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ABSTRACTS

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SYSTEMATIC REVISION OF SOUTH AMERICAN FOSSIL PENGUINS (SPHENISCIFORMES)

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A phylogenetic and morphometric analysis of South American fossil penguins has been done using skull and appendicular skeleton characters. Our current studies lead us to identify two groups substantially equivalent to those proposed originally by Simpson though abandoned later by himself after examining fossil New Zealand penguins: Palaeospheniscinae and Paraptenodytinae, and a third group belonging to a new subfamily Madrynornithinae. However, we have reevaluated both subfamilies, and when necessary we have amended the respective diagnoses. Only nine of the 35 previously named species are recognized, therefore the diversity would not have been so high as it was supposed. Herein we propose the following systematic arrangement: (1) PALAEOSPHENISCINAE Simpson, 1946 (Early Miocene of Argentina and Middle Miocene- Pliocene of Chile and Peru), characterized by humerus with a bipartite fossa tricipitalis, a high crus dorsale fossae, a laterocraneal fossa over the tuberculum ventrale and a sulcus ligamentaris transversus divided in two parts; tarsometatarsus with elongation index higher than two, a flattened metatarsal II, and a foramen vasculare proximale medialis only open in cranial side, including *Eretiscus tonni* (Simpson, 1981), *Palaeospheniscus bergi* Moreno and Mercerat, 1891, *P. patagonicus* Moreno and Mercerat, 1891, and *P. biloculata* nov. comb. (2) PARAPTENODYTINAE Simpson, 1946 (Late Eocene - Late Miocene of Argentina and Middle Miocene of Chile) characterized by a straight humerus with a single fossa tricipitalis (lacks of crus dorsale fossae), a lateral fossa over the tuberculum ventrale and a undivided sulcus ligamentaris transversus; tarsometatarsus with elongation index smaller than two, a foramen vasculare proximale lateralis bigger than the medialis and a strongly divergent trochlea II, including *Paraptenodytes robustus* (Ameghino, 1895), *Paraptenodytes antarcticus* (Moreno y Mercerat, 1981), and *Arthrodytes andrewsi* (Ameghino, 1901); and finally (3) MADRYNORNITHINAE nov. subfam. (early Late Miocene of Argentina) showing a straight humerus, a lateral fossa over the tuberculum ventrale, a bipartite fossa tricipitalis, a low crus dorsale fossae and a sulcus ligamentaris transversus divided in two parts; tarsometatarsus with elongation index about 1.79, an extremely small foramen vasculare proximale mediale, and strongly divergent trochlea II.
These three groups are recorded exclusively in South America and are morphologically closer to living species than either any pre-Miocene penguins or the Neogene taxa recorded in others regions of the Southern Hemisphere. This suggests, in first instance, that the evolutionary and biogeographic history of South American Miocene penguins would have followed different routes from those of the Eocene of Antarctica and New Zealand-Australia, which share taxa of specific level.

THE VALIDITY OF THE FOSSIL *AYTHYA ARETINA* (PORTIS) AND *AYTHYA SEPULTA* (PORTIS) (AVES, ANATIDAE) ON THE BASIS OF NEW FINDING IN THE ITALIAN EARLY PLEISTOCENE

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In 1889 Alessandro Portis (1889, Gli Ornitoliti del Valdarno Superiore e di alcune altre località Plioceniche di Toscana. *Mem. Regio Istituto di Studi superiori e Pratici*: 1-20) described two new extinct species of *Aythya*, under the old generic name *Fuligula*, *A. aretina* and *A. sepulta* from two different Pliocene fossil localities in the Uupper Valdarno Basin, (Firenze, Central Italy). In particular the fossil remains described by Portis have been found in the locality of Montecarlo and Le Strette, associated with mammals of the Middle and Late Villafranchian (MN 17-18). The validity of the two taxa has never been discussed and, after Brodkorb (1964, Catalogue of fossil birds: Part 2. *Bull. of Florida State Museum*, 8(3): 195-335) they have been placed, still as valid taxa, in the modern genus *Aythya*. In his revision of the Anatidae of the Miocene of France, Cheneval (1987, Les Anatidae (Aves, Anseriformes) du Miocene de France. Révision systematique et évolution. *Docum. Lab. Geol. Lyon*, 99: 137-157), after the analysis of Portis's type material, put the two fossil species in the genus *Anas*, following their morphological characteristics, without further discussion on their validity at specific level. More recently Mlíkovský (2002, *Cenozoic birds of the World, part 1: Europe*. Ninox Press Praha, 405 pp.) discussed the systematic position of these two species; Mlíkovský (2002, op. cit.) followed the opinion of Cheneval about the generic attribution of these two species, and also synonymysed them with the living species *Anas platyrhynchos*. In a recent revision of the Plio-Pleistocene Italian fossil birds, Bedetti (*Le avifaune fossili del Plio-Pleistocene italiano: sistematica, paleoecologia ed elementi di biocronologia*. Unpublished PhD Dissertation, Università "La Sapienza" di Roma, 188 pp., Roma) restudied the Portis type material together with new material collected in the Pietrafitta mine. Pietrafitta is a lignite mine situated in the Tiberino Basin (Perugia, Central Italy), where several bird bones have been found together with a rich mammal association of the Early Pleistocene (MN 18). The revision of Portis's type material of both *Aythya aretina* and *A. sepulta* confirms that they belong to the genus *Aythya*, and not *Anas*, as stated by Cheneval. Only a distal ulna, originally described as *Aythya sepulta*, shows the morphological characteristics of the genus *Anas*. Moreover the analysis of the material from Pietrafitta, which contains the same osteological elements as the type material and some more elements, like humeri, ulnae and coracoids, allows us to confirm the validity of these two taxa and better illustrate their osteological characteristics. In particular *Aythya aretina* is a big species, as big as *Somateria mollissima*, and so bigger than any other *Aythya* species already known; *Aythya sepulta* is much smaller, but can be separated from the similar-sized living species by some morphological characteristics in the coracoid and in the proximal humerus. The two species *Aythya aretina* and *A. sepulta* are known only from the Upper Pliocene-Early Pleistocene and seem to be endemic to the Plio-Pleistocene lacustrine basins of Central Italy and they have not been found in earlier Italian bird assemblages (Bedetti, 2003 op. cit.). So, together with other extinct bird species, some of them already described by Portis, they are part of the Plio-Pleistocene bird fauna which became extinct at the end of the Villafranchian (MNQ 19).

