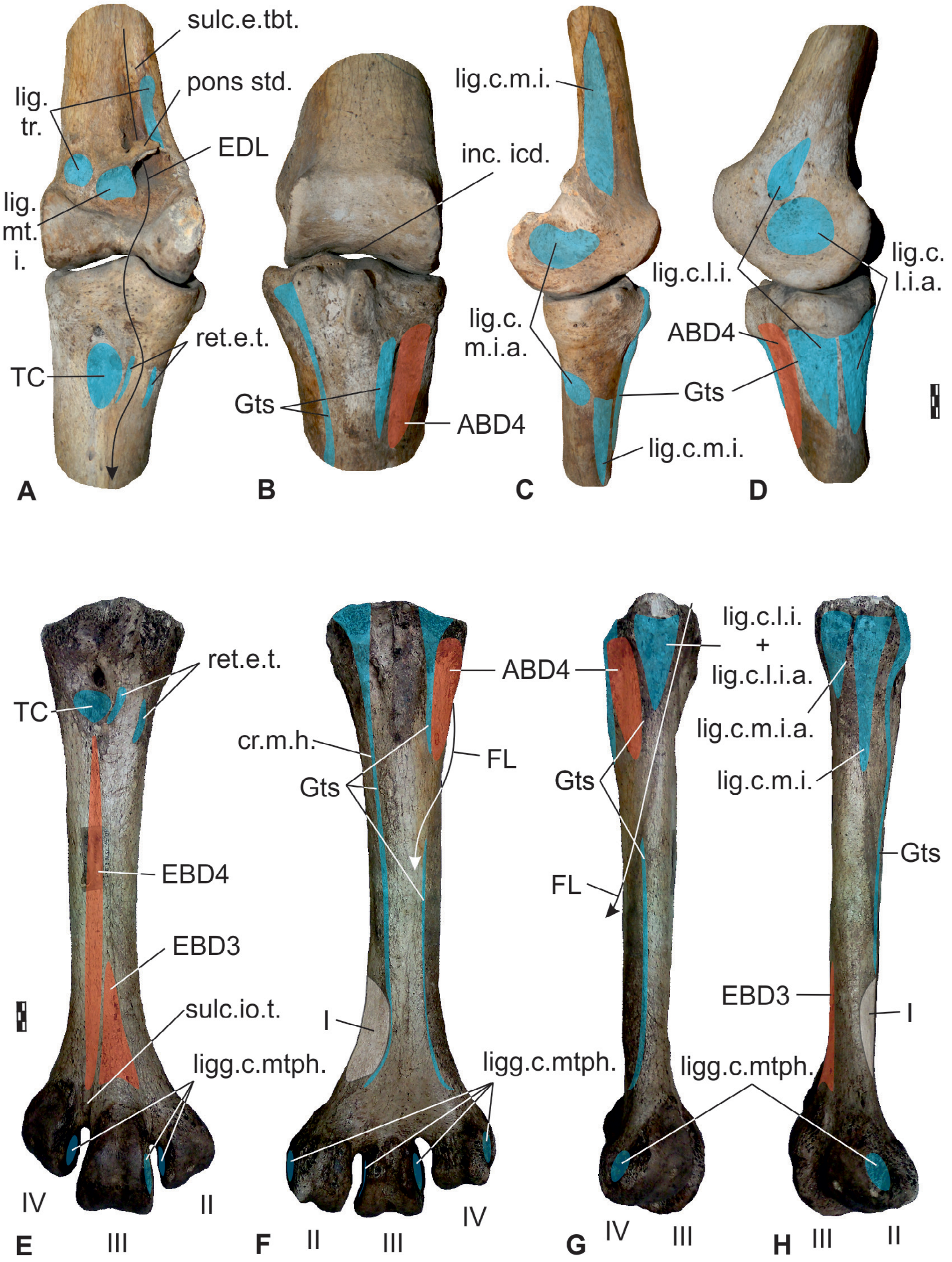

FIGURE 5. Right intertarsal joint of *Emeus crassus* (MB. Av. 1571), **A–D**, cranial, caudal, medial and lateral aspects; right tarsometatarsus of *Dinornis robustus* (MG. Av. 1570) **E–H**, dorsal, plantar, lateral and medial aspects, showing attachments of some muscles and ligaments. I-IV, metatarsal elements (I is missing).
Abbreviations: ABD4, m. abductor digiti 4; cr. m. h., crista medialis hypotarsi; EBD3, m. extensor brevis digiti 3; EBD4, m. extensor brevis digiti 4; EDL, m. extensor digitorum longus; FL, m. fibularis longus; Gts, m. gastrocnemius tendinous sheath; inc. icd., incisura intercondylaris; lig. c. l. i., lig. collaterale laterale intertarsi; lig. c. l. i. a., lig. collaterale laterale intertarsi accessorium; lig. c. m. i., lig. collaterale mediale intertarsi; lig. c. m. i. a., lig. collaterale mediale intertarsi accessorium; lig. tr., lig. transversum; ligg. c. mtph., ligamentai collateralia metatarsophalangealia; pons std., pons supratendineus; ret. e. t., retinaculum extensorium tarsometatarsi; sulc. e. tbt., sulcus extensorius tibiotarsi; sulc. io. t., sulcus interosseus tendineus; TC, m. tibialis cranialis.

formed a marginal rim and corresponds to the observations by Coughtrey (1874b). The lateral articular surface of the tarsometatarsus and its corresponding condyle showed less congruency. It was achieved by the presence of meniscus lateralis intertarsi, whose cornu caudale attached in the fossa on the caudal margin of area intercotylaris tarsometatarsi (Fig. 4G). The presence of meniscus lateralis intertarsi is also reported by Coughtrey (1874b). The cranial insertion of the lateral meniscus (its cornu craniale) was through lig. meniscotibiale intertarsi on the prominent tubercle, lateral to the distal opening of pons supratendineus tibiotarsi. There were no traces of lig. intercondylare (Fig. 4F, G), which is therefore presumed to be absent in moa. A large sesamoid bone is reportedly attached to the caudal rim of the lateral tarsometatarsal cotyla (Coughtrey 1874b). It was connected to the lateral meniscus by lig. meniscosesamoideum intertarsi, indirectly reported by the same author. The tibial cartilage, mentioned above, is also associated with the intertarsal joint.

Muscles of the foot

The foot possesses a group of intrinsic muscles (Figs 5, 6) associated with individual toes. These muscles in birds are usually small owing the well developed extrinsic (starting proximally to tarsometatarsus) synergists (Zinoviev 2011). Unfortunately, intrinsic muscles rarely leave prominent traces on the tarsometatarsus and thus many of them cannot be reconstructed in detail. M. extensor hallucis longus, m. adductor digiti 2, m. extensor digitorum brevis lateralis (Zinoviev 2003b) and m. lumbricalis were almost certainly present in moa, but did not leave traces on the bones of the material available for examination. Radiological studies of mummified moa feet might greatly improve our understanding of the muscles and ligaments of the foot of Dinornithiformes. Here I describe three muscles, which either left traces on bones or have been described by other authors.

***M. abductor digiti 2* —** M. abductor digiti 2 is the only intrinsic muscle of the foot, reported by Coughtrey (1874b) from his examination of a mummified specimen of *D. robustus*. He failed to identify it but described its characteristic tendinous insertion. The extent of which the muscle's belly expanded over the craniomedial surface of the tarsometatarsus remains unclear (Fig. 6A, C).

Comparison — The muscle is present and moderately developed in all members of the Ratitae, excluding *Struthio* (Zinoviev 2010).

***M. abductor digiti 4* —** The belly of m. abductor digiti 4 originated from a depressed and slightly rugose area just distal to the proximal end of the tarsometatarsus and lateral to crista lateralis hypotarsi (Kooyman 1991) (Figs 5B, D, F, G; 6I, J, L). The muscular belly rapidly tapered towards the terminal tendon, which ran along the lateral side of an aponeurotic sheath formed by the terminal tendon of mm. gastrocnemii. The insertion of m. abductor digiti 4 on the lateral surface of the proximal end of the basal phalanx of the toe is not well-marked. The area of fleshy origin is most clear in *D. robustus* and much fainter in *E. crassus.*

Comparison — The proximal displacement of the muscle's belly is quite typical for Ratitae and many other long-legged birds (Zinoviev 2010). There is often a small proximal head, but its presence in moa cannot be proved.

***M. extensor brevis digiti 4* —** The size of lateral intermetatarsal sulcus shows the shape and development of m. extensor brevis digiti 4 (Figs 5E, 6I, K). It was long and thin in *D. robustus*, starting from the distal level of tuberositas m.

FIGURE 6. Right foretoes of *Dinornis robustus* (MG. Av. 1570): **A–D,** second; **E–H**, third; **I–L**, fourth, dorsal, plantar, medial and lateral aspects, showing attachments of some muscles and ligaments. Attachments are not shown on the ungual phalanx of the fourth toe, since it is artificial.
Abbreviations: ABD2, m. abductor digiti 2; ABD4, m. abductor digiti 4; EBD3, m. extensor brevis digiti 3; EBD4, m. extensor brevis digiti 4; EDL, m. extensor digitorum longus; FDL, m. flexor digitorum longus; FPD2, m. flexor perforatus digiti 2; FPD3, m. perforatus digiti 3; FPD4, m. flexor perforatus digiti 4; FPP2, m. flexor perforans et perforatus digiti 2; FPP3, m. flexor perforans et perforatus digiti 3; ligg. c. iph. 2, ligamenta collateralia interphalangealia digiti 2; ligg. c. iph. 3, ligamenta collateralia interphalangealia digiti 3; ligg. c. iph. 4, ligamenta collateralia interphalangealia digiti 4.

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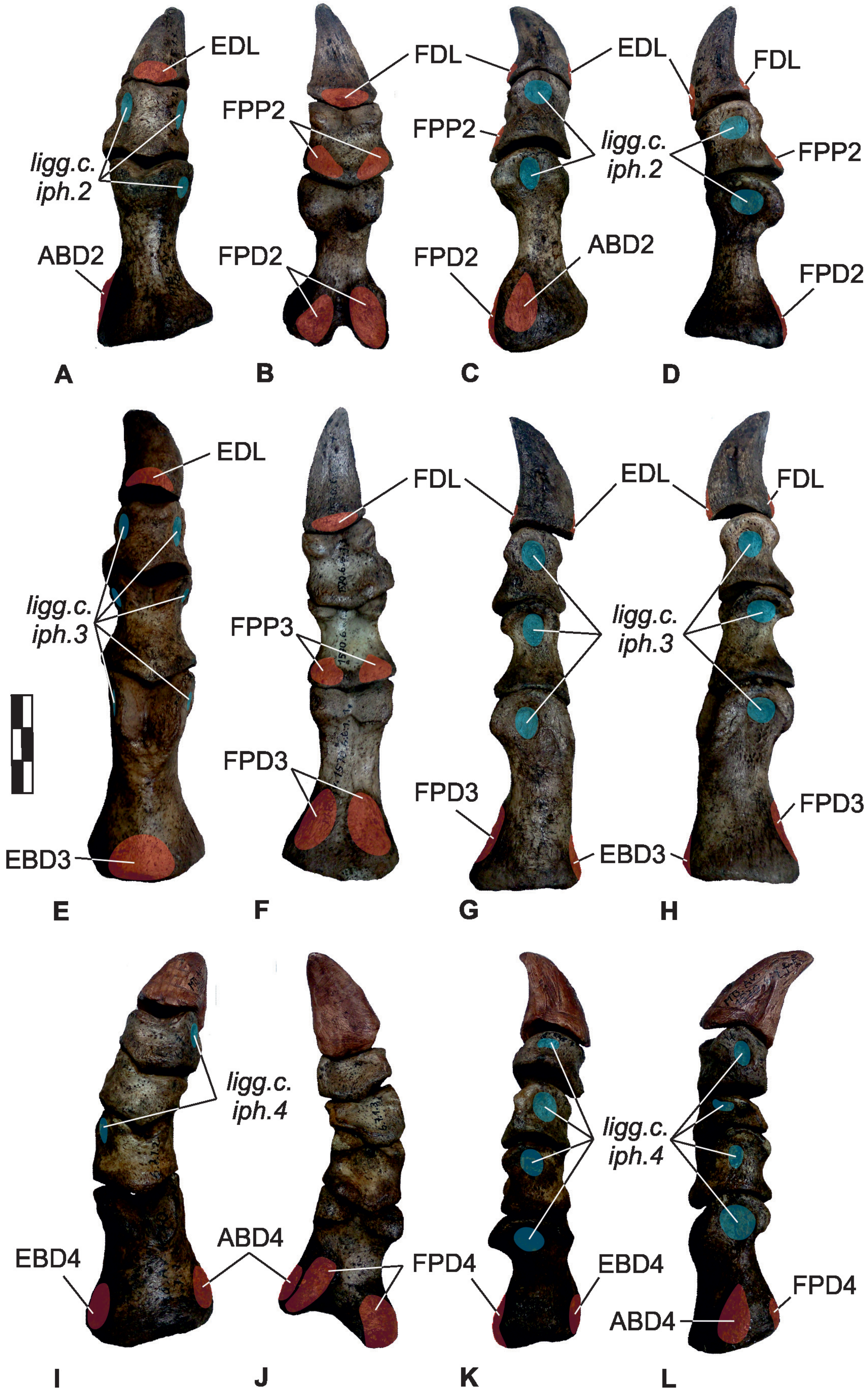
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tibialis cranialis. Its shape is not clear in *E. crassus* due to the absence of definite impressions on the bone. The terminal tendon of m. extensor brevis digiti 4 passed through sulcus interosseus tendineus between the third and fourth trochleae to insert on the dorsomedial side of the base of the first phalanx of the fourth toe.

Comparison — The length of the belly of m. extensor brevis digiti 4 was variable among moa (Kooyman 1991). In the majority of birds, the terminal tendon passes through canalis interosseus tendineus, but that structure is absent in moa and, reportedly in Struthioniformes and Apterygiformes. It is also absent in juvenile *Dromaius*, but present in the adult (Patterson 1983).

***M. extensor brevis digiti 3* —** M. extensor brevis digiti 3 is a short extensor of the third toe that had a fleshy origin from the distal half of the dorsal surface of the tarsometatarsus (Figs 5E, H; 6E, G, H). The belly lay on the elevated surface of the third metatarsal. The terminal tendon must have inserted on the dorsal surface of the base of the first phalanx of the third toe.

Comparison — The muscle is quite uniform in birds. In the majority of Ratitae its belly is restricted to the distal half of the tarsometatarsus.