A PHYLOGENETIC REASSESSMENT OF THE FOSSIL RECORD OF TINAMOUS (PALEOGNATHAE: TINAMIDAE)

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The scant fossil record of tinamous is mostly limited to isolated bones. Although ghost lineage inference (based on the Paleocene record of its sister-group, the ratites) indicates a much deeper origin, the known fossil record of tinamous is limited to the Early Miocene-Present interval. The earliest fossils are from the Pinturas and Santa Cruz formations of southern Patagonia (Argentina). Fossil tinamous are also known from the Lower-Middle Monte Hermoso Formation and the Upper Pleistocene (Buenos Aires and Chapadmalal formations) of this country. No Tertiary fossils have been recorded outside Argentina — only Pleistocene remains are known from Peru and Brazil. While Tertiary records appear to belong to extinct taxa (e.g., unnamed taxa from the Early Miocene and the Lower-Middle Pliocene *Eudromia olsoni* and *Nothura parvula*), most Quaternary tinamous have been assigned to living species (the sole published exception is *Nothura paludosa* from Argentina). In order to assess the phylogenetic placement of these fossils, we have scored their morphological information within a data matrix of 107 osteological characters and 40 living species of tinamous. The distribution of these fossils within the resultant cladograms is discussed in light of their significance for the understanding of the evolution of the two main ecological subdivisions of these birds—the forest-dwelling taxa (traditionally classified in the paraphyletic taxon "Tinaminae") and the open-area tinamous (the monophyletic Nothurinae).

THE EXTINCT CALIFORNIA TURKEY FROM RANCHO LA BREA VERSUS MODERN SPECIES: OSTEOLOGICAL EVIDENCE FOR RELATIONSHIPS WITHIN THE GENUS *MELEAGRIS*

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Although the subject of several studies, the relationship of the extinct, late Pleistocene California Turkey, *Meleagris californica*, to the modern taxa *Meleagris gallopavo* and *M. ocellata* had not been definitively established. Fossil remains of the California Turkey at Rancho La Brea are not only numerous, but also very well preserved. These attributes made possible thorough studies of all major, and many minor, skeletal elements, including statistical analyses. The shortage of modern comparative specimens of these variable taxa had hindered attempts to resolve the problem of relationships in the past, but this issue was not a factor in this study. Mensural and osteological characters differentiating the three taxa will be presented, and the taxonomic implications will be discussed.

SYSTEMATICS OF THE AUSTRALIAN GIANT MEGAPODES *PROGURA* (AVES: MEGAPODIIDAE)

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Australia's largest megapode was *Progura gallinacea* De Vis, 1888, from Plio-Pleistocene deposits in southeastern Queensland. A second species, *P. naracoortensis* Van Tets, 1974, from southeastern South Australia, was initially distinguished by different leg proportions and size; it was later suggested that there might be only a single, sexually dimorphic species. An examination of extensive collections of unstudied material from the Naracoorte Caves indicates that there is only a single species, with size differences apparently individual in nature. The genus *Progura* is not separable from the modern genus *Leipoa*, and *P. gallinacea* appears to be the megafaunal representative of the living *Leipoa ocellata* (Malleefowl).

A NEW PALEOCENE-EOCENE AVIFAUNA FROM MOROCCO: THE EARLY DIVERSIFICATION OF THE PSEUDO-TOOTHED BIRDS (AVES, ODONTOPTERYGIFORMES)

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The phosphatic beds of the Ouled Abdoun Basin (Morocco) range from Upper Cretaceous to Lower Eocene in age. These marine deposits have yielded a very rich vertebrate fauna. The first avian remains have been collected in the course of a joint paleontological fieldwork, which has begun in 1996 in collaboration with the Ministère de l'Energie et des Mines and the Office Chérifien des Phosphates of Morocco. Fossil birds are found in beds dated as upper Paleocene (Thanetian) and Lower Eocene (Ypresian). Most of them, however, come from a bone-bed located in a level dated as Lower Eocene (basal Ypresian). They consist of partial skulls and isolated long bones preserved in three dimensions. They constitute the oldest neornithine avifauna in Africa.

A new Prophaethontidae has been described on the basis of a single skull [BOURDON, E.; BOUYA, B. & IAROCHÈNE, M. Earliest african neornithine bird: a new Prophaethontidae (Aves) from the Paleocene of Morocco. *Journal of Vertebrate Paleontology*, in press]. Other remains have been associated with the holotype. This new species is fairly abundant in the Ouled Abdoun Basin. The pseudo-toothed birds (Aves, Odontopterygiformes) are the best-represented taxon in the Ouled Abdoun avifauna. They are very similar to the contemporaneous pseudo-toothed birds from the London Clay of the Isle of Sheppey, England. Two new species are assigned to the genus *Odontopteryx* Owen, 1873, and three new species in two new genera are tentatively assigned to the Dasornithidae Harrison and Walker, 1976. These new species are among the oldest known representatives of the pseudo-toothed birds and represent the most diversified odontopterygiform fauna. At least seven species that do not belong to the two predominant taxa are present in the Ouled Abdoun Basin.

A preliminary cladistic analysis shows that Odontopterygidae and Dasornithidae form a monophyletic group. Among the synapomorphies that support this clade are the presence of elongated basipterygoid processes at the ventral corners of the parasphenoidal rostrum, a very small temporal fossa, a greatly enlarged area of origin of the pseudotemporalis superficialis muscle, a unique conformation of the cotyles for articulation with the quadrate bone, and an elongated pneumotricipital fossa of the humerus. Monophyly of the Procellariiformes, Gallo-Anseriformes, and a group that comprises Balaenicipitidae, Scopidae and members of the Steganopodes sensu Cracraft [CRACRAFT, J. 1985. Monophyly and phylogenetic relationships of the Pelecaniformes: a numerical cladistic analysis. *The Auk*, **102**: 834-853] is well supported. The pseudo-toothed birds are not nested within one of these clades. This analysis also shows that the Pelecaniformes are not monophyletic.

NEW REMAINS OF THE GIANT BIRD *GASTORNIS* FROM THE PALAEOGENE OF FRANCE

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Remains of the giant ground bird *Gastornis* were first reported from the basal Eocene of Meudon, near Paris, in 1855. Since then, only a few French localities have yielded *Gastornis* specimens, most of them coming from the Late Palaeocene (Thanetian) of Cernay and Berru, near Reims, in the eastern Paris Basin. Recent finds from both an already known locality in the Paris Basin and a new one in southwestern France shed new light on both the anatomy and the geographical distribution of European *Gastornis*.

A Gastornis mandible from the Thanetian of Berru (Marne, eastern France)

A well preserved lower jaw has been found in the Late Thanetian fluvial beds of the Mouras quarry, at Berru, near Reims. It is of approximately the same age as the *Gastornis* remains described by Lemoine (1878, 1881) from the nearby locality at Cernay. This specimen bears no resemblance whatsoever to the so-called lower jaw referred to *Gastornis* by Lemoine, which was shown by Martin (1992) to be a composite of turtle and fish elements. With its robust build, it long symphysis, and its prominent coronoid region bearing a strongly marked muscle scar on its lateral surface, it very closely resembles in all respects the mandible of "*Diatryma*" *gigantea* from the Lower Eocene of North America. These close resemblances support the idea, already advocated by Buffetaut (1997, 2000), that *Diatryma* Cope, 1876 is a junior synonym of *Gastornis* Hébert, 1855, so that the proper name for the giant ground birds of the Palaeocene and Eocene of both Europe and North America is *Gastornis*.

A Gastornis tibiotarsus from the Sparnacian of Saint-Papoul (Aude, southern France)

A well preserved left tibiotarsus has been found in non-marine Sparnacian beds in a quarry near the village of Saint-Papoul, west of the city of Castelnaudary (Aude, southwestern France). It is similar in size and shape to the (now lost) lectotype of *Gastornis parisiensis* from the basal Sparnacian of Meudon, but is more complete, in that the proximal end, missing from the Meudon specimen, is almost completely preserved. The proximal end shows great similarities with that of "*Diatryma*" tibiotarsi from North America, further reinforcing the conclusion that *Gastornis* and "*Diatryma*" are congeneric.

This is the first record of *Gastornis* from southern France, and its southernmost European occurrence so far. Fragments of large bird eggshells have long been known from the continental Sparnacian of both Provence and Languedoc, in southern France, and have sometimes been tentatively referred to gastornithids. However, no skeletal remains of such birds were hitherto known from the Palaeogene of southern France. The specimen from the Sparnacian of Saint-Papoul shows that *Gastornis* did occur there, and lends support to the idea that the large bird eggs from the Palaeogene of Languedoc and Provence are indeed gastornithid eggs (although only the discovery of embryonic remains *in ovo* could unambiguously demonstrate it).

PYROCLASTIC LAGERSTÄTTEN IN MESOZOIC SEDIMENTS OF NORTHEASTERN CHINA

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A remarkable number of well-preserved fossil birds have come from early Cretaceous deposits in Liaoning Province, China. The preservation of feathers and body outlines are well known in many of these, especially *Confuciusornis*. Additionally, 1000's of *Confuciusornis* specimens occur in a single mass death assemblage in the lower Yixian Formation. Taphonomy has not yet solved how vast numbers of these birds were deposited. Questions remain about how they may have been killed and preserved in large numbers. An examination of the geologic processes active during this time give further insight into the taphonomy as well as preservation of these early birds.

Tectonic activity in northeastern China included faulting that produced numerous basins and intense volcanism during the Mesozoic. These basins filled with lacustrine and volcanoclastic sediments as well as the remains of flora and fauna living in the surrounding biota as well. The organisms killed during the volcanic activity in the area included *Confuciusornis*. Articulated skeletons, soft tissues, and integument preservation suggests rapid burial by excess sedimentation after the volcanic eruptions. Enhancing the quality of the preservation during diagenesis was the release of chemical constituents from the alteration of the volcanic ash. The above combined geologic processes resulted in a remarkable fossil *Konservat-Lagerstätte* termed the Jehol Biota.

The fallout tuff layers in this area also provide isotopic age dates critical to the understanding of paleonenvironment, paleoecology, and evolution of the faunal and floral elements. Furthermore, analyses of volatile contents of these sediments have been reported as coincident with the mass death assemblages, but from different gaseous components. Data indicates the volcanic eruptions that produced the sediments occurred in a narrow window of time and provided mechanisms for death such as atmospheric poisoning and greenhouse effects. Additionally, the volume of volcaniclastic ash suggests it was a highly explosive 'supervolcano' and plinian in nature.