Metatarsophalangeal and interphalangeal joints

Ligg. collateralia metatarsophalangealia as well as lig. collateralia interphalangeales of all the foretoes were well-developed and started in fossae on the lateral sides of the trochleae or on the sides of distal ends of phalanges, other than unguals (Figs 5, 6). They inserted laterally and medially to the bases of the corresponding distal phalanges. Coughtrey (1874b) found them all except lig. collaterale metatarsophalangeale mediale digiti 2. Nevertheless this ligament was present in moa and possessed a prominent fossa at its origin (Fig. 5E). Coughtrey also reported the presence of grooved cartilagines subarticulares metatarsophalangeales digitorum 2, 3 et 4 as well as cartilagines subarticulares interphalangeales digitorum secundi, tertii et quarti. He also observed vaginae fibrosae sheathing separately flexorial tendons to the third and fourth toes, and those to the second toe.

Discussion

D. robustus and *E. crassus* represent two branches of locomotory adaptation in moas. *Dinornis* is more agile whereas *Emeus* is less (Alexander 1983a, b; Kooyman 1985, 1991). Nevertheless, the number and the position of their hindlimb muscles are almost identical. The locomotory specializations appear to depend on the relative development of particular muscles associated with the length of the leg elements. The overall anatomy of the hind limbs in these species resembles that, inferred for other primitive birds (Hudson 1937; Zinoviev 2010). In particular, the hindlimb anatomy and syndesmology of moa resemble that of the Tinamiformes, whose ancestors are now accepted as being close to ancestral palaeognaths. They are also similar to geographically close Apterygiformes and Casuariiformes. Other member of Ratitae, such as Rheiformes and especially Struthioniformes show significant differences related to their own distinct locomotor adaptations.

There are, however, certain traits in hindlimb morphology that characterize the Dinornithiformes. First of all, the enormous development of m. iliofemoralis externus far surpasses the bulk of this muscle in other birds. It is truly unfortunate that information on this muscle in *Aepyornis* is missing. Generally reduced in most birds, this muscle abducts the femur, preventing passive adduction of this bone during the single support stance phase of locomotor cycle. As in other massive ratites with wide pelves, moa must have exerted the maximal power of femoral abductors (m. iliofemoralis externus, m. iliotibialis lateralis pars acetabularis) to keep the body balanced. M. iliotibialis in moa was also very powerful.

A caudal shift in the center of gravity, proposed for moa in comparison to other birds (Alexander 1983a) and especially for *Dinornis* in relation to other moa (Kooyman 1985, 1991), does not have anatomical support. Proceeding from the position of antitrochanter, the femur of the moa was carried in the same position as in other cursorial birds. Thus their center of gravity must have been aligned with the knee joints.

The proposed insertion of m. iliofemoralis internus is unusual and may represent another unique characteristic for moa. M. iliofemoralis internus appears to have inserted just distally to the femoral neck on the cranial surface of femoral shaft. Such a position implies a change in function from that of a weak, outward rotator of the femur. The significance of such a shift is unclear and needs to be reexamined in additional mummified remains. Of other pelvic muscles m. iliofemoralis had an unusually long attachment on the posterior surface of the femoral shaft. Outside of Dinornithiformes such a feature is seen only in *Apteryx* (McGowan 1979).

Femoral and tibiotarsal muscles are well-developed, which is expected in cursorial birds. Traces of their origin on the femur are more pronounced in *E. crassus*, which, however, may not be related to the degree of femoral muscle development. Muscles of the shank in moa were long-bellied, as in *Apteryx*. In cursorial birds, there is strong selection to lighten the distal components of the limb but there is no such pressure on graviportal species. Thus cnemial crests of moa were relatively small, since the bulk of the shank muscles were more evenly distributed along the length of tibiotarsus. Most of the shank muscles, including powerful mm. gastrocnemii, originated on the common aponeuroses whose configuration appears to have been similar to that in the majority of birds. Movements in the intertarsal joint, which lacked lig. anticum and its stabilizer, m. fibularis brevis, were restricted to flexion and extension, as in many specialized cursorial birds, including members of the Ratitae. The relative length of the tarsometatarsus is greater in *Dinornis*, which corresponds to its greater agility. Although the majority of the intrinsic muscles must have been preserved in moa, their relative development is difficult to assess due to the faintness of traces that they left on the tarsometatarsus. Abductors of the second and fourth toes and extensors of the third and fourth toes were slender and long, corresponding to the length of the tarsometatarsus. Terminal tendons of the long digital flexors to the second toe were, at least in *D. robustus*, separated from those to the other foretoes. This feature might indicate, that the second toe might have played a major role in the scratching and digging reported as a foraging activity of moa attempting to obtain fern rhizomes (Owen 1849b, 1883b; Kirk 1875; White 1925; Burrows *et al.* 1981).

Conclusions

The muscular anatomy of hind limbs in moa was modified according to their weight and their degree of graviportal locomotion. The retention of the wide pelvis makes their pelvic muscles look less modified than comparable muscles in their narrow hipped relatives in the Apterygiformes, Casuariiformes, and Struthioniformes. Resembling in the overall hindlimb anatomy geographically close species of *Apteryx* and *Dromaius*, moas were probably adapted to scratching and digging.

Hopefully, in the future, I will be able to test these anatomical hypotheses on more abundant material.

Acknowledgements

I am grateful to Oliver Hampe (Museum für Naturkunde, Humboldt Universität zu Berlin) for access to specimens. I thank Alan Tennyson (Museum of New Zealand Te Papa Tongarewa), Trevor Worthy (Department of Biological, Earth and Environmental Sciences of the University of New South Wales, Australia) and especially Paul Scofield (Canterbury Museum in Christchurch, New Zealand), who kindly helped me in the identification of moa remains and made useful suggestions on the content of manuscript. I would like to thank Peter Ballman (Cologne, Germany) and one anonymous reviewer for their thorough review and comments, many of which significantly improved the paper. Gary Kaiser (Royal BC Museum, Canada) very kindly assisted with the manuscript's language.

The research was supported by the DAAD program "Forschungsaufenthalte für Hochschullehrer und Wissenschaftler" (2010) and joint program of DAAD and Ministry of Education and Science of Russian Federation "Michail-Lomonosov-Forschungsstipendien und -aufenthalte" (2011).

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Paleornithological Research 2013

Proceed. 8th Internat. Meeting Society of
Avian Paleontology and Evolution

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Ontogenetic change of morphology and surface texture of long bones in the Gray Heron (*Ardea cinerea*, Ardeidae)

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Abstract — Although the importance of assessing ontogenetic age or developmental stage of fossil materials is widely recognized, information on avian postnatal skeletal ontogeny, which forms a basis for ageing criteria for bird fossils, is seriously lacking. One potentially useful ontogenetic ageing method in avian paleontology is textural ageing, in which surface textures of long bones are examined to assess developmental stage. To date, ontogenetic change of surface textures in long bones has been intensively described in only one species, the Canada Goose (*Branta canadensis*). In this study, through original preparation and examination of an ontogenetic series of specimens, which consists of 13 chicks (including one fledgling), two juveniles (birds under one-year-old) and two adults, postnatal ontogenetic changes of macroscopic morphology and surface texture of six major long bones (humerus, ulna, carpometacarpus, femur, tibiotarsus and tarsometatarsus) of the Gray Heron (*Ardea cinerea*, Ardeidae) are described and illustrated. Most long bones continue to grow in length until reaching their adult size range around the time of fledging. Epiphyses are generally not ossified before fledging; in both ends of femur and proximal end of tibiotarsus, distinct ossification centers can be observed. Generally, long bones of chicks are characterized by rough surface textures, including striated structures near epiphyses and fibrous/porous surface with frequent penetrating pits in the midshaft. Long bones of juveniles are characterized by faint grooves and/or dimples, but rough striated structure may remain in the proximal regions of tibiotarsus and tarsometatarsus. In adults smooth surface pattern dominates. Inter-elemental variation in surface texture in one species is likely to represent taxon-specific patterns of relative timings of maturity among long bones, which would be related to various aspects of skeletal ontogeny in birds. At this time, textural ageing on birds with interrupted growth might be somewhat problematic because of a lack of sufficient data.

Key words: bone growth, textural ageing, epiphysis, Ardeidae

Introduction

Assessing ontogenetic age or developmental stage (ontogenetic ageing) of fossil materials is an essential and crucial step in most paleontological investigations, including taxonomical, paleoecological, faunistic, and evolutionary studies. Incorrect ontogenetic ageing will easily lead to taxonomical confusion or other misled conclusions in such studies. In avian paleontology, except for very rare cases, fossil remains are almost always skeletal elements, which are often isolated and damaged. Among them, long bones are of particular importance for their relative abundance as fossil remains and ease of identification. Reliable ontogenetic ageing criteria for (isolated) avian long bones are desired. As a basis for such criteria, precise and detailed understanding of the ontogeny of avian long bones is necessary.

Although embryological development of the avian skeleton has been intensively investigated (*e.g.*, Fujioka 1955; Rogulska 1962; Starck 1993), there have been relatively few studies investigating postnatal ontogeny. Examples of previous studies which investigated postnatal ontogeny of avian skeletons include those focusing on metrical aspects (*e.g.*, Marples 1930; Klíma 1965; Cane 1993; Hayward *et al.* 2009; Picasso 2012), histological aspects (*e.g.*, Starck & Chinsamy 2002; de Margerie *et al.* 2004) and mechanical/functional aspects (*e.g.*, Bjordal 1987; Carrier & Leon 1990; Dial & Carrier 2012). However, there have been very few studies focusing on macroscopic morphological aspects of the avian skeleton in postnatal ontogeny, which would be useful for establishing ontogenetic ageing criteria for bird fossils. Previous studies that gave partial descriptions or illustrations on macroscopic morphology in avian postnatal skeletal ontogeny include; Huggins *et al.* (1942), who described and illustrated stained skeletons of the growing House Wren (*Troglodytes aedon aedon*); Beale (1985, 1991), who investigated ontogeny of long bones of a growing kiwi (*Apteryx australis mantelli*) through ten years of radiological study; and Picasso (2012), who studied ontogenetic allometry in the hindlimb skeleton of the Greater Rhea (*Rhea americana*) and figured hindlimb long bones at various ages. To form a basis for ontogenetic ageing criteria for bird fossils and for other morphological studies, it is desirable to accumulate data on skeletal ontogeny of various avian taxa with comprehensive descriptions and illustrations.

As a practice in many previous avian paleontological and zooarchaeological studies, “incompletely ossified” skeletal materials were considered to represent immature or juvenile individuals, often without firm justification (*e.g.*, Howard 1929). Degrees of ossification in skeletal specimens of immature individuals have been sporadically described or illustrated by some authors for comparative purpose (Callison & Quimby 1984; Sanz *et al.* 1997; Serjeantson 2002). Recently, Tumarkin-Deratzian *et al.* (2006) gave a comprehensive review on this topic and evaluated surface texture of the humerus, femur and tibiotarsus as an ontogenetic indicator in the Canada Goose (*Branta canadensis*). They examined over 80 skeletal specimens of the species, described the relationship between surface textures of long bones and developmental stages, as well as their underlying histological features, and formed a basis for a practical ontogenetic ageing criterion. Given the fact that birds have diverse ontogenetic strategies (*e.g.*, precocial-altricial spectrum; Starck & Ricklefs 1998), further studies are needed to test the presence or nature of taxon-specific variation.

In this study, to form a basis for ontogenetic ageing criteria for bird fossils, a postnatal ontogenetic series of skeletal specimens of a common Recent species, the Gray Heron (*Ardea cinerea* Linnaeus, 1758, Family Ardeidae), was prepared and examined. Ontogenetic changes of macroscopic morphology and surface textures of six major long bones (humerus, ulna, carpometacarpus, femur, tibiotarsus and tarsometatarsus) are described and illustrated. Some additional features of morphological interests are also described, such as epiphysial ossification centers in femur and tibiotarsus.

Materials and Methods

Sampled species. In this study, an ontogenetic series of the Gray Heron (*Ardea cinerea*) was collected and prepared in order to observe ontogenetic changes of morphology and surface texture of long bones. *Ardea cinerea* is a large heron species whose adults reach 90–98 cm in length and 1020–2073 g in weight (Kushlan & Hancock 2005). Some subspecies can be recognized based on geographical variation in plumage. All individuals studied were collected in Japan, thus are from the East Asian subspecies *A. c. jouyi* Clark, 1907 (Yamashina 1941; Kushlan & Hancock 2005). Sexual variation in skeletal dimensions is generally significant but slight (about 2–4 %; Boev 1987). In the breeding season, they build colonies in the forest canopy and drop chick carcasses, facilitating collection of large samples of chicks. In Japan, eggs are laid from April to early May, and chicks hatch after 25–28 days of incubation (Yamashina 1941). Chicks are (semi-)altricial: hatchlings are fed by parents, covered by down, have open eyes and can stand within a day (Starck & Ricklefs 1998; Kushlan & Hancock 2005). They can clamber away from nests at about six weeks old, and fledge and become capable of flight at seven to eight weeks old (Yamashina 1941). Individual developmental stages can be determined by distinctive age-related plumage (Yamashina 1941; Milstein *et al.* 1970). It is commonly thought that they breed after the second winter, but breeding by yearlings is not exceptional (Milstein *et al.* 1970; Kushlan & Hancock 2005). Thus, sexual maturity could be attained around (or perhaps before) one-year-old in this species.

In this study, three postnatal developmental stages are recognized: chick, juvenile, and adult. Note that definitions of these terms might be different from both ornithological and paleontological conventions (see below). Each individual is classified into one of the three stages based on its plumage. Exact absolute age was not available for any of the individuals, so they are ordered in a presumed ontogenetic sequence. In chick stage, individuals are ordered by increasing external measurements. Juveniles are ordered by their collection date (from earlier to later). Ordering in adults is done arbitrarily.

Description of sample series. The study series consists of 13 chicks, two juveniles and two adults. Each individual is labeled with a prefix ("C" for chicks, "J" for juveniles and "A" for adults), and a number to represent its place in the ontogenetic sequence defined above (*i.e.*, C1, C2,..., C13, J14, J15, A16 and A17). All individuals were collected in and around Kyoto, Japan, so the geographical variation within the series is considered to be minimal. Sexes of most individuals could not be determined, so both sexes were pooled to form a single series. Definitions and descriptions of three developmental stages are given below. Date of death and external measurements of each individual are summarized in Tab. 1. The study series is stored at the Department of Geology and Mineralogy, Kyoto University, Kyoto, Japan. See Tab. 1 for repository numbers of the specimens.