THE WRIST AND MANUS OF ARCHAEOPTERYGIANS: AVIAN, NOT MANIRAPTORAN

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Recent confirmation that the digits of the avian manus are II, III, and IV, and not I, II, and III as in theropods, brings into question the purported homologies recognized by many as existing between the wrist and manus of birds and those of theropods. A close examination of the wrist and manus of five archaeopterygians confirms the presence of numerous previously recognized, as well as unrecognized, derived avian characters. These include, but are not limited to, metacarpal II very short, “affixed” to, and slightly wrapping under, metacarpal III for most of length; metacarpal II with small Processus extensorius for attachment of M. extensor metacarpi radialis; metacarpal IV with proximal end lying well distal to proximal ends of metacarpals II and III, wrapping under and “affixed” to “palmar” surface of metacarpal III; joint between metacarpal II and phalanx 1 typically avian, very restricted; joints between metacarpals III and IV and their respective phalanges relatively immobile; and “palmar” surfaces of all distal phalanges facing anteroventrad when wing extended. The above features are not found in maniraptoran theropods, but their more highly derived counterparts are found in all modern birds with wings. The avian structure of the wrist and manus of archaeopterygians indicates significant functional differences compared to that of theropods, which is not surprising given that different digits are involved.

JUVENILE ENANTIORNITHINE BIRDS FROM THE LOWER CRETACEOUS OF LAS HOYAS (SPAIN)

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Discoveries of exquisite avian remains contained in the Lower Cretaceous lacustrine limestones of Las Hoyas, central Spain, have provided critical information for understanding the diversity and evolution of early birds. Among these fossils is a bone aggregate of at least four similarly ossified individuals, that was previously interpreted as a pellet. The presence of open neurocentral sutures and the lack of fusion of several elements forming compound bones (i.e., carpometacarpus, tibiotarsus, tarsometatarsus) indicates an early juvenile age for these individuals. Qualitative and quantitative characters of the skeletons contained in this aggregate indicate the presence of three different types of birds, all of which show synapomorphies of Enantiornithes. One of these skeletons displays several unique characters—primarily in the tail—that indicate that it belongs to a new enantiornithine species. The remaining two types of birds are less easily identifiable and whether or not they correspond to early juveniles of any of the previously identified enantiornithines from Las Hoyas (*Iberomesornis romerali*, *Concornis lacustris*, and *Eoalulavis hoyasi*) remains unclear. The anatomy of the fossils contained in the bone aggregate is discussed in this paper. These juvenile enantiornithines provide evidence of new morphologies for the group and anatomical information relevant to the understanding of the evolutionary origin of the avian pygostyle.

BONE MICROSTRUCTURE OF EXTANT AND EXTINCT BIRDS

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Much of our understanding of the bone microstructure of extinct birds derives from comparisons with modern bird taxa and other vertebrates. Studies on a variety of modern vertebrates have demonstrated that bone microstructure is affected by a host of different factors. In this presentation, results of studies undertaken to examine the effect of ontogenetic growth, ovulation, dietary stress, lifestyle adaptations and bone depositional rates on various modern bird taxa is presented. The bone microstructure of several fossil birds (represented by both ornithurine and non-ornithurine Mesozoic taxa, and Cenozoic Neornithes) will also be presented. By comparing the bone microstructure of the extant and extinct taxa, insight into various aspects of the biology of the fossil taxa can be reasonably deduced.

NEW AVIALAN REMAINS FROM THE CRETACEOUS AND EOCENE OF MONGOLIA: IMPLICATIONS FOR THE TIMING AND PATTERN OF AVIAN DIVERSIFICATION

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We report new avialan material from the Cretaceous and Eocene of Mongolia and the implications from phylogenetic placement of these new fossils for constraining the timing and pattern of the origin of crown clade lineages. Three new specimens were recovered from the Maastrichtian? Nemegt Formation exposed at the Gobi Desert locality of Tsaagan Khushu (Omnogov Aimag). All are partial bones with a limited number of preserved morphologies (i.e., proximal tibia, distal tibia and proximal humerus) but have a resolved phylogenetic placement as part of Ornithurae. Of these three specimens, two are not supported as part of the avian crown clade and placement of the third is unresolved with respect to Aves. These are the first avialan remains from the Nemegt Formation to be evaluated in phylogenetic analyses. Previously described specimens referred to neognath subclades of the avian crown lack synapomorphies of Aves and Neognathae and support for these referrals must be considered weak. No material from the Cretaceous of Mongolia can with confidence be referred to the avian crown; more complete specimens or further character data supporting the placement of previously described specimens is necessary.

Survey of Late Cretaceous avialan diversity from Mongolia reveals that ornithurine and enantiornithine birds are both known from the Nemegt Formation and the underlying Djadokhta/Barun Goyot Formations although ornithurine remains are more common in the Nemegt. No Djadokhta, or Barun Goyot avialan species are also known from the Nemegt Formation and the species from these formations do not appear more closely related to each other than to other avialans. The new remains further understanding of the Late Cretaceous diversity of Mongolia as small dinosaur and, indeed, small vertebrate remains generally have been rare from the Nemegt Formation.

A well-preserved avian tarsometatarsus was collected from upper Eocene deposits exposed at the eastern Gobi Desert locality of Alag Tsav (Dornogov Aimag). The new specimen is identified as part of an Eogruidae clade, although it is unclear whether it is appropriately the holotype of a new species within this clade or referable to a previously named species. The clade Eogruidae has as its current contents species named as part of the 'families' Eogruidae and Ergilornithidae, which include several lineages of completely didactylous and apparently flightless birds. These taxa have been proposed to be a dominant part of Eocene to Miocene Asian faunas as referred remains are relatively abundant in Eurasian localities across this period. Referral of the new fossil to the clade Eogruidae is on the basis of derived reduction/loss of the metatarsal II trochlea.

Phylogenetic placement of Eogruidae within Aves was investigated using a more completely known eogruid, *Eogrus aeola,* as an exemplar taxon. *Eogrus aeola* is identical to the new tarsometatarsus for all evaluated characters in common and is placed in an unresolved trichotomy with Psophiidae and Gruidae (Trumpeters and Cranes) when included in the Mayr and Clarke (2003) dataset. Given the results of this analysis, Eogruidae was analyzed in the Grues dataset of Livezey (1998) and was placed as the sistertaxon to an Aramidae + Gruidae clade. Monophyly of traditional 'order' Gruiformes has been questioned and the outgroups used in the original Grues dataset were identified through analyses assuming monophyly. Placement of Eogruidae is robust to both removing these outgroup assumptions, however, and to swapping in the more incomplete new fossil as an exemplar for Eogruidae. Eogruidae is the first phylogenetically placed fossil calibration a part of Gruoidea (≈Psophiidae + Aramidae + Gruidae). Its placement constrains the divergence of stem lineage Aramidae + Gruidae from Psophiidae to have occurred by the middle Eocene.

WRECKS AND RESIDENTS: THE SUBFOSSIL GADFLY PETRELS (PTERODROMA SPP.) OF THE CHATHAM ISLANDS, NEW ZEALAND

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The remarkable assemblages of Holocene subfossil bird remains known from the Chatham Islands, some 860 km east of New Zealand, have revealed that the archipelago formerly supported one of the world's richest and most diverse breeding communities of petrels. Some 31 species of Procellariiformes have been recorded from dune, midden and cave deposits. However, dominating the petrel assemblage are the remains of gadfly petrels *Pterodroma* sp., of which at least 6 species have been previously identified, including both breeding residents and likely vagrants. Particularly abundant are bones of the now critically endangered endemic species Chatham Island Taiko *P. magentae* and Chatham Island Petrel *P. axillaris*. Specimens of another common species have frequently been compared with Mottled Petrel *P. inexpectata*, but have also been suggested as representing a third possible endemic species, now extinct. In this presentation, we will critically review the identification of Pterodroma remains from the Chatham Islands, with a view to determining the status of the unknown taxon. If this potentially undescribed species can be reliably diagnosed, it will be the first confirmed global extinction of a petrel in the Chatham Islands.

A NEW SPECIES OF OWL (AVES: STRIGIFORMES) FROM THE EOCENE WASATCH FORMATION, WYOMING AND A SYSTEMATIC REVISION OF FOSSIL OWLS

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The owls have a long evolutionary history and several taxa have been described from the Paleocene and onwards. I will here present a new taxon collected in the middle Eocene Green River formation in Wyoming U.S.A. I also conduct a phylogenetic analysis of recent and fossil owls in order to shed light on their intra-ordinal relationships. The phylogenetic analysis resulted in a largely unresolved tree, but some groupings of owls were discovered. The new species is closely related to two species of the genus *Necrobyas* of the Paleogene of Europe. It is argued that this genus is another example of terrestrial organisms that were distributed in both Europe and North America during the Eocene.

THE PHYLOGENY OF PALAEOGNATHOUS BIRDS: ADDING FOSSILS TO THE BASE OF THE TREE

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By use of 166 osteological, integumentary and eggshell characters, we present a comprehensive phylogenetic analysis of all extant (and most extinct) palaeognathous birds. Significantly, our matrix includes 60 cranial characters, the bulk of which are formulated for cladistic analysis for the first time. Adding to a solid framework topology comprising the extant ratites and tinamou, we have further extended our analysis to include the recently extinct moas as well as the elephant bird (*Aepyornis*). We also incorporated into the matrix a new and exceptionally well-preserved specimen of the Lower Eocene fossil palaeognath Lithornis. The Cretaceous ornithurines *Ichthyornis* and *Hesperornis* were employed as outgroups alongside representatives of Galliformes and Anseriformes. A heuristic parsimony analysis under equal weights was performed using the program TNT. The resolution of the tree obteined was complete and has a length of 440 steps. The analysis recovered monophyly of Palaeognathiformes and places Tinamidae as the most basal branch wthin palaeognaths (contrary to ome recent molecular analyses), followed by *Lithornis* and the traditional grouping of ratites as a monophyletic group. Significantly, our analysis provides morphological support for the placement of elephant birds, kiwi and moas together within a single clade.

THE DISTAL END OF THE AVIAN FEMUR: MORPHOLOGY AND TERMINOLOGY

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Birds have the lateral condyle of the femur subdivided into the fibular trochlea and the tibial facet. The two parts are separated by a usually prominent edge known as the tibiofibular crest (Baumel & Witmer, 1993). Traditionally, three terms have been applied to the distal projections of the avian femur (Howard, 1929): “internal condyle” for the medial condyle, “external condyle” for the medial part of the lateral condyle (i.e., the tibial facet and the tibiofibular crest), and “fibular condyle” for the lateral part of the lateral condyle. This traditional scheme continues to be occasionally used, e.g., for *Avimimus* (Vickers-Rich et al., 2002), except that the terms “internal” and “external” are replaced by “medial” and “lateral”, leading to a confusing concept of the avian lateral condyle that comprises only the medial part of the lateral condyle in the widely used, comparative sense. Although the comparative definition of the lateral condyle has been extended to the avian femur in current terminological standards (Baumel, 1979; Butendieck et al., 1981; Witmer and Baumel, 1993), two important and well-defined structures, the fibular condyle and the external condyle, have been left without names.