Chick — This stage refers to birds after hatching and before leaving the colony. Birds of this stage are typically characterized by functionally immature plumage, including sheathed flight feathers. All chick individuals included in the study series were found dead at a breeding colony in Kyoto, Japan. A total of 23 chicks were

TABLE 1. List of the individuals included in the study series. Linear measurements (in mm), body weight (in grams), and collection date (year. month. day) are given. Body length is measured from the bill tip to the tip of the tail with the back on a flat plane and the neck extended. Asterisks indicate underestimated values due to damage on carcasses.

Individual code	Repository number	Collection date	Body length	Body weight	Culmen length	Tarsus length
C1	RAJ-1	2009.06.07	401	488	51	68
C2	RAJ-2	2010.04.21	417*	470*	50	77
C3	RAJ-3	2009.05.19	456*	520*	61	78
C4	RAJ-4	2010.06.02	462*	820*	60	90
C5	RAJ-5	2011.06.13	474*	700*	61	91
C6	RAJ-6	2010.04.29	495*	840*	62	93
C7	RAJ-7	2009.05.27	484*	682*	65	91
C8	RAJ-8	2009.05.22	530*	782*	69	99
C9	RAJ-9	2011.05.31	530*	940*	70	102
C10	RAJ-10	2009.05.24	564*	835*	74	109
C11	RAJ-11	2009.05.24	576*	790*	80	112
C12	RAJ-12	2009.05.19	552*	940*	80	132
C13	RAJ-13	2009.06.07	886	1362	100	146
J14	RA-1002	1995.06.18	980	1220	118	171
J15	RAJ-27	1999.08.02	960	1180	115	162
A16	RAJ-28	2012.03.15	910*	1600*	127	168
A17	RA-1001	(not recorded)	940	1050*	112	145

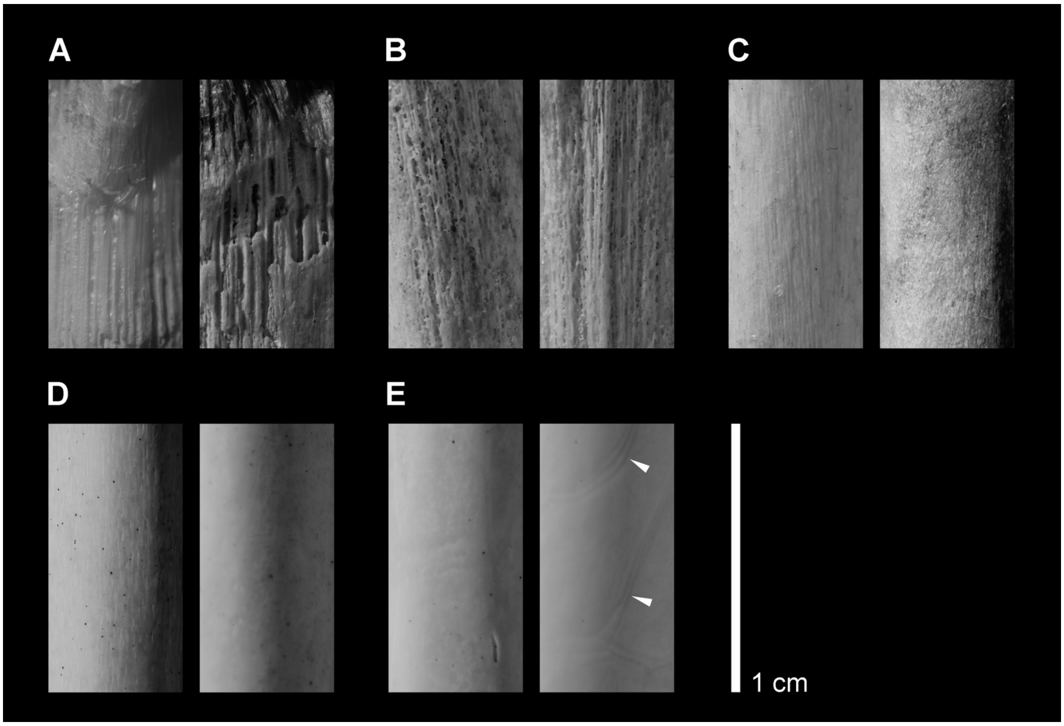


FIGURE 1. Examples of surface textural patterns. **A**) pattern A: left, proximal tibiotarsus in C5, cranial view, showing striated pattern running longitudinally with few transverse struts; right, damaged surface of proximal tibiotarsus in C8, medial view, showing low bone density underlying this pattern. **B**) pattern B: left, proximal humerus in C11, ventral view, showing striated structure with frequent transverse struts; right, proximal tarsometatarsus in C11, cranial view. **C**) pattern C: left, midshaft of humerus in C11, cranial view, showing fibrous structure with shallow grooves; right, midshaft of femur in C11, caudal view, showing densely distributed dimples. **D**) pattern D: left, midshaft of humerus in J14, caudal view, surface showing short longitudinal grooves and dimples; right, midshaft of ulna in J14, dorsal view, showing shallowly dimpled surface. **E**) pattern E: midshaft of humerus in A17, ventral view, with a nutrient foramen on right bottom; right, distal tibiotarsus in A17, caudal view, with vascular grooves (white arrowheads). Upper side of each photograph is proximal side of the long bone.

obtained, and 13 of them had a nearly complete set of long bones and thus were included in the study series. The largest chick studied (C13) had both an almost complete plumage including flight feathers and remains of natal down at the tip of the crest. Thus it is considered to represent the fledgling period, or seven to eight weeks old (Yamashina 1941; Milstein *et al.* 1970). All others (C1–C12) had not yet fledged, so they are considered to be younger than C13.

Juvenile — This stage includes birds having left the colony and are under one year old. Juveniles are readily distinguishable from adults by their distinct plumage, including gray forehead and neck and less developed crown. Yearlings, or one-year-old birds, have a similar plumage, but they can be distinguished by several distinctive features, including the color pattern of the bill (Milstein *et al.* 1970). Two juveniles were included in the study series, both of which were collected around Kyoto in their first summer (thus are considered to be about two to four months old).

Adult — In this study, this stage refers to all birds after attaining the second year external coloration (*i.e.*, one-year-old and older). Although further distinction (*e.g.* yearlings, subadults and adults) within this stage is possible based on plumage, this was not attempted because the sample size was too small to allow meaningful comparison. Two adults, collected around Kyoto, were included in the study series.

Preparation of specimens. All collected individuals were temporarily stored frozen until preparation. After thawing, left long bones (humerus, ulna, carpometacarpus, femur, tibiotarsus [+ fibula] and tarsometatarsus) were isolated from the carcasses by dissection, and the surrounding soft tissue was carefully removed from the bones. Isolated bones were soaked in dilute solution of hydrogen peroxide (ca. 2 %) until they were bleached (usually after 12–24 hours). After bleaching, they were further cleaned manually and then dried. This procedure deforms cartilages on epiphysial area of long bones from their original shape, but it makes them translucent to a certain degree, which allows ossification centers to be observed. The rest of the body was refrozen for future studies.

Classification of surface textures. Surface textures of long bones, which have been suggested to be an useful ontogenetic indicator in the Canada Goose (*Branta canadensis*) by Tumarkin-Deratzian *et al.* (2006), are described and figured in the study series. They show considerable variation among individuals and elements, and even within a single element (see below for detail). For comparisons among individuals and elements, various surface textures are classified into the five patterns described below. These patterns are applied to surface texture in certain area on a bone, rather than to the texture of an entire bone, unlike the "texture types" in Tumarkin-Deratzian *et al.* (2006). Examples of surface patterns are shown in Fig. 1.

Variation of textural patterns in a single element is most prominent in its longitudinal direction; longitudinally, one bone show up to four texture patterns at one transverse position of its shaft, whereas transversely (or circumferentially), one bone show no more than two patterns at one longitudinal position of its shaft. Thus one-dimensional longitudinal distribution of textural patterns in a long bone can be used as a representation of overall distribution of patterns in that bone. In practice, the dominant textural pattern at one longitudinal position is regarded as the representing pattern at that position; the dominant pattern here refers to that the pattern is more widely distributed transversely than any other patterns, without concerning articular surfaces and apparent muscular/ligamental attachment sites. Longitudinal distribution of one pattern is defined as the length of longitudinal section where the pattern is dominant, and is measured between the two points at which the pattern occupies 50 % of transverse circumference of the shaft (measured with a tape measure rolled on the shaft). This simplified one-dimensional distribution is used for graphical presentation and comparison among elements and individuals.

Pattern A (Fig. 1A) — This pattern is defined as a striated structure with smooth surface and few transverse struts. Typically, it shows loose structure formed by relatively thick longitudinal ridges and shallow furrows without transverse struts. This pattern is always accompanied by epiphysial cartilages on one side. When seen from the epiphysis, it shows a rather porous appearance.

Pattern B (Fig. 1B) — This pattern is defined as a striated structure with rough surface and frequent transverse struts. This pattern shows the roughest appearance among the five, and is composed of thin ridges, or trabeculae, deep grooves running longitudinally and with frequent transverse struts.

Pattern C (Fig. 1C) — This pattern is defined by the absence of structures characterizing the above patterns, and the frequent presence of shallow longitudinal grooves and/or dimples, which occasionally form penetrating pits on the bone wall. When present, grooves often reach five millimeters or more in length. This pattern gives a fibrous/porous and non-glossy appearance.

Pattern D (Fig. 1D) — This pattern is defined by the absence of apparent striated patterns and penetrating pits, and the presence of faint longitudinal grooves and/or dimples. Typically, grooves and dimples are less densely distributed, and length of grooves are smaller (several millimeters at maximum) than in pattern C. This pattern gives an overall glossy appearance, but grooves and dimples can easily be observed with a hand lens.

Pattern E (Fig. 1E) — This pattern is defined by the absence of striated structure, penetrating pits, and grooves/dimples (except at the attachment sites of muscles, ligaments or articular capsules). Occasional traces of vascular canals can be observed on this pattern. This pattern gives an overall glossy and smooth appearance.

Terminology and measurements. Osteological terminology follows that of Baumel & Witmer (1993). The term "epiphysis" as used here

FIGURE 2. Ontogenetic morphological change of the humerus in *Ardea cinerea*. From left to right, C1, C2, C5, C8, C9, C11, C12, C13, J14, J15, A16 and A17.

refers to either end of a long bone, not specifically to independent ossification centers; the latter is called "epiphysial ossification center" to avoid confusion. But the term "diaphysis" of a long bone is used to refer either to the primary ossification center of the shaft, or to the shaft in general. Dimensions of long bones were measured after drying, thus they might underestimate actual values in incompletely ossified bones; such underestimated values are marked in the table of measurements (Tab. 2). The dimension "ossified length" was measured in incompletely ossified bones and refers to the approximate length of ossified diaphysis and fused epiphysial ossification centers, if applicable. In wing bones (humerus, ulna, and carpometacarpus), "width" refers to dorsoventral width and "depth" refers to craniocaudal depth; whereas in leg bones (femur, tibiotarsus, and tarsometatarsus), "width" refers to mediolateral width and "depth" refers to craniocaudal depth. In humeri, greatest and smallest diameters of the shaft at the midpoint are presented, which are slightly diagonal to the width and depth, respectively, of the shaft. In tibiotarsi, length of the bone is measured from the proximal articular surface, rather than from the cnemial crest, to the distal condyles. Measurements on skeletal elements were performed with a digital caliper (Mitutoyo Corp., Japan; precision = ± 0.02 mm) to the nearest tenth millimeter.

Description of morphology

Overall morphology of long bones in *Ardea cinerea* show considerable ontogenetic change from chick through juvenile to adult stage. Detailed morphological description, with emphasis on ontogenetic variable characters, are given below. Long bones of selected individuals are illustrated in Figs 2–6. Details of skeletal features described are illustrated in Figs 7 and 8. Selected osteological measurements are given in Tab. 2.

Humerus (Figs 2, 7A, 7B). *Chick* — Overall shape of the bone is relatively uniform longitudinally, with less developed osteological features on both ends. Caput humeri, Tuberculum ventrale, Incisura capitis, Tuberculum dorsale, and Sulcus transversus are all cartilaginous in C1–C12. In C13, they are all present, but Caput humeri is less developed than in juveniles and adults, with porous surface and flat proximal margin. Impressio coracobrachialis and Linea m. latissimi dorsi are observable only in C13. Crista deltopectoralis is almost absent in C1–C7, present as a blunt projection with slightly convex dorsal surface in C8–C12, and developed with concave dorsal sur-

FIGURE 3. Ontogenetic morphological change of the ulna in *Ardea cinerea*. From left to right, C1, C2, C5, C8, C9, C11, C12, C13, J14, J15, A16 and A17.

face in C13. Foramen pneumaticum (pf in Fig. 7A) is open in the cartilaginous proximal end in C1–C12, and the surrounding area is ossified in C13; its distal margin is always extending distally to form a prominent fossa on the ossified area, which is covered by periosteum and occasional thin bone wall (Fig. 7A). Foramina nutrientia are present on Margo ventralis in the midshaft region, and single in C1–C4, C7, C8, C11, and C13, but double in C5, C6, C9, C10, and C12; they are almost always with large openings (about 3.5 × 0.7 mm, with long axis parallel to the shaft; Fig. 7B), and one of the double foramina is occasionally covered by thin bone wall. Condyli dorsalis et ventralis are cartilaginous in C1–C12, ossified but with porous surface in C13. Epicondyli dorsalis et ventralis are cartilaginous in C1–C12, ossified in C13. Proximal margin of Fossa m. brachialis is observable on ossified area, but its distal margin is indistinct.

Juvenile — Caput humeri is developed proximocaudally, rounded, and surrounded by numerous foramina on its margin (Fig. 7A). Tuberculum ventrale, Incisura capitis, Tuberculum dorsale, Crista deltopectoralis, and Linea m. latissimi dorsi are developed as in adults. Foramen pneumaticum (pf in Fig. 7A) is long proximodistally; its distal part is covered by periosteum (Fig. 7A) and serves as attachment for M. humerotriceps. Foramen nutriens is single in all cases, and opens on Margo ventralis at around the midpoint of the shaft with an apparently larger opening than in adults (about 4.0 × 0.4 mm, with long axis parallel to the shaft; Fig. 7B). Condyli dorsalis et ventralis are developed as in adult, but with numerous foramina on their margins. Epicondyli dorsalis et ventralis, and Fossa m. brachialis are developed as in adults.