The fibular condyle is part the lateral condyle, and thus referring to it as a condyle leads to a unwieldy conceptual construct of a condyle in a condyle. The external condyle comprises a more or less convex tibial facet with its lateral margin protruding as the tibiofibular crest which separates the tibial facet from the fibular trochlea. The tibial facet has been ignored by the current terminological standard (Witmer and Baumel, 1993: fig. 4.16), inviting the use of the name “tibiofibular crest” for the entire external condyle. This may seem *prima facie* plausible as in the majority of modern birds the external condyle is essentially reduced to a prominent tibiofibular crest with the tibial facet on its medial side. However, applying the name “tibiofibular crest” to the entire external condyle is misleading because the external condyle is primarily a condyle, that is, an articular structure, and in some birds, such as the cormorants, it is broad and cannot be sensibly conceptualized as a crest. In order to make the terminology consistent and complete, two new terms are proposed, *semicondylus fibularis* for the fibular condyle and *semicondylus tibiofibularis* for the external condyle (inclusive of the tibiofibular crest). Both semicondyles are parts of the lateral condyle.

The proposed terminology helps clarify the homologies of the distal femoral details. The theropods have a prominent ectocondylar tuber projecting caudally from the lateral condyle. The ectocondylar tuber varies in shape from cuboid with a flattened caudal facet to lenticular with a narrow edge. Apparently influenced by Baumel’s (1979) terminology, Rowe (1989) identified the entire lenticular tuber of *Syntarsus* as the tibiofibular crest and Chiappe (1996) put forward an explicit hypothesis that the ectocondylar tuber is homologous with the avian tibiofibular crest, that is, the tibiofibular semicondyle, which is relatively broad in all basal birds including the Enantiornithes (Chiappe and Walker, 2002).

THE STAPES OF THE OILBIRD *STEATORNIS* IS UNIQUE WITHIN AVES.

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The morphology of the bony stapes (columella) in the vast majority of birds represents the primitive condition for the Class Aves, and is similar to the plesiomorphic element in most reptiles, including dinosaurs, characterized by a flat footplate and slender bony shaft. Unique pockets of derived morphologies have been useful in corroborating relationships, particularly in suboscine passerines and in major coraciiform families, including trogons. The stapes of *Steatornis*, illustrated here, is characterized as somewhat resembling a 'bullet casing with half of the side removed'. This structure is unique within the Caprimulgiformes and the Class Aves and is therefore of little interest in providing information on the relationship of the oilbird.

THE AVIAN AUTOPOD – DIGIT HOMOLOGY, AN ALTERNATIVE VIEW.

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The seemingly intractable problem of the identification of the avian manual digits has been characterized as a dilemma of conflicting developmental and paleontological data (and phylogenetic systematics), the former supporting an avian hand with digits II-III-IV, the latter, a reduction pattern similar to theropod dinosaurs, with a tridactyl hand composed of digits I-II-III. The identification of the digits of the avian hand as II-III-IV, is based on a highly conserved pattern of development among amniotes, in which there is a stereotyped, early developmental pattern characterized by a Y-shaped condensation. The strongly staining, postaxial element forms a "primary axis", a linear array that invariably identifies, in sequence, ulna-ulnare-distal carpal IV – and ultimately –digit IV. The basic pentadactyl ground plan of the avian manus has been confirmed recently by a variety of independent studies, including early ostrich embryology, in which the anlagen for all five digits are present, but the anlagen for digits I and V are vestigial, the former disappearing by day 17. A homeotic shift of digits I-III into digits II-IV in theropods has been invoked to account for the conflicting data. Another explanation may be that birds come from a separate lineage from the 'main-line' theropods, and that the so-called maniraptoran theropods with avian-like hands are secondarily flightless birds, or remnants of the early avian radiation with varying degrees of flight capability. The discrepancies that arise between different methods draw attention to how one deals with developmental patterns as a means of establishing homologies in phylogenetic reconstruction. Drawing broad inferences from cladistic analyses can be risky given the track record of this methodology in avian systematics.

A DIMINUTIVE, LATE OLIGOCENE ALBATROSS (DIOMEDEIDAE) FROM THE LINCOLN CREEK FORMATION, PACIFIC COUNTY, WASHINGTON STATE

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Three concretions containing bird bones have been collected along the north shore of the Columbia River near the townsite of Knappton, in Pacific County, Washington. The concretions are derived from deep-water strata of the upper part of the Lincoln Creek Formation. Molluscan and foraminiferan fossils, along with recent magnetostratigraphic data, indicate that these rocks are Late Oligocene in age. The bird fossils (LACM 130330, 130331, and USNM 526218) are associated bones from three individuals, and all appear to be the same species of a small albatross, family Diomedeidae. Preliminary study indicates that they represent an albatross much smaller than any living species of Diomedeidae, possibly related to species of *Plotornis* from Early and Middle Miocene rocks in France and other small albatrosses from Late Oligocene to Middle Miocene rocks in South Carolina and Maryland. The new fossils from Washington are the oldest known albatrosses from the Pacific Ocean.