Adult — Caput humeri is developed proximocaudally and rounded, with few foramina on its margin. Tuberculum ventrale, Incisura capitis, Tuberculum dorsale are all well developed. Crista deltopectoralis is well developed craniodorsally with concave dorsal surface. Linea m. latissimi dorsi is prominent. Foramen pneumaticum (pf in Fig. 7A) is just slightly longer longitudinally than dorsoventrally; its distal margin extending no more distally than the base of Crus dorsale fossae. Foramen nutriens is single in all cases, and opens on Margo ventralis at around the midpoint of the shaft, with a minute opening (about 2.0 × 0.3 mm; Fig. 7B). Condyli dorsalis

TABLE 2. Osteological measurements of the study series (in mm). Daggers indicate those including dried cartilaginous area (and thus underestimated values). Asterisks indicates underestimated values because of damage to bones. See Materials and Methods for notes on measurements.

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	J14	J15	A16	A17
Humerus																	
length	†69.6	†84.0	†91.3	†95.9	†98.0	†110.1	†102.7	†127.3	†125.7	†130.0	†139.6	†150.7	164.8	173.3	176.9	178.3	162.7
ossified length	61.3	76.9	82.7	85.9	89.5	100.6	93.7	115.8	120.1	121.9	129.4	141.0	—	—	—	—	—
proximal width	†9.5	†13.2	†12.7	†16.9	†15.9	†15.5	†13.5	†15.8	†17.1	†16.9	†18.7	†18.7	22.8	25.7	24.9	25.2	24.6
greatest diameter at midpoint	4.0	5.1	5.0	5.6	6.0	6.6	5.9	7.0	7.5	7.2	7.5	8.2	8.6	9.9	9.9	10.5	10.1
smallest diameter at midpoint	3.7	4.4	4.5	5.4	5.3	5.6	5.1	6.4	7.1	6.5	7.0	7.2	7.7	8.8	8.7	8.9	8.5
distal width	†9.3	†10.6	†13.3	†14.4	†13.6	†14.0	†13.1	†15.1	†15.9	†15.6	†16.9	†18.5	20.6	22.5	22.4	23.4	21.8
Ulna																	
length	†68.6	†84.4	†88.9	†97.8	†98.7	†116.5	†103.6	†132.6	†153.7	†137.4	†154.5	†162.8	194.0	209.6	214.8	208.8	194.3
ossified length	60.0	71.6	78.0	82.9	89.8	105.8	91.8	118.5	121.7	124.8	145.3	155.0	—	—	—	—	—
proximal width	†6.9	†9.1	†9.4	†10.8	†11.0	†11.5	†8.4	†11.3	†10.1	†10.3	†10.4	†13.2	14.8	16.0	15.7	15.8	15.4
shaft width at midpoint	3.1	3.4	3.2	4.0	4.2	4.0	4.1	5.1	5.4	4.7	5.4	5.8	6.6	7.4	7.5	7.8	7.5
shaft depth at midpoint	2.5	3.3	2.6	3.2	3.1	3.2	3.1	3.9	4.1	4.0	4.7	4.6	5.7	6.0	6.2	6.3	6.1
distal width	†4.3	†5.3	†4.6	†6.2	†6.7	†7.4	†5.9	†6.7	†8.1	†6.1	†7.4	†8.2	10.3	10.1	11.7	10.5	10.7
Carpometacarpus																	
length	†35.1	†43.6	†45.2	†48.2	†50.4	†58.7	†52.9	†65.3	†67.1	†67.4	†75.3	†80.2	87.8	95.0	97.5	93.7	85.9
ossified length	28.8	35.7	39.0	40.4	44.9	50.8	43.9	56.6	59.0	60.0	69.1	71.2	—	—	—	—	—
width of major metacarpus	2.7	2.7	2.7	3.1	3.2	3.2	3.3	3.5	3.8	3.5	4.0	4.2	4.6	5.2	5.6	5.7	5.1

TABLE 2. (continued)

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	J14	J15	A16	A17
Femur																	
length	†62.0	†68.9	†73.2	†75.4	†75.1	†78.1	†75.2	†82.2	†84.3	†83.2	†79.8	—*	85.6	92.8	94.3	93.5	84.0
ossified length	55.1	61.4	65.1	66.4	66.9	71.0	67.1	75.4	76.2	76.6	74.5	—*	—	—	—	—	—
proximal width	†8.9	†10.4	†12.4	†11.2	†11.6	†11.6	†10.9	†11.8	†11.7	†12.0	†12.8	—*	14.4	15.4	15.6	15.5	14.5
shaft width at midpoint	4.6	4.9	5.4	6.0	6.0	5.7	5.5	5.6	6.4	5.9	6.2	—*	5.8	7.5	6.7	6.8	7.3
shaft depth at midpoint	4.8	5.0	5.0	6.0	5.9	5.3	5.5	5.7	6.6	6.2	6.1	—*	6.2	7.0	6.9	6.9	6.5
distal width	†10.3	†11.2	†12.5	†12.2	†12.6	†12.3	†12.0	†12.1	†13.9	†13.5	†14.0	—*	14.4	15.5	15.5	15.8	14.0
Tibiotarsus																	
length	†83.6	†91.8	†101.9	†109.3	†105.7	†116.9	†110.7	†127.2	†131.0	†132.1	†138.8	†150.8	196.4	224.2	221.1	216.3	202.1
ossified length	73.5	80.8	88.9	92.7	93.9	103.8	98.9	113.1	116.2	116.9	127.6	143.1*	—	—	—	—	—
proximal width	†6.8	†10.1	†9.1	†9.8	†9.9	†10.9	†8.6	†10.2	†11.1	†11.0	†11.4	—*	12.2	13.4	12.9	13.6	12.7
width below proximal end	6.7	7.8	8.2	9.5	9.4	10.0	8.7	10.0	10.7	10.7	12.0	11.8	9.1	7.8	7.7	8.1	8.2
depth below proximal end	10.3	13.2	13.0	14.3	14.3	15.1	12.9	14.4	16.2	15.8	15.2	15.9	10.7	9.6	10.0	11.9	9.5
narrowest shaft width	4.1	4.1	4.3	4.9	4.9	4.4	4.7	4.7	5.1	4.8	5.8	5.9	5.1	6.0	6.0	5.9	5.8
distal width	9.7	12.2	11.9	12.8	12.6	12.9	12.4	12.5	13.0	12.0	12.0	12.5	12.2	12.8	13.3	13.6	12.1
Tarsometatarsus																	
length	†62.7	†68.4	†77.3	†85.5	†82.6	†88.0	†89.9	†100.9	†105.4	†102.9	†111.9	†131.7	144.7	169.6	161.3	172.9	145.6
ossified length	51.6	56.8	65.0	73.1	70.8	75.9	78.4	89.1	90.1	93.9	101.1	119.9	—	—	—	—	—
proximal width	10.2	12.5	12.7	14.4	14.5	15.0	14.1	14.9	15.5	15.5	16.1	16.8	13.8	14.7	14.9	14.8	13.3
shaft width below hypotarsus	9.1	11.3	11.7	13.2	12.3	13.3	12.3	13.6	14.2	13.9	14.8	15.6	9.2	9.6	8.2	7.2	6.6
narrowest shaft width	5.0	5.3	4.9	5.5	5.5	5.3	5.3	5.0	5.4	5.5	5.4	5.6	5.0	5.4	5.3	5.6	5.3
distal width	11.0	11.1	11.4	12.0	12.3	12.1	12.5	12.8	13.1	13.1	13.6	14.0	13.2	13.9	14.8	14.3	13.5

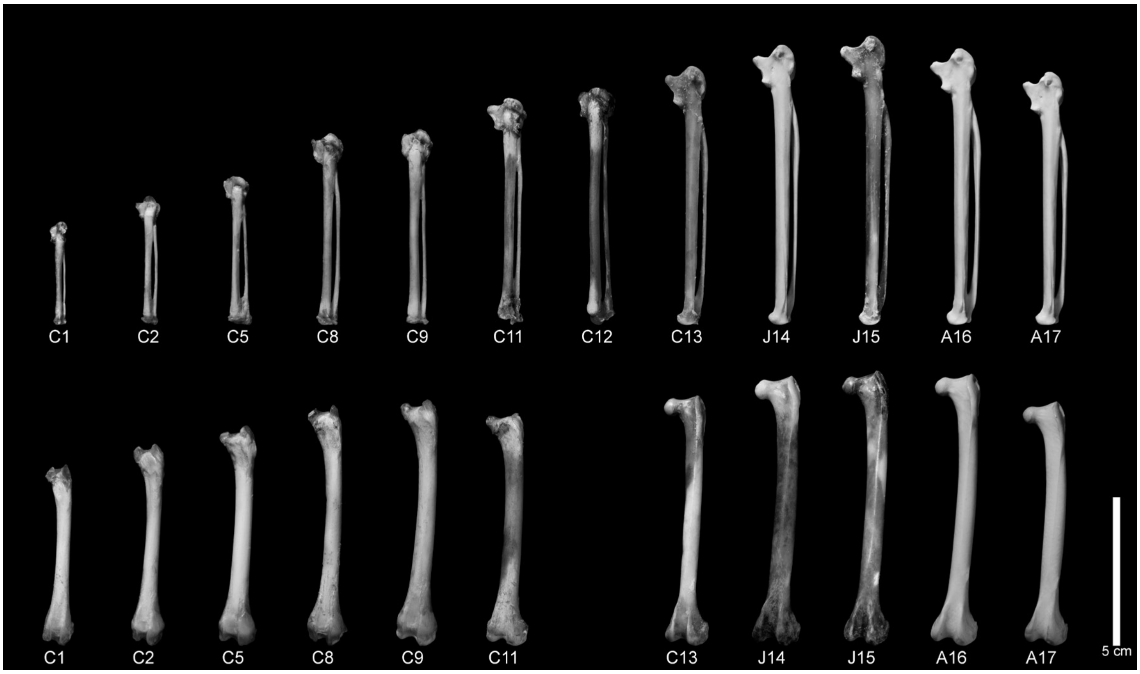


FIGURE 4. Ontogenetic morphological changes of the carpometacarpus (top) and femur (bottom) in *Ardea cinerea*. From left to right, C1, C2, C5, C8, C9, C11, C12 (missing for the femur), C13, J14, J15, A16 and A17 for each.

et ventralis are developed craniodistally, with few surrounding foramina. Epicondyli dorsalis et ventralis are well developed. Entire margin of Fossa m. brachialis is distinct.

Ulna (Fig. 3). *Chick* — Shaft curvature is less prominent in C1–C12, and slightly more weakly curved in C13 than in adults. Extremitas proximalis ulnae is cartilaginous in C1–C12, and ossified in C13 with porous surface on Crista intercotylaris and Olecranon. Impressio brachialis is almost unobservable in C1–C12, and present with indistinct distal margin in C13. Foramina nutrientia is present on Margo interosseus at various positions on the proximal half, double in C7 and C8, single in all others, with large opening (5.3 × 1.0 mm in maximum). Papillae remigales caudales are absent (but observable on periosteum in live bird) in C1–C12, and eight prominent papillae observable (as ossified structures) in C13. Papillae remigales ventrales are absent in all cases. Linea intermuscularis is absent in C1–C12, and present but less distinct in C13. Extremitas distalis ulnae is cartilaginous in C1–C12, and ossified in C13.

Juvenile — Shaft curvature is as in adults. Extremitas proximalis ulnae is ossified, but with porous surface on Cotylae dorsalis et ventralis. Distal margin of Impressio brachialis is somewhat less distinct than in adults. Foramen nutriens is present on Margo interosseus at around the two-fifth of the shaft from the proximal end, and is always single, with larger opening than that in adults (about 3.5 × 0.5 mm). Papillae remigales caudales, 13 papillae are present, with three distalmost papillae indistinct. Papillae remigales ventrales, 10 prominent papillae are present, with three distalmost papillae in adults unobservable. Linea intermuscularis is as in adult. Extremitas distalis ulnae, numerous foramina are present on Sulcus intercondylaris, Labrum condyli dorsalis, and Depressio radialis.

Adult — Extremitas proximalis ulnae is ossified, with few foramen on and around. All muscular/ligamental attachments on the proximal end are distinct. Foramen nutriens is present on Margo interosseus at around the two-fifth of the shaft from the proximal end, and is always single, with a minute opening (about 1.5 × 0.2 mm). Papillae remigales caudales, 13 prominent papillae are present. Papillae remigales ventrales, 13 prominent papillae are present. Linea inter-

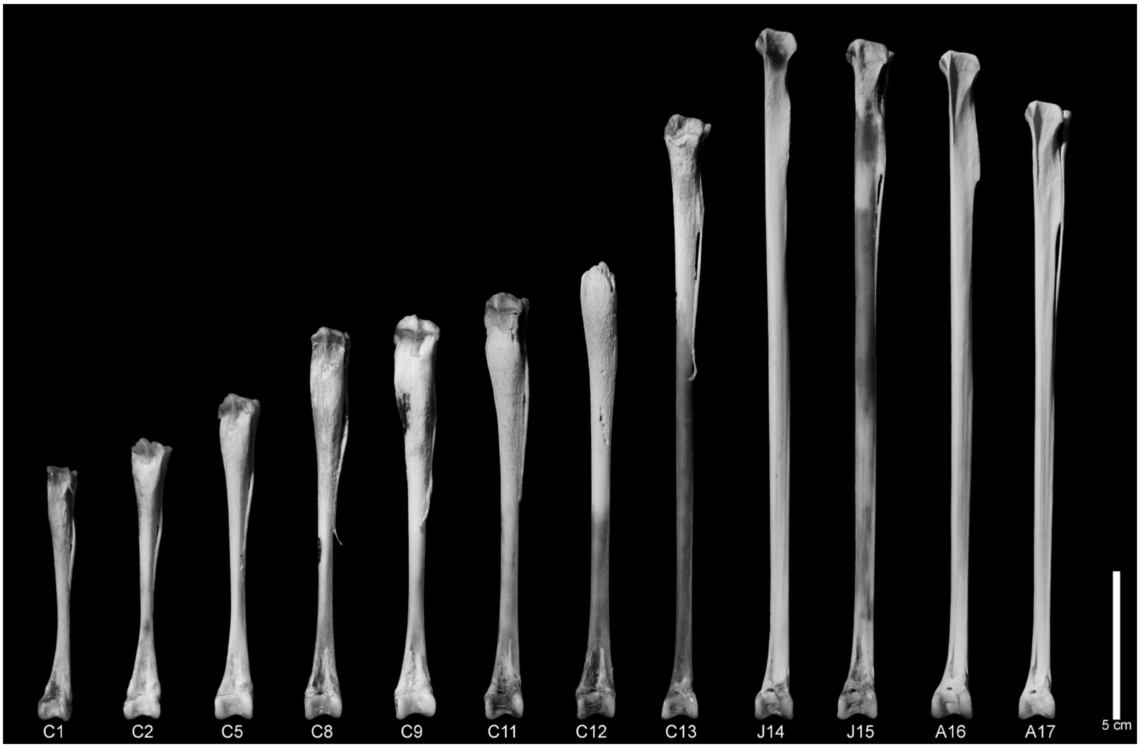


FIGURE 5. Ontogenetic morphological change of the tibiotarsus in *Ardea cinerea*. From left to right, C1, C2, C5, C8, C9, C11, C12 (proximal end damaged), C13, J14, J15, A16 and A17.

muscularis is present on the proximal region of Margo caudalis with a distinct ridge. Extremitas distalis ulnae, with occasional foramina on Sulcus intercondylaris, Labrum condyli dorsalis, and Depressio radialis.

Carpometacarpus (Figs 4, 8A). *Chick* — Five independent elements, including three metacarpi and two carpi, can be recognized; Os metacarpale alulare, Ossa metacarpale majus et minus, one carpus forming the proximal margin of Trochlea carpalis (dca in Fig. 8A), and another carpus for the distal margin of the ventral rim of Trochlea carpalis and the base of Processus pisiformis (dcb in Fig. 8A). The three metacarpi are ossified in all cases, and the two carpi are observable in C3 and larger. They are unfused to one another in C1–C12, but fused in C13. Margin of Trochlea carpalis is formed mostly by cartilage in C1–C10, formed mostly by unfused carpi in C11 and C12, and completely formed by fused carpi in C13. Processus pisiformis is not ossified in C1–C8, formed by one of the carpus (dcb in Fig. 8A) with cartilaginous tip in C9–C12, and ossified in C13. Sulcus tendineus is absent in C1–C12, and prominent throughout the distal one-third of the shaft in C13. Foramen nutriens is present on the caudal margin of Os metacarpale majus at around the midpoint, with moderate size of opening (about 1.0 × 0.5 mm). Almost no trace of muscular/ligamental attachments is observable in C1–C12: most of them are observable in C13, but less distinct than in juveniles and adults. Extremitas distalis carpometacarpi is cartilaginous in C1–C12, and ossified to form Symphysis metacarpalis distalis in C13.

Juvenile — All elements are completely ossified and fused (Fig. 8A). On Extremitas proximalis carpometacarpi, numerous foramina are present along the base of Os metacarpale alulare and around Processus pisiformis. Trochlea carpalis, Processus pisiformis, and Sulcus tendineus are ossified as in adults. Foramen nutriens is present on the caudal margin of Os metacarpale majus at around the midpoint, with moderate size of opening (about 0.6 × 0.3 mm). Extremitas distalis carpometacarpi is ossified, and foramina are present in Sulcus interosseus and on Facies articularis digitalis major.

Adult — All elements are completely ossified

FIGURE 6. Ontogenetic morphological change of the tarsometatarsus in *Ardea cinerea*. From left to right, C1, C2, C5, C8, C9, C11, C12, C13, J14, J15, A16 and A17.

and fused (Fig. 8A). On Extremitas proximalis carpometacarpi, a distinct foramen is present in Fossa infratrochlearis, and foramina can be present along the base of Os metacarpale alulare. Trochlea carpalis and Processus pisiformis are well marked. Sulcus tendineus is well marked throughout the distal half of the shaft. Foramen nutriens is present on the caudal margin of Os metacarpale majus at around the midpoint, with minute opening (about 0.2 × 0.2 mm). Extremitas distalis carpometacarpi is ossified, with few foramina in Sulcus interosseus. Foramina can be present on Facies articularis digitalis major.

Femur (Figs 4, 7C, 7D). *Chick* — Both ends can be either cartilaginous, with epiphysial ossification centers, or ossified. Extremitas proximalis femoris is cartilaginous with slight indication of Caput femoris on the ossified shaft in C1–C11 (femur of C12 was not available), and ossified but silghtly porous in C13. In C10 and C11, an irregularly-shaped ossification center is present in the proximal tip of cartilaginous Trochanter femoris (poc in Fig. 7C). Impressiones mm. et ligg. trochanteris are absent in C1–C10, only the distalmost one of them is observable in C11, and all are present but the proximalmost one is indistinct in C13. Linea intermuscularis cranialis is absent in C1–C11, and indistinct in C13. Lineae intermusculares caudales are absent C1–C11, and the medial one (on caudal margin) is blunt and the lateral one (on the caudolateral margin) is indistinct in C13. Foramina nutrientia are present on Facies caudalis et medialis, with various size of openings (2.0 × 1.0 mm in maximum). The tuberculum for Ansa m. iliofibularis is absent in C1–C10, indistinct in C11, and present as in adults in C13 (ta in Fig. 7D). Extremitas distalis femoris is entirely cartilaginous in C1–C3, containing an ossification center in C4–C11 (doc in Fig. 7D), and ossified with porous surface in C13 (Fig. 7D); the ossification center appears in cartilaginous Condylus medialis in C4, then expands to form Condyli lateralis et medialis and Trochlea fibularis in C10 and C11, and fuses with the diaphysis with little trace of suture in C13.

Juvenile — Both ends are ossified. On Extremitas proximalis femoris, numerous foramina sometimes present in Fovea lig. capitis and the craniolateral margin of Facies articularis antitrochanterica. Impressiones mm. et ligg. trochanteris are as in adults. Lineae intermusculares cranialis et caudales are as in adults. Foramina nutrientia are present on Facies caudalis et medialis, with various size of openings (2.0 × 0.5 mm in maximum). The tuberculum for Ansa m. iliofibularis (ta in Fig. 7D) is developed as in adults. Extremitas distalis femoris is almost completely

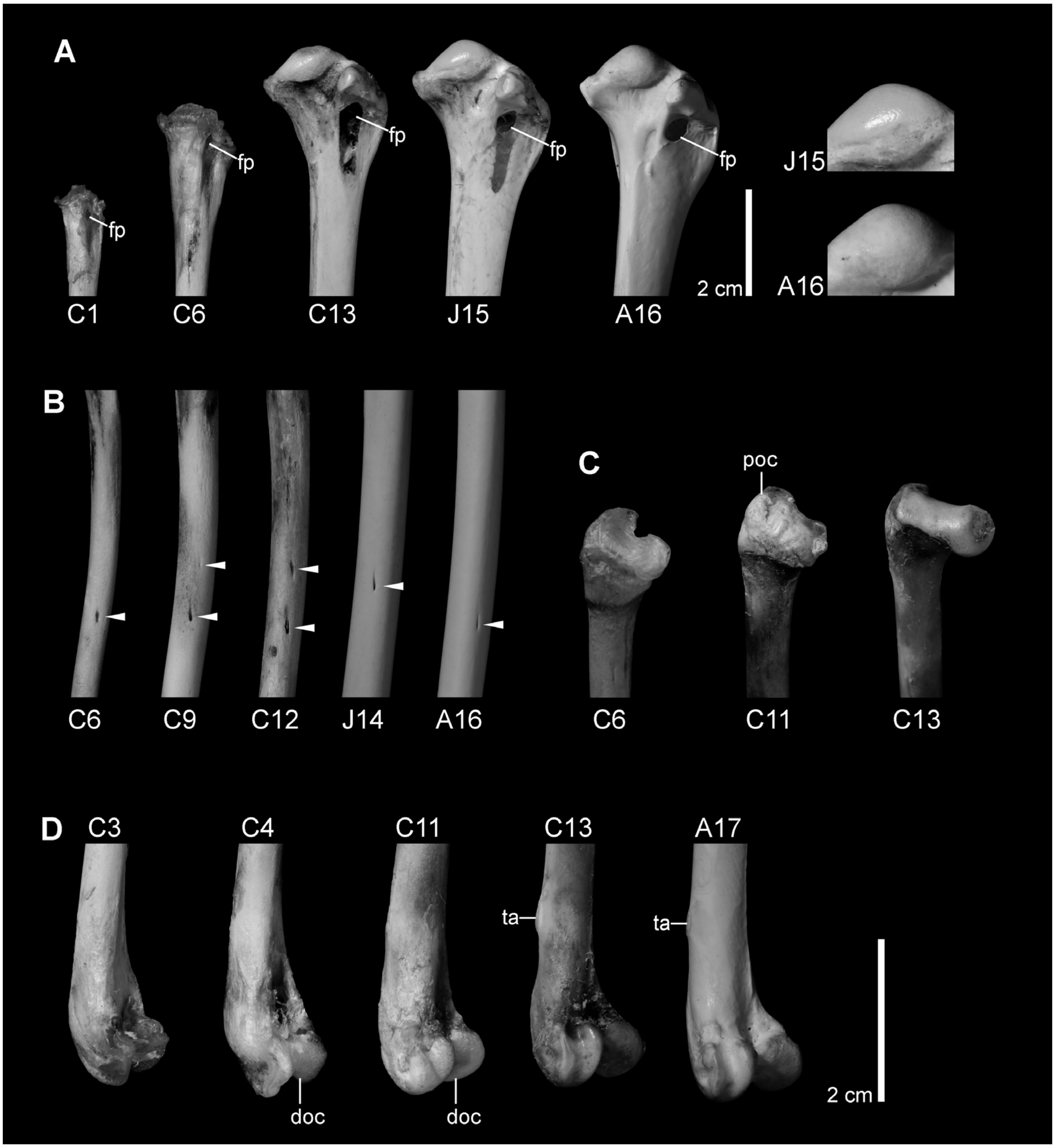
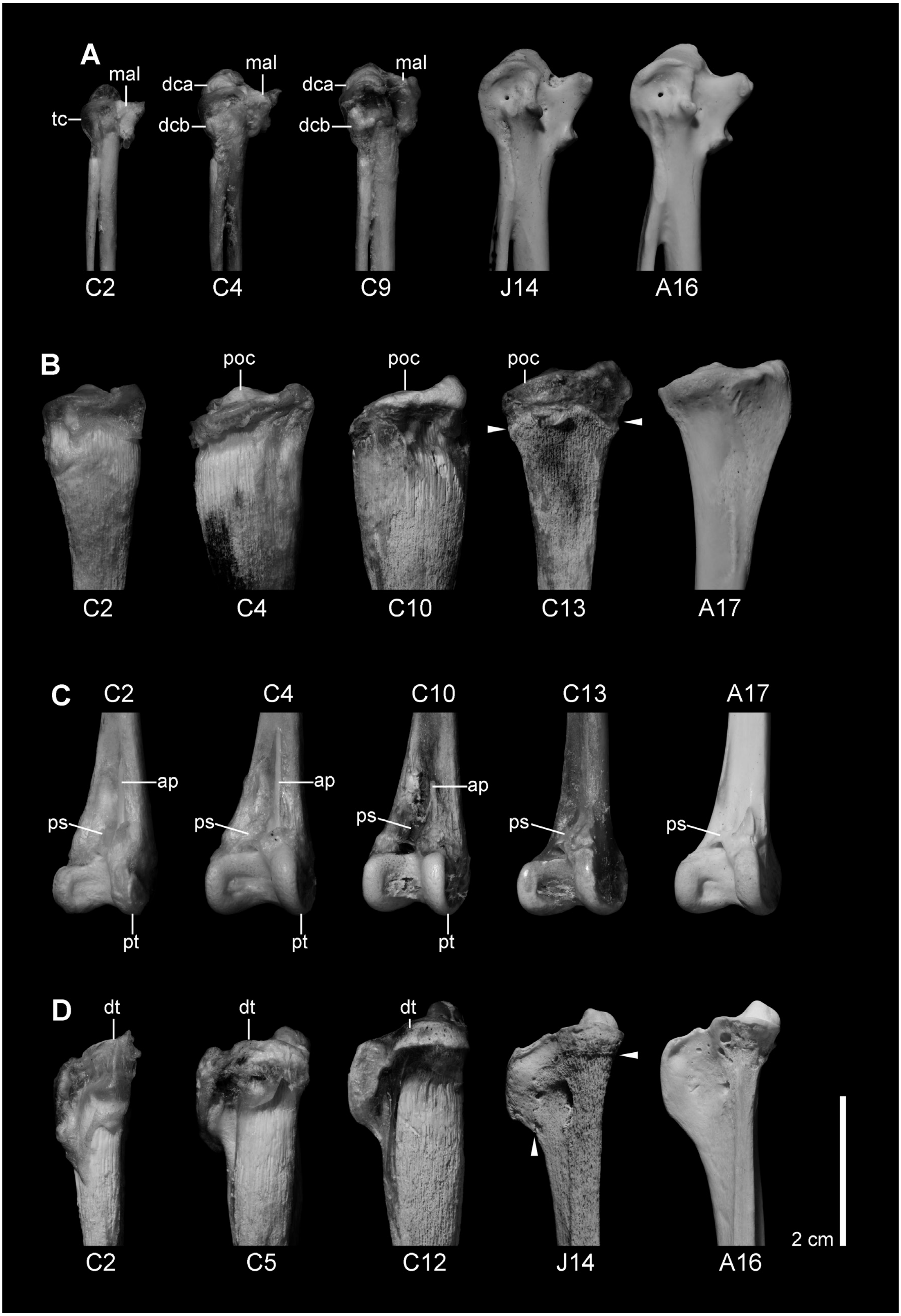


FIGURE 7. Ontogenetic morphological change in humerus and femur. **A**) proximal end of humerus, caudoventral view, in C1, C6, C13, J15 and A16 (from left to right). Caput humeri in J15 and A16 are magnified in the right insets. Foramen pneumaticum (fp) can be observed on the cartilaginous epiphysis in C1 and C6; in C13, periosteum is removed to show the opening of Foramen pneumaticum extending distally to form a fossa; and in J15, periosteum covering the fossa is left as it was in live bird. Note the porous nature of the margin of Caput humeri in J15 compared to that in A16 (right insets). **B**) ventral margin of humeral shaft, ventral view, in C6, C9, C12, J14 and A16 (from left to right). Positions of Foramina nutrientia are indicated by white arrowheads. Scale as in A. **C**) proximal end of femur, caudoproximal view, in C6, C11 and C13 (from left to right). In C6, proximal end is completely cartilaginous; in C11, an ossification center (poc) is present in cartilaginous Trochanter femoris; and in C13, proximal end is ossified. Scale as in D. **D**) distal end of femur, laterocaudal view, in C3, C4, C11, C13 and A17 (from left to right). In C3, distal end is completely cartilaginous; in C4 and C11, an ossification center (doc) is present to form distal condyles; and in C13 and A17, distal end is completely ossified. The tuberculum for Ansa m. iliofibularis (ta) is also shown.


A
tc
mal
dca
dcb
mal
dca
dcb
mal
C2
C4
C9
J14
A16
B
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C2
C4
C10
C13
A17
C
C2
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C10
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ps
pt
ap
ps
pt
ap
ps
pt
ps
ps
D
dt
dt
dt
C2
C5
C12
J14
A16
2 cm

ossified with no trace of suture; prominent foramina are occationally present in Sulcus patellaris and Fossa poplitea.