THE PENGUINS (SPHENISCIDAE) FROM THE NEOGENE PISCO FORMATION IN PERU

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The Pisco Formation is well known for its abundant marine vertebrate fauna of Miocene to Pliocene age; the marine bird fauna is the richest from the Neogene of South America.
Already Noriega & Tambussi [1989, Un Spheniscidae (Aves, Sphenisciformes) del Mioceno Tardio de la costa sur de Peru. – Abstract of VII Jornadas Argentinas de Paleontologia de Vertebrados. – *Ameghiniana*, **26**(3-4): 247] and Cheneval [1993, L'avifaune Mio-Pliocène de la formation Pisco (Pérou).Étude préliminaire. - *Docum. Lab. Géol. Lyon*, **125**: 85-95] mentioned a probable new penguin taxon in the Pisco Formation. Recently, two new fossil penguin species from the Pisco Formation have been named and have been referred to the actual genus *Spheniscus*: *S. urbinai* Stucchi, 2002 [Una nueva especie de *Spheniscus* (Aves: Spheniscidae) de la Formatión Pisco, Perú. – *Boletín de la Sociedad Geológica del Perú*, 94: 17-24] from different sites of Late Miocene to Early Pliocene age, and *S. megaramphus* Stucchi, Urbina & Giraldo, 2003 [Una nueva specie de Spheniscidae del Mioceno Tardío de la Formacíon Pisco, Perú. – *Bulletin de l'Institut Français d'Études Andines*, 32 (2): 361-375] from the Late Miocene of Montemar. These two species are of same size, similar to recent *S. humboldti*, and are described as differing only by cranial characters.

An extraordinary rich material of several hundreds isolated bones, but also several partial and subcomplete skeletons, as well as two complete skeletons of fossil penguins from the Pisco Formation of Peru (from the Muséum National d'Histoire Naturelle Paris and the Staatliches Museum für Naturkunde Karlsruhe) is now studied. The fossils come from different localities in the Sacaco area and the more northern Department of Ica and are of Middle Miocene to Early Pliocene age: Cerro la Bruja (Middle Miocene, 12-14 Ma), El Jahuay (~9 Ma), Late Miocene; Aguada de Lomas (~7-8 Ma), Late Miocene; Montemar (~6 Ma), Late Miocene; Sud-Sacaco (~5 Ma) and Sacaco (~3,5 Ma), both Early Pliocene.
Within this material a distinction of the two taxa *S. urbinai* and *S. megaramphus* is not possible, but an additional, small sized penguin taxon is recorded from the Middle Miocene.

REVISION OF THE PHASIANIDS (AVES, GALLIFORMES) FROM THE LOWER MIOCENE OF ST.-GÉRAND-LE-PUY (FRANCE)

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Three phasianid species of *Palaeortyx*, differing by their size, have been described from the Lower Miocene of St.-Gérand-le-Puy; they are *Palaeortyx brevipes* Milne-Edwards, 1869, *Palaeortyx gallica* Milne-Edwards, 1869, *Palaeortyx phasianoides* Milne-Edwards, 1869, Later, *Palaeortyx intermedia* Ballmann 1969, a taxon originally described from the Early Miocene of Wintershof-West (Southern Germany), was additionally mentioned from St.-Gérand-le-Puy.

Recently, *Palaeortyx brevipes* has been synonymized with *Palaeortyx gallica*, and *Palaeortyx intermedia* has been synonymized with *Palaeortyx longipes* Milne-Edwards, 1869 by Mlíkovský 2000 (Early Miocene quails (Aves: Phasianidae) from Saint-Gérand-le-Puy, France. *Časopis Národního Muzea Rada Přírodovědná*, 169 (1-4), 91-96). The latter was described from the Middle Miocene of Sansan (France) and recognized formerly by Ballmann 1969 (Les oiseaux miocènes de La-Grive-Saint-Alban (Isère). *Geobios*, 2, 157-204.) as a junior synonym of *Palaeortyx phasianoides*.

This present revision of the phasianids from St.-Gérand-le-Puy, based on "old" and new fossil material [Göhlich & Mourer-Chauviré (in press): Revision of the phasianids (Aves, Galliformes) from the Lower Miocene of St.-Gérand-le-Puy (France). *Paleontology*], leads to differing results: We confirm the presence of four different species of *Palaeortyx* in St.-Gérand-le-Puy; *Palaeortyx brevipes*, *Palaeortyx gallica*, and *Palaeortyx phasianoides* are recognized to be separate and valid taxa. *Palaeortyx intermedia* is synonymized with *Palaeortyx prisca*, which was described from the Middle Miocene of Sansan (France).

Additionally, it was recently proposed (Mlíkovský 2002: *Cenozoic birds of the world, part 1: Europe*. Ninox Press, Praha, 406 pp) to refer the species *Palaeortyx gallica* to the recent genus *Coturnix* as well as *Palaeortyx prisca* to the recent genus *Alectoris*. However, the present morphological comparisons and metric variability statistics on some recent quails and partridges of the genera *Coturnix*, *Perdix*, and *Alectoris* show osteological differences between these Recent and Miocene taxa and confirm the distinction of the Tertiary genus *Palaeortyx*.

FIRST RECORD OF *OSTEODONTORNIS* (AVES: PELAGORNITHIDAE) FROM MEXICO

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A very large, distal end of the right humerus of a bird was found in marine strata near Rancho Trinidad in Baja California Sur, Mexico. These rocks are mapped as the lower part of the Trinidad Formation, and are Late Miocene in age on the basis of microfossils (diatoms and radiolarians) and mollusks. They were deposited at depths of at least 100 meters (mid-platform). The bone is referred to the extinct Pelagornithidae because of its large size, its extremely thin bone-walls, and similarity to other described pelagornithid fossils. The Late Miocene holotype skeleton of *Osteodontornis orri* Howard from California is crushed and does not allow for much in the way of comparisons other than to say that the Trinidad Formation bone represented a bird that was about the same size or only slightly smaller. Other vertebrate fossils found in the Trinidad Formation are sharks, rays, a Blue Marlin (*Makaira nigricans*) and other teleosts, and cetaceans. The Trinidad Formation bone is tentatively referred to *Osteodontornis orri*, and is the first bird fossil reported from the formation, and only the second record of the Pelagornithidae from Mexico.