Adult — Both ends are ossified. On Extremitas proximalis femoris, several foramina are present on each of Fovea lig. capitis, cranial surface of Collum femoris, the area just medial to Trochanter femoris, and the caudal surface just distal to Facies articularis antitrochanterica. Impressiones mm. et ligg. trochanteris are distinct, with five scars observable. Linea intermuscularis cranialis is present, and running obliquely from Crista trochanteris toward Condylus medialis. Lineae intermusculares caudales are present on the caudal and caudolateral margins of the shaft. Foramina nutrientia are present on Facies caudalis et medialis, with minute openings (less than 1.0 × 0.4 mm). The tuberculum for Ansa m. iliofibularis is present on the distal region of the craniolateral margin of the shaft (ta in Fig. 7D). Extremitas distalis femoris is completely ossified with no trace of suture (Fig. 7D); minute foramina and a large foramen are present in Fossa poplitea.

Tibiotarsus (Figs 5, 8B, 8C). *Chick* — The shaft is generally wide and deep proximally. Extremitas proximalis tibialis is entirely cartilaginous in C1–C3, and cartilaginous with a distinct epiphysial ossification center in C4–C13 (poc in Fig. 8B); the ossification center appears in cartilaginous Area interarticularis of Caput tibiae, extends first laterally (from C6) then caudally (from C9) to form ossified Caput tibiae, and in C13 it is about to fuse with diaphysis with a distinct suture (Fig. 8B). The shaft distal to Caput tibiae is first flaring distally and then tapering distally to midshaft in C1–C12, and tapering relatively less steeply than in adults to the midshaft in C13. Crista cnemialis cranialis and Crista fibularis are indistinct and continuous with the shaft. Facies gastrocnemialis is convex. Fossa flexoria is absent. Foramen nutriens is present on the caudal side of Margo lateralis with an opening forming a large fossa (often more than 20.0 × 1.0 mm). On Extremitas distalis tibiotarsi, fused Ossa proximalia tarsi are observable as a single ossification center in the cartilaginous epiphysis in C1–C10 (pt in Fig. 8C), the tarsi are about to fuse to diaphysis of tibia with a distinct suture in C11 and C12, and the tarsi are fused to diaphysis of tibia with little trace of suture in C13. Condyli lateralis et medialis are cartilaginous caudally in C1–C3, and overall shape is formed by tarsi but surface porous with fine foramina in C4–C13 (Fig. 8C). Pons supratendineus (ps in Fig 8C) is a cartilaginous bridge between the “ascending process” (ap in Fig. 8C) of fused tarsi and diaphysis of tibia in C1–C12, and ossified in C13 (Fig. 8C).

Juvenile — The shaft is slender, relatively uniform in width and depth. Extremitas proximalis tibiotarsi is ossified with no trace of suture, with overall shape similar to adult; porous surface with numerous foramina dominates the area on and around Caput tibiae. Crista cnemialis cranialis is indistinct with the distal margin fading. The area between Crista cnemialis cranialis and Crista fibularis is almost flat. Foramen nutriens is present on the caudal side of Margo caudalis with an opening forming a slender fossa extending proximally (more than 7.0 × 0.7 mm). Extremi-

FIGURE 8. Ontogenetic morphological change in carpometacarpus, tibiotarsus and tarsometatarsus. **A**) proximal end of carpometacarpus, ventral view, in C2, C4, C9, J14 and A16 (from left to right). In C2, Os metacarpale alulare (mal) is the only ossified element in the proximal end, and Trochlea carpalis (tc) is cartilagenous; in C4 and C9, two carpi (dca and dcb) can be observed in proximal and distal portion of Trochlea carpalis, respectively. All elements are fused in J14 and A16. **B**) proximal end of tibiotarsus, medial view, in C2, C4, C10, C13 and A17 (from left to right). In C2, proximal end is completely cartilaginous; in C4 and C10, an ossification center (poc) is present to form (part of) the proximal articular surface; in C13, the ossification center is about to fuse with diaphysis of tibia with a distinct suture (white arrowheads); in A17, proximal end is completely ossified. **C**) distal end of tibiotarsus, craniolateral view, in C2, C4, C10, C13 and A17 (from left to right). In C2, C4 and C10, Ossa proximalia tarsi (pt) can be observed as a single ossification center, and form distal condyles, and Pons supratendineus (ps) is a cartilagenous bridge between diaphysis of tibia and the "ascending process" (ap) of Ossa proximalia tarsi; in C13 and A17, Ossa proximalia tarsi are fused to diaphysis of tibia. **D**) proximal end of tarsometatarsus, medial view, in C2, C5, C12, J14 and A16 (from left to right). In C2, C5 and C12, Os distale tarsi (dt) is present in the cartilaginous proximal end and Hypotarsus; In J14, it is fused to shaft of fused metatarsi with a distinct suture (white arrowheads); in A16, the suture is less obvious.

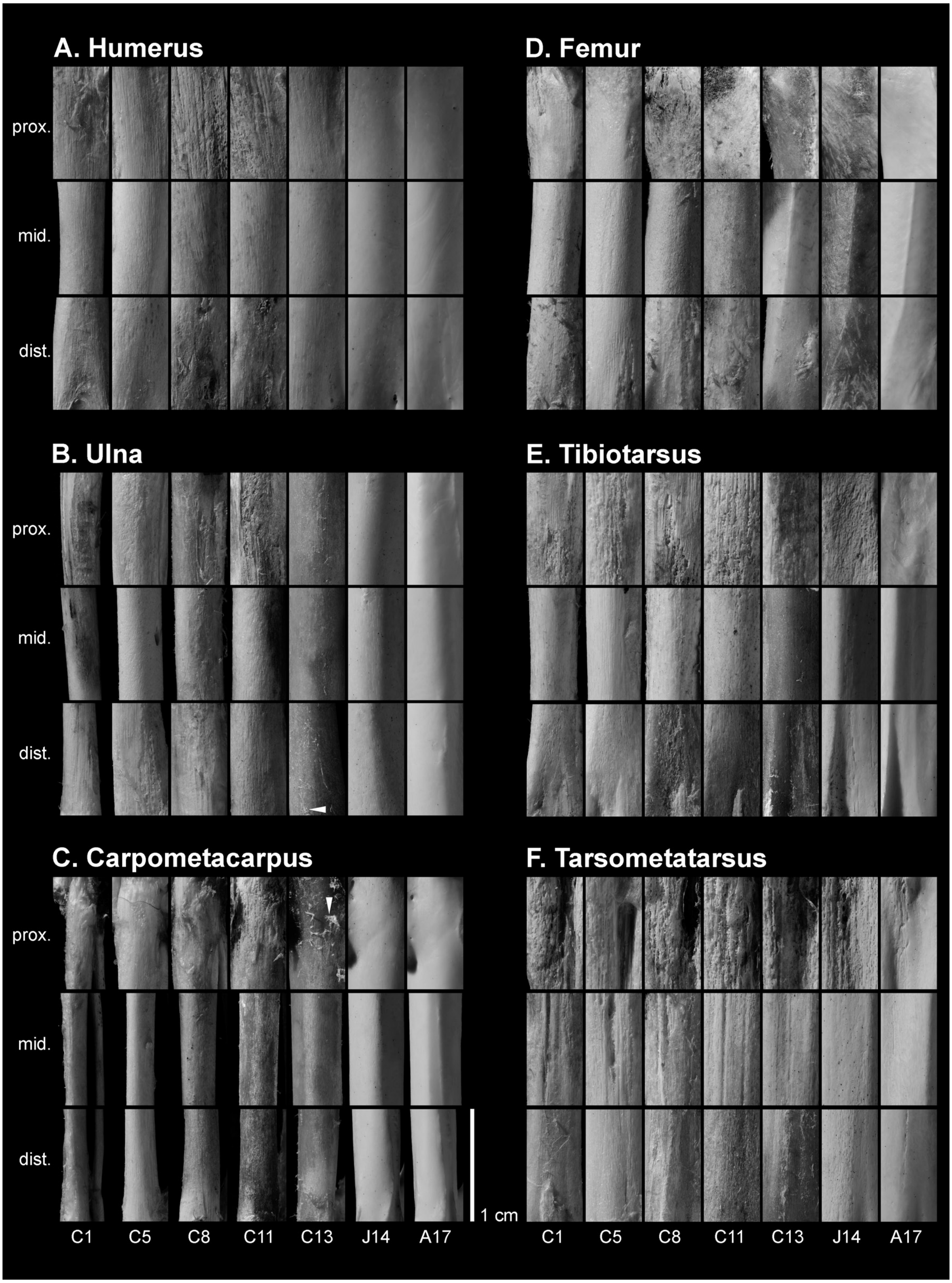

FIGURE 9. Bone surface textures on selected regions of long bones through ontogeny. **A**) humerus, **B**) ulna, **C**), carpometacarpus (Os metacarpale majus for the midshaft region), **D**) femur, **E**) tibiotarsus and **F**) tarsometatarsus. For each bone, proximal, midshaft and distal regions (from top to bottom) in C1, C5, C8, C11, C13, J14 and A17 (from left to right) are shown. Note the occasional presence of periosteum remains, which give fluffy appearance (see white arrowheads in the distal region of ulna and the proximal region of carpometacarpus in C13 for examples).

tas distalis tibiotarsi is ossified with no trace of suture; numerous foramina are present on medial surface of Condylus medialis and lateral surface of Condylus lateralis, and in Incisura intercondylaris and Sulcus extensorius.

Adult — The shaft is slender, with relatively uniform width and depth. On Extremitas proximalis tibiotarsi, numerous minute foramina are present on and around the margin of Caput tibiae (Fig. 8C). Facies gastrocnemialis and Fossa flexoria are sloping steeply from Caput tibiae to the shaft. Crista cnemialis cranialis is well developed with distal margin reaching distally to the position of the midpoint of Crista fibularis. The area between Crista cnemialis cranialis and Crista fibularis is flat to somewhat concave. Foramen nutriens is present on the caudal side of Margo caudalis with a long but thin opening (about 5.0 × 0.2 mm). Extremitas distalis tibiotarsi is ossified with no trace of suture (Fig. 8C); numerous minute foramina are present on medial surface of Condylus medialis and lateral surface of Condylus lateralis, and in Incisura intercondylaris.

Tarsometatarsus (Figs 6, 8D). *Chick* — The shaft is extremely broad proximally, with width and depth reducing gradually distally, and the depth is relatively uniform mediolaterally. Extremitas proximalis tarsometatarsi and Hypotarsus are cartilaginous, with ossified Os distale tarsi within them in C1–C12 (dt in Fig. 8D). Os distale tarsi is observable as a single ossification center, forming first Extremitas proximalis tarsometatarsi (from C1) and then Hypotarsus (from C4), and fusing to the shaft of the fused metatarsi in C13. Sulcus extensorius is broad with blunt margins. Foramina vascularia proximalia are very long, reaching to the proximal epiphysial cartilage in C1–C12. Tuberositas m. tibialis cranialis is almost unobservable. The rims of Trochleae metatarsorum II, III et IVare cartilaginous in C1–C8, mostly ossified but porous in C9–C12, and almost completely ossified in C13.

Juvenile — The shaft is relatively slender, width reducing gradually distally from the proximal suture then maintaining uniform width, and depth shallowing medially and slightly distally. Extremitas proximalis tarsometatarsi and Hypotarsus are ossified, and Os distale tarsi is fused with the fused metatarsi with a distinct suture (Fig. 8D). The area between Extremitas proximalis tarsometatarsi and the suture line is uniform in width unlike in adults where the area is tapering distally, and with numerous foramina. Margins of Sulcus extensorius are less developed cranially than in adults and fading proximal to the midpoint of the shaft. Foramina vascularia proximalia are long (the dorsal openings are more than 4 mm in longitudinal length). Tuberositas m. tibialis cranialis is indistinct. Trochleae metatarsorum II, III et IV are as in adults.

Adult — The shaft is slender, its width is tapering from the position just distal to the margin of Extremitas proximalis tarsometatarsi and then relatively uniform throughout the shaft, and its depth is deepest proximolaterally, shallower medially and tapering gradually distally. Extremitas proximalis tarsometatarsi and Hypotarsus are ossified with no trace of suture, with large surrounding foramina (Fig. 8D). Margins of Sulcus extensorius are well developed and extending distal to the midpoint of the shaft. Foramina vascularia proximalia are short longitudinally (the dorsal openings are about 1.5 mm in longitudinal length). Tuberositas m. tibialis cranialis is prominent. Trochleae metatarsorum II, III et IV are completely ossified with few foramina on and around.

Surface texture

Surface textures of long bones showed considerable variation among developmental stages. They can also vary among elements within a single individual, and even within a single element. Surface textures of various regions of long bones are illustrated in Fig. 9, and longitudinal distribution of textural patterns of long bones, measured as described in Materials and Methods, in selected individuals are shown in Fig. 10. Results for individuals not shown did not differ considerably from those shown in the same developmental stage.

In general, long bones of chicks show rough surface textures (mostly patterns A–C), those of juveniles are smoother but weakly grooved and/or dimpled (mostly pattern D), and those of adults are smooth with little grooves or dimples (mostly pattern E). Surface textures in smallest chicks (C1 and C2) can show a slightly smoother appearance than in larger ones; a striated structure with transverse struts (pattern B) was not observed in some bones, and fibrous/porous texture (pattern C) in the midshaft have less penetrating pits than in larger ones. Elements within a single individual show similar sorts of surface textures, but certain elements tend to have smoother or rougher surface textures than other elements (see below). Within a single element, surface texture is relatively uniform transversely, and is much more variable longitudinally. Generally, loose, striated texture and rough surface (patterns A and B) appear near proximal and distal epiphyses (especially when the epiphysis is not ossified), then they are replaced by less rough fibrous texture diaphysially (typically patterns C and D), and the density of grooves and dimples are least in midshaft region (Fig. 9). Specific characteristics of each element are described below.

Humerus (Figs 9A, 10A) — Humeri show the typical ontogenetic variation described above. In most chicks, C1–C12, surface texture can be classified into either patterns A, B or C, whereas in the largest chick observed, C13, surface texture shows few penetrating pits through most of the shaft, thus classified as pattern D. Longitudinal grooves, rather than dimples, are common in the midshaft region. The proximal shaft, especially caudal surface of Crista deltopectoralis, shows rougher surface texture compared to other part. Numerous distinct penetrating pits can be observed in the area proximal to Fossa m. brachialis (Fig. 9A; bottom row). In juveniles, surface texture is overall smooth, but with faint grooves (pattern D). In adults, surface texture is smooth with few grooves or dimples (pattern E).

Ulna (Figs 9B, 10B) — Overall pattern of ontogenetic variation of surface texture in ulnae is similar to that described in the humerus. The area occupied by striated structure (patterns A and B) is relatively long in the distal end. In both ends, the area of pattern A extends further toward diaphysis in convex caudal margin, whereas it is immediately replaced by pattern B in concave cranial margin. In C13 and J14, the areas next to both ends show slightly fibrous texture with penetrating pits (pattern C). In J15, the shaft is almost entirely without penetrating pits (pattern D), and in adults it is overall smooth (pattern E).

Carpometacarpus (Figs 9C, 10C) — Carpometacarpi show little deviation from the typical ontogenetic variation described above. Both Ossa metacarpi majus et minus show similar sort of patterns. In the midshaft region in chicks, dimples are more common than longitudinal grooves.

Femur (Figs 9D, 10D) — Femora show somewhat smoother surface textures when compared to other bones of the same individual. In chicks, patterns A and B are restricted to small areas near epiphyses. In C10 and C11, surface texture with few penetrating pits (pattern D) can be observed, contrasting to other elements in the individuals. In the midshaft region, few longitudinal grooves appear and dimples dominate. In C13, J14 and J15, all of the shaft is occupied by a texture with numerous faint dimples and little penetrating pits (pattern D). In adults, the shaft is entirely smooth (pattern E).

Tibiotarsus (Figs 9E, 10E) — Tibiotarsi show pronounced intra-elemental variation of surface textures. In chicks, striated structures (patterns A and B) occupy most of the surface on the flared proximal shaft, giving larger proportions within the bone than most other bones. Rough surface textures (patterns B and C) persist in the proximal region until juvenile stage (J14 and J15), unlike most other bones. The distal shaft is relatively smoother, and there is a distinct area with few penetrating pits (pattern D) in the region in C12. In rough surfaces of the proximal to midshaft regions, longitudinal grooves are more common than dimples, whereas in the distal region dimples are more common. The entire shaft is occupied by smooth surface texture (pattern E) in adults.

Tarsometatarsus (Figs 9F, 10F) — Tarsometatarsi show considerable intra-elemental variation, even in juvenile and adult stages. In chicks, the flared proximal shaft is occupied by striated structures (patterns A and B), as in the tibiotarsus. The striated structure with transverse struts (pattern B) also appears in the proximal shaft in juveniles. Even in C13, J14 and J15, where the shaft of most other elements have surface texture with few penetrating pits (pattern D), the pattern appears only in the distalmost shaft. In adults, smooth surface texture (pattern E) appears only in the distalmost shaft, and large proportion

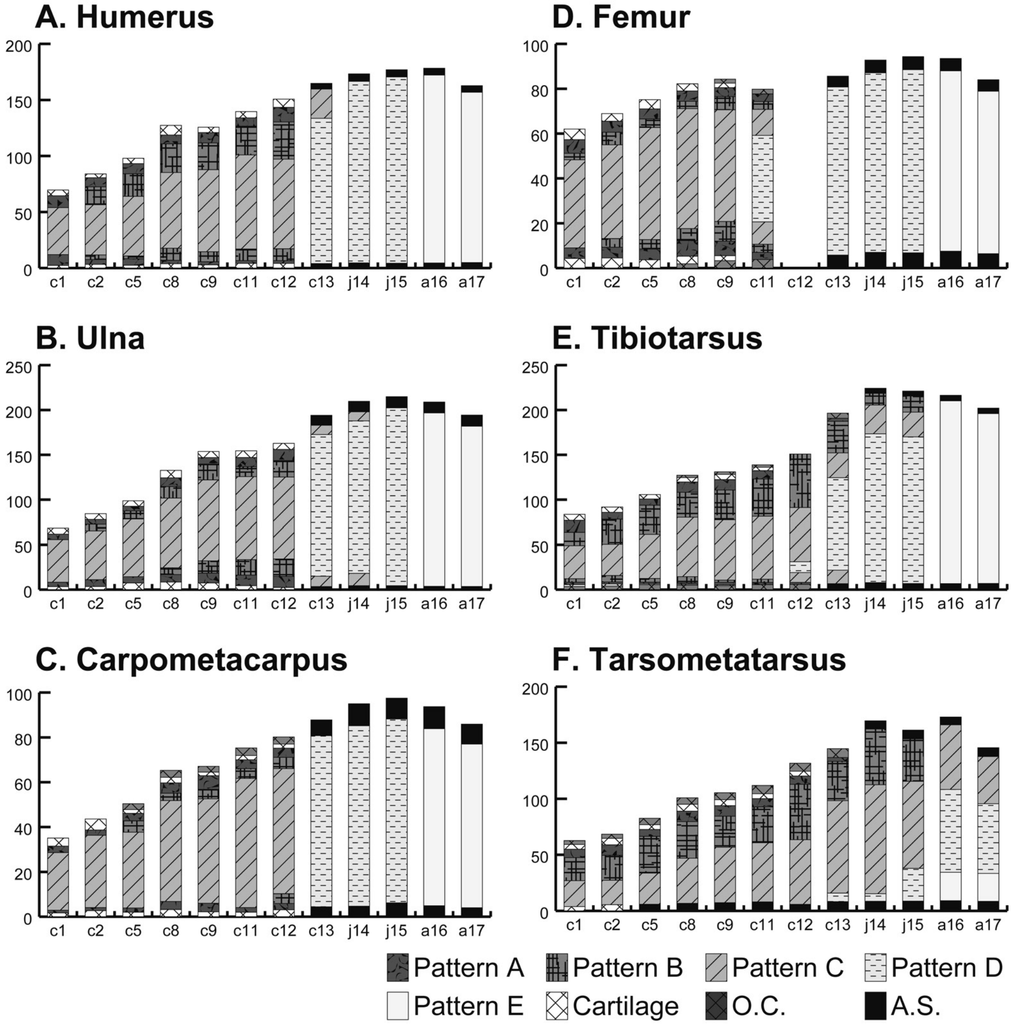

FIGURE 10. Longitudinal distributions of surface textural patterns in six long bones through ontogeny. A) humerus, B) ulna, C), carpometacarpus (Os metacarpale majus), D) femur, E) tibiotarsus and F) tarsometatarsus. For each bone in selected individuals (same ones as in Figs 2–6), longitudinal distributions of patterns A to E, as well as epiphysial cartilages, ossification centers (O.C.) and articular surfaces (A.S.), are shown with distal end at bottom. Vertical axes in millimeter (mm). See Materials and Methods for the definition and measurement of longitudinal distribution of patterns.

is occupied by textures with faint longitudinal grooves (patterns C and D). Longitudinal grooves are common in rough surface in chicks and juveniles. In adults, they are relatively rare and short in length.

Discussion

Ontogeny of long bones. In the study series of the Gray Heron (*Ardea cinerea*), macroscopic morphology and surface textures of all six long bones show ontogenetic variation. Long bones show various degrees of change in linear dimensions (Figs 2–6, Tab. 2). In general, they increase gradually through the chick stage and reach adult size range as early as the time of fledging (except for tibiotarsus and tarsometatarsus, where length of each bone of the largest chick are slightly smaller than that in older individuals), although some dimensions of shaft thickness of leg bones reach their peak before this time and then decrease (see below for further discussion). Epiphysial areas of long bones are cartilaginous and can contain a distinct ossification center through most of the chick stage. Most of epiphyses are ossified at or slightly before the time of fledging (C13; with the exceptions of the proximal ends of tibiotarsi and tarsometatarsi, where complete fusions occur between C13 and J14), but they show slightly more porous surface than adults until the juvenile stage. Epiphysial areas are completely ossified in adult stage (Figs 2–8). Most osteological landmarks and muscular/ligamental attachment scars are not observable as ossified structures through most of the chick stage. At fledging they are more or less observable on the ossified area, but margins are less distinct than in the later stages. In the juvenile stage, they are mostly similar to those in the adult stage, although there are distinct ontogenetic changes between the two stages in some features including Foramen pneumatica of humerus and Crista cnemialis cranialis of tibiotarsus (Figs 2–8). Distinctly large Foramina nutrientia on bone walls in chicks

TABLE 3. Summary of proportions of longitudinal distributions of five textural patterns in six long bones through ontogeny. Proportions of longitudinal distributions of patterns A to E are expressed in percent (%) to the ossified length of the bone. For each combination of long bones and developmental stages, minimum and maximum values among individuals (C, chick; J, juvenile; A, adult) are shown. $N = 13$ for chicks (12 for femur), 2 for juveniles and 2 for adults. See Materials and Methods for the definition and measurement of longitudinal distribution of patterns.

Humerus					
	A	B	C	D	E
C	0.0–32.5	0.0–31.6	16.8–67.5	0.0–83.2	0.0
J	0.0	0.0	0.0	100.0	0.0
A	0.0	0.0	0.0	0.0	100.0
Ulna					
	A	B	C	D	E
C	0.0–19.1	0.0–29.9	12.2–81.1	0.0–87.8	0.0
J	0.0	0.0	0.0–12.3	87.7–100.0	0.0
A	0.0	0.0	0.0	0.0	100.0
Carpometacarpus					
	A	B	C	D	E
C	0.0–17.6	0.0–13.0	0.0–89.4	0.0–100.0	0.0
J	0.0	0.0	0.0	100.0	0.0
A	0.0	0.0	0.0	0.0	100.0
Femur					
	A	B	C	D	E
C	0.0–20.4	0.0–19.6	0.0–75.7	0.0–100.0	0.0
J	0.0	0.0	0.0	100.0	0.0
A	0.0	0.0	0.0	0.0	100.0
Tibiotarsus					
	A	B	C	D	E
C	1.6–22.1	19.1–43.9	23.2–57.9	0.0–55.8	0.0
J	0.0	6.2–8.6	13.2–15.2	78.2–78.6	0.0
A	0.0	0.0	0.0	0.0	100.0
Tarsometatarsus					
	A	B	C	D	E
C	2.6–17.4	27.3–54.5	33.9–64.1	0.0–6.0	0.0
J	0.0	26.1–32.4	53.7–63.2	4.4–20.2	0.0
A	0.0	0.0	32.6–36.8	47.1–48.1	16.1–19.3

(Fig. 7B) could be correlated to active blood flow and bone metabolism (see Seymour *et al.* (2012) and references therein). The occasional presence of Foramen nutriens covered by thin bone wall indicate that they can be opened or closed during ontogeny. Surface textures of long bones also show considerable ontogenetic change. Through most of the chick stage, fibrous/porous surface texture with frequent penetrating pits (pattern C) dominates in the midshaft region, whereas striated structures (patterns A and B) dominate near both epiphyses of long bones (with some exceptions). In larger chicks, smoother surface texture with faint grooves/dimples and few penetrating pits (pattern D) appears in the midshaft region of femur and the distal shaft of tibiotarsus. At the time of fledging, rough surface textures (patterns A and B) are mostly replaced by smoother one (pattern D) with occasional remains of rougher textures on epiphysial areas (particularly in the proximal regions of tibiotarsus and tarsometatarsus). This state persists through the juvenile stage. In the adult stage, smooth surface texture with few grooves/dimples (pattern E) dominates on all long bones except for tarsometatarsus, where rougher surface (patterns C and D) occupies considerable portion of overall area (Figs 9 and 10). Proportions of longitudinal distribution of surface texture patterns, expressed as a percentage to ossified length of a bone, in each developmental stage are summarized in Tab. 3.

The presence of inter-elemental variation of surface textures among six long bones results in differences in relative timing of the appearance of smooth surface textures. Of the six elements examined, the femur is the first element to attain pattern D (in C10), the tibiotarsus is the second (in C12; although limited to the distal shaft), and all others follow (in C13). Rough surface textures (patterns A–C) disappear earliest in the carpometacarpus and femur (at latest in C13), followed by the humerus (in J14), ulna (in J15), and tibiotarsus (in A16), and persist through all of the series in tarsometatarsus. One possible reason for the tarsometatarsus to retain relatively rough surface texture (patterns C and D) in the adult stage is that it is firmly attached to podotheca (Baumel & Witmer 1993). It is notable that the proximal ends of tibiotarsus and tarsometatarsus, where complete ossification of epiphysis occurs later than in the other bones, retain rougher surface until later period of development. This fact, along with longitudinal distribution of surface textures in long bones, suggests that striated structures (patterns A and B) might be partly relevant to active longitudinal growth of long bones, as well as bone remodeling process. The possible biological significance of this inter-elemental variation is further discussed below.

The combination of observations on surface textures and histology of long bones in the Canada Goose (*Branta canadensis*) have revealed that rough surface textures on long bones are underlain by actively growing fibrolamellar bone tissue, characterizing immature long bones (Tumarkin-Deratzian *et al.* 2006). Their discussion is based primarily on estimated relative developmental stages of the samples, which are based mainly on possession of osteological landmarks, with several other supportive evidences (length of the bones, and date of death of individuals). The current study, based on originally prepared specimens of the Gray Heron (*Ardea cinerea*), confirms that lack of osteological landmarks and rough surface textures do occur in the immature chick stage. It is remarkable that most individual surface textures observed in *Ardea* in the current study (Figs 1 and 9), such as a rough striated texture with frequent transverse struts (pattern B), a fibrous/porous texture with frequent longitudinal grooves/dimples (pattern C), and a smooth texture with few longitudinal grooves/dimples (pattern E), are almost qualitatively identical to those observed in *Branta* in Tumarkin-Deratzian *et al.* (2006: figs 5–7).

In addition, the overall pattern of transition of surface texture from striated, fibrous texture into smooth surface observed in *Ardea cinerea* is similar to that reported by Tumarkin-Deratzian *et al.* (2006) in *Branta canadensis*. They defined seven texture types, type I to VII in the order of decreasing degree of roughness, to describe the overall composition of surface textures of a long bone, which are considered to represent relative developmental stages within each element. According to their definition of texture types (Tumarkin-Deratzian *et al.* 2006: pp. 143–148 and tab. 6), long bones of the study series of *Ardea cinerea* in the current study can be classified as in Tab. 4. Although some of the seven texture types could not be recognized in the study series of *Ardea cinerea*, the table shows that the ontogenetic sequence of surface texture types observed in *Ardea* is consistent with that identified in *Branta*, confirming the previous authors' hypothesis that "ontogenetic patterns of bone texture change in other species may be similar to those observed in *B. canadensis*" (p. 159). This similarity confirms the reliability of surface textures as a ageing criterion for bird fossils.

According to Tumarkin-Deratzian *et al.* (2006), bones of birds that have not yet reached the adult size range show texture type I; birds that have reached adult size ranges but are not yet fully skeletally mature show texture types II–V; and birds attained both adult size and skeletal maturity show texture types VI and VII. This statement appears roughly true also in *Ardea cinerea*, where all bones of chicks that have not yet reached the adult size range (C1–C12) show texture type I, and most bones of birds that attained adult size range (C13–J15) show texture types III and IV. However, it should be noted that rough striated surface textures, whose presence define texture type I, can be observed in the proximal shaft of tibiotarsi and tarsometatarsi of those that have reached adult size range (C13–J15). This fact does not significantly diminish the reliability of surface textures as a criterion for ontogenetic ageing because the overall pattern of transition is quite consistent for each bone. But the presence of such inter- and intra-elemental variation should be taken in mind when dealing with isolated/fragmental fossil bones. Tumarkin-Deratzian *et al.* (2006) also concluded, from the distribution of textural maturity against date of death, that adult surface with grossly smooth texture (texture types VI and VII) is attained in the winter of the hatching year in that species. Unfortunately, as the two juveniles available to this study were both collected in the first summer (June and August; Tab. 1), exact timing of attaining smooth surface in *Ardea* could not be determined in this study.

Inter-elemental variation. One interesting difference between ontogenies of surface textures of long bones in *Ardea cinerea* (this study) and *Branta canadensis* (Tumarkin-Deratzian *et al.* 2006) is found in inter-elemental difference of relative timing of attaining mature surface textures. Tumarkin-Deratzian *et al.* (2006) examined sur-

TABLE 4. Texture types (Tumarkin-Deratzian *et al.* 2006) applied to the long bones of *Ardea cinerea*. Each long bone is classified into one of the seven texture types (types I to VII) according to the definition and description given by Tumarkin-Deratzian *et al.* (2006).

	Humerus	Ulna	Carpometa-carpus	Femur	Tibiotarsus	Tarsometa-tarsus
C1	I	I	I	I	I	I
C2	I	I	I	I	I	I
C3	I	I	I	I	I	I
C4	I	I	I	I	I	I
C5	I	I	I	I	I	I
C6	I	I	I	I	I	I
C7	I	I	I	I	I	I
C8	I	I	I	I	I	I
C9	I	I	I	I	I	I
C10	I	I	I	I	I	I
C11	I	I	I	I	I	I
C12	I	I	I	—	I	I
C13	III	III	IV	IV	I	I
J14	IV	III	IV	IV	I	I
J15	IV	IV	IV	IV	I	I
A16	VII	VII	VII	VII	VII	V
A17	VII	VII	VII	VII	VII	V

face textures of three long bones, humerus, femur and tibiotarsus, in *B. canadensis*, and pointed out the tendency of the humerus to retain immature rough surface textures longer than the other two bones in that species. In contrast, in *A. cinerea*, the tibiotarsus retains immature rough surface longer than humerus and femur (Figs 9 and 10, Tab. 4).

Assuming that attaining smooth surface texture corresponds to cessation of active bone growth, relative timing of attaining smooth surface texture can be regarded as relative timing of maturity among long bones. So it is likely that the relative timing of attaining smooth surface textures among long bones reflects some biological aspects of avian ontogeny, such as resource allocation among limb sections and allometric/heterochronic change in limb growth. There are two possible explanations for interspecific difference of the relative timing of attaining smooth surface textures between *Ardea cinerea* and *Branta canadensis*. First, the difference may reflect different locomotor requirements in early ontogeny between the two species. In the Family Anatidae, including *Branta*, chicks generally hatch in precocial condition, and have to walk and swim to follow the parents and to feed for themselves immediately after hatching (Starck & Ricklefs 1998; Bowler 2005). In order to achieve sufficient locomotor ability early in ontogeny, anatid chicks mature their hindlimbs much earlier than forelimbs and pectoral girdle (Hohtola & Visser 1998; Dial & Carrier 2012). In contrast, in the Family Ardeidae, including *Ardea*, chicks hatch in (semi-)altricial condition, in which they stay in the nest for a certain period (about six weeks in *Ardea cinerea*, when chicks can clamber away from nests to the forest canopy of the colony; Yamashina 1941) and are fed by their parents until fledging (at about seven to eight weeks old in *Ardea cinerea*, and 2–3 to 12–13 weeks among Ardeidae (Yamashina 1941, Starck & Ricklefs 1998; Kushlan & Hancock 2005). In this condition, hindlimbs would be released from drastic development in early ontogeny, allowing bone growth to continue until late ontogeny. Second, the difference could be related to the different proportion of limb sections between the two species, such as the extremely long distal leg in *Ardea*. If there exist any constraints on longitudinal growth rates in long bones (see Carrier & Auriemma 1992), extremely long leg bones in *Ardea* would need a longer time period to reach adult size. Of course, these two explanations are not mutually exclusive, and it is fairly possible that the difference results from both factors. Comparative studies with more sample taxa, including long-legged precocial species (*e.g.*, gruids, ratites, etc.), would be fruitful.

Ossification centers. The presence of epiphysial ossification centers in long bones of birds has not been widely accepted (see Baumel & Witmer 1993: Annotation 2; but see also Starck 1994: footnote in p. 121). In spite of repeated mentions to "epiphysis" by earlier authors (Latimer 1927; Huggins *et al.* 1942), Haines (1942) and Bellaris & Jenkin (1960) considered them as misidentifications. One exception is an ossification center in the proximal end of tibiotarsus. Hogg (1980) reported and figured a distinct ossification center at the cranial margin of the proximal end of tibiotarsus in the domestic fowl under the name of "proximal tibial centre" (pp. 735, 741, figs 11, 12, 14, 15) (but curiously his later study (Hogg 1982) did not mention it). Hall (2005) recognized its presence in the domestic fowl as a secondary ossification center, and considered it to be relevant to the rapid growth rate of tibiotarsus. Through a radiological study on a kiwi (*Apteryx australis mantelli*), Beale (1985, 1991) showed the presence of an ossification center at the equivalent position, and called it "patella" (Beale 1985: p. 190–191, fig. 5). Turvey & Holdaway (2005), studying ontogeny of the extinct Giant Moa (*Dinornis*), also figured and described this structure as "patella" (p. 73, fig. 3). A distinct ossification center in *Grus grus* from an archaeological site was figured by Serjeantson (1998). Recently, through their examination of osteological characters, Livezey & Zusi (2006) concluded that the ossification center at that position is not a patella but a distinct "tibial epiphysis" (p. 322).

The study series of *Ardea cinerea* clearly demonstrated the presence of a distinct epiphysial ossification center in the proximal tibiotarsus and supports Livezey & Zusi's (2006) view, because the ossification center in this species first appears at the middle part of the articular surface, rather than at the cranial margin where the patellar tendon inserts (Fig. 8B). This ossification center then extends craniolaterad, and later caudad to form the entire Extremitas proximalis tibiotarsi. It apparently starts fusing with the diaphysis of tibia around fledging, and the suture disappears in the early juvenile stage. The study series also showed the presence of distinct epiphysial ossification centers in the proximal and distal ends of femur. To date, there appears to be no definite descriptions of them in the literature. The one in the proximal end of femur appears in the middle chick stage (C10) in the proximal margin of cartilaginous Trochanter femoris (Fig. 7C). The one in the distal end of femur appears earlier (in C4) at the caudal margin of the distal condyles, and then extends to form entire Extremitas distalis femoris (Fig. 7D). Unfortunately, the process of fusion of these ossification centers could not be observed. Both proximal and distal ends of femur are ossified at the time of fledging with little trace of sutures. It is not clear whether these ossification centers are induced in response to mechanical loadings (Carter *et al.* 1998) or not. Further studies are required to clarify phylogenetic distribution and histological nature of epiphysial ossification centers in birds.

Bone growth. Long bones grow both longitudinally and circumferentially. Longitudinal growth occurs through endochondral ossification in epiphyses, or in epiphysial growth plates (Wolbach & Hegsted 1952; Starck 1996), whereas circumferential growth occurs through membranous ossification, or direct deposition of new bone tissue on existing bone surface in periosteum (Bellaris & Jenkin 1960). In the ontogenetic series of *Ardea cinerea* observed in this study, most long bones of the largest chick studied, C13, have equivalent length to those in small adults studied (Figs 2–6, Tab. 2), suggesting that long bones reach adult size range in length during chick stage (except for tibiotarsus and tarsometatarsus). At the same time, both ends of long bones are ossified to retain no trace of epiphysial growth plates (except for the proximal ends of tibiotarsus and tarsometatarsus, where fusion of epiphysial ossification center and Os distale tarsi, respectively, with each diaphysis is completed slightly later). These two facts suggest that longitudinal growth of long bones in this species ceases at (or slightly after) the end of the chick stage, or the time birds become capable of flight and leave birth colonies.

In contrast, circumferential growth of long bones does not appear to cease at this time in *Ardea cinerea*. Almost all dimensions of shaft diameters in long bones are larger in all adults and juveniles than in largest chicks (except for shaft depth at the midpoint in femur; Tab. 2). Although the sample size is too small for statistical tests, it would be reasonable to suppose that circumferential growth of long bones continues for a certain period after cessation of longitudinal growth in this species. Rough surface textures in chicks and juveniles, indicating active bone growth (Tumarkin-Deratzian *et al.* 2006), support this hypothesis. Also, in the House Sparrow (*Passer domesticus*), it has been reported that most long bones of adults are significantly thicker, but not longer, than those of first year birds in females (though not in males; Bjordal 1987).

Interestingly, the proximal shafts of tibiotarsus and tarsometatarsus are considerably thicker in chicks than in juveniles and adults (Figs 5, 6, 8B, 8D, Tab. 2). These regions are characterized by extremely rough surface textures (Figs 9 and 10), suggesting active bone remodeling in these regions (see above). This fact strongly suggests that intensive resorption of bone tissue is taking place in the cortex of these leg bones in the ontogeny of *Ardea cinerea*. Although the exact significance of this resorption is not clear, one possible explanation is that the thick bone shaft in leg bones of *Ardea* chicks compensates for less dense, weak immature bone tissue, providing the leg bones with sufficient strength to sustain growing body weight. Carrier & Leon (1990) observed thick bone walls in leg bones of the California Gull (*Larus californicus*) chicks, and concluded thick bone walls might compensate for weak bone tissue in rapidly growing animals. Similar compensation might take place in the leg bones of *Ardea* chicks.

Ontogenetic ageing in bird fossils. Recent birds, in general, are considered to undergo rapid growth in early ontogeny and attain skeletal maturity within a year (*e.g.*, Padian *et al.* 2001).

As far as for surface textures of long bones, available data on skeletal ontogeny in *Branta canadensis* (Tumarkin-Deratzian *et al.* 2006) and *Ardea cinerea* (this study) are consistent with the idea. However, there are some exceptions. In kiwi (*Apteryx*), epiphyses of leg bones may retain unfused independent ossification centers for more than four years (Beale 1985, 1991), and histological studies revealed that they undergo cyclical interrupted growth for five to six years (Bourdon *et al.* 2009). Similar growth pattern have been suggested for extinct moas (Turvey *et al.* 2005; Turvey & Holdaway 2005). It should also be noted that some basal birds are likely to have had distinct growth strategies than modern birds, in which cortical bone deposition is frequently interrupted (Chinsamy-Turan 2005).

Through the study of both surface textures and histology of long bones in the American Alligator (*Alligator mississippiensis*), Tumarkin-Deratzian *et al.* (2007) showed that an apparently smooth surface texture can occur on the long bones of immature individuals in animals with cyclical interrupted growth, and cautioned that textural ageing on fossil animals with unknown growth strategies would be problematic. At this time, textural ageing on fossil birds with unknown or interrupted growth strategies should be similarly problematic, as there are no detailed data on ontogenetic change of surface texture in birds with interrupted growth or longer growth periods. Clearly more studies are needed to establish reliable ageing criteria for bird fossils.

Conclusion

Postnatal ontogenetic changes of macroscopic morphology and surface texture in major long bones of the Gray Heron (*Ardea cinerea*) were described and illustrated. Both macroscopic morphology and surface texture of each element showed relatively consistent shifts through ontogeny, and thus these changes would be useful in ontogenetic ageing of fossil bird materials. Long bones of chicks are typically characterized by indistinct muscular/ligamental attachments and cartilaginous epiphyses. Those of adults are characterized by distinct muscular/ligamental attachments and completely ossified epiphyses. Those of juveniles (here, birds under one-year-old) can be distinguished from adults by some qualitative characters, including articular surfaces with more porous margins, large nutrient foramina, Foramen pneumatica of humerus extending distally to form a fossa, less distinct distal Papillae remigales of ulna, less developed Crista cnemialis cranialis of tibiotarsus, and much larger Foramina vascularia proximalia of tarsometatarsus. Long bones of chicks typically have a striated surface texture near both epiphyses and rough fibuous/porous surface textures with distinct longitudinal grooves and/or dimples and penetrating pits in the midshaft. Those of juveniles are dominated by an overall smooth surface texture with faint longitudinal grooves and/or dimples and few penetrating pits; surface textures with frequent penetrating pits can remain near either or both epiphyses. Adult long bones are characterized by an overall smooth surface texture with few longitudinal grooves and dimples, except for tarsometatarsus.

However, there can be considerable variation of surface textures among elements even within a single individual. For instance, a rough striated structure can be observed on the proximal regions of tibiotarsus and tarsometatarsus in juveniles of *Ardea cinerea*, whereas their distal regions and most other elements show only faint grooves or dimples. The presence of such variation suggests that assessment of ontogenetic age of an individual based on a single isolated fossil bone should be made with caution.

Preliminary comparisons suggest the presence of taxon-specific inter-elemental variation of surface textures. Provided that this variation represents differential sequence of the relative timing of maturity among long bones, the nature of the variation could be correlated to differences in limb proportions and/or ontogenetic strategies among various avian taxa. Comparative work among birds with various body sizes, limb proportions, life histories and phylogenetic positions is needed to evaluate the significance of the variation, as well as to establish reliable ageing criteria for bird fossils.

Acknowledgements

This study is largely based on graduate work by JW under the guidance of HM at the Department of Geology and Mineralogy, Kyoto University. Completion of the work is largely thanks to generous assistance and valuable discussions by the members of the department. Attendance at the 8th International Meeting of the Society of Avian Paleontology and Evolution by JW was supported by an "Accommodation Grant" by the organizing committee of the meeting. Sincere gratitude is expressed to U. Göhlich (Naturhistorisches Museum Wien) for kind editorial support, and A. Tumarkin-Deratzian (Temple University, Philadelphia) and K. Campbell (Natural History Museum of Los Angeles County) for constructive comments on the manuscript that greatly improved the manuscript.

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Verlag Naturhistorisches Museum Wien
ISBN 978-3-902421-82-1