EVOLUTION OF AVIAN REPRODUCTIVE CHARACTERS IN NON-AVIAN SAURISCHIAN DINOSAURS.

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The reproductive characters of crocodiles and birds greatly differ but a series of evolutionary features found among non-avian dinosaurs mitigates the existing gap in reproductive disparity of these extant groups of archosaurs. This study examines the evolution of several reproductive characters within well-identified saurischian dinosaurs. The most primitively known stage is represented by titanosaur sauropods, which retain the crocodilian type of *en masse* ovideposition within nests likely covered with vegetation, minimal parental care, and single-layered symmetrical eggs with relatively thick and nodular eggshells. A significant departure from this primitive reproductive condition is found among non-avian theropods. Brooding and an avian type of monoautochronic ovideposition can be inferred for the oviraptorid *Citipati osmolka*. In addition, its elongate eggs show a slight degree of asymmetry (one pole is somewhat bigger and more rounded than the other). The eggshell of *C. osmolka* is also bi-layered, with aprismatic (well-distinct) crystallographic layers, evolutionary features that are congruent with the principles of mechanical stress resistance where multiple laminations increase resistance to extrinsic forces. A similar eggshell structure is found in the dromaeosaurid *Deinonychus antirrhopus*. Some evidence also supports the presence of brooding behaviour in this theropod taxon. Similar reproductive characters are also present in the troodontid *Troodon formosus*. However, the eggs of this taxon differ from *D. antirrhopus* and *C. osmolka* by their well-developed asymmetry and their prismatic (not well-distinct) eggshell crystallographic layers. Furthermore, these eggs are recovered in sub-vertical position, narrow pole down in the substrate, within an open U-shaped rimmed nest as opposed to the sub horizontal position of the eggs of *C. osmolka*. Eggs of another troodontid, *Byronosaurus jaffei,* are smaller but overall similar to those of *T. formosus* yet, clutches of *B. jaffei* show a definitively unpaired distribution. Egg shape and clutch spatial arrangement suggest that *B. jaffei* might have shared with extant birds the presence of a single functional ovary. All these maniraptors display diverse degrees of avian reproduction traits strongly supporting the theropod ancestry of birds but all had a body mass that would not be congruent with the expected skeletal size reduction observed at the transition from non-avian to avian theropods, a body size reduction that should be mirrored by a coeval decrease in egg volume.

Reproductive traits supports the theropod-bird evolution by the acquisition of various avian oological characters among diverse theropods lineage and as for integuments demonstrates that these characters thought to be exclusively avian were already present in non-avian saurischian taxa.

EVIDENCE FOR A LATE EVOLUTION OF AVIAN ENDOTHERMY AND IMPLICATIONS FOR THE ORIGIN OF FEATHERS.

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Basal birds (e.g., *Archaeopteryx*, enantiornithines) are often presumed to have been endothermic simply because they have feathers and could fly. However, several lines of evidence suggest that non-ornithurine birds may not have attained a fully endothermic metabolic status: 1) available skull material indicates that the nasal cavity of *Archaeopteryx* and *Cathayornis* retained a comparatively primitive morphology, with large paranasal sinuses and a constricted nasal passage that likely lacked complex respiratory turbinates; 2) the ribcage and sternum of *Archaeopteryx* and enantiornithine birds still lack the specialized hinged ribs and sternocostal joints associated with lung ventilation in modern birds. In contrast, both the nasal cavity and the ribcage skeleton of Early to Late Cretaceous ornithurine birds were drastically modified beyond those of their ancestors, and closely resemble those of modern birds. These observations suggest that the expansion of aerobic capacity, which resulted in the evolution of avian endothermy, took place principally in ornithurines. This is consistent with the emerging paleoecological picture: many Cretaceous ornithurine birds appear to have occupied marine and shorebird-like niches, wherein resources are often spread thinly over long distances. Increased aerobic capacity would thus have provided considerably selective advantage to these taxa. In contrast, enantiornithine and other basal birds apparently were largely terrestrial birds with perching capabilities, which lived in relatively more compact resource environments, such as forests, that did not require long-distance foraging. In these environments, ectothermically-powered flight may still have been adequate. However, this scenario of endothermy evolving well after powered flight necessitates a reexamination of possible selective factors in the origin of feathers.

A DEVELOPMENTAL VIEWPOINT OF THE BIRD WING SKELETON & ITS HOMOLOGIES.

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The paper will consider the following issues. The developing bird wing as a specialisation of the general developmental 'bauplan' for the pentadactyl skeleton. Evidence from the chick embryonic wing skeletogenic pattern in establishing homology in the definitive wing skeleton, especially the main digits. These appear to be 2,3,4 on the basis of timing, position & connections. Specialisations (eg of the digital arch & ulnare) of the wing skeletogenic pattern and implications for establishing homology. Critical discussion of the 'frame shift' hypothesis of molecular identity transformation that theropod identities for 1,2,3 become shifted to avian digit blastemas 2,3,4. Difficulties raised by the embryological evidence that wing digits are 2,3,4 for the 'dinosaur-bird' theory.

TERRESTRIAL LOCOMOTION ADAPTATIONS IN BURROWING OWL, AS COMPARED WITH LITTLE OWL

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The present study is an attempt to evaluate some locomotion adaptations in the Burrowing Owl (*Athene cunicularia*), which is highly modified for a terrestrial life-style, as compared with the Little Owl (*A. noctua*). The Burrowing Owl is characterized by the following morphological features of the hind limb that as we suppose are connected with mastering of cursorial way of life.

Elongation and thinning of the distal limb elements (tibiotarsus and especially tarsometatarsus) and reduction of the femur caused pace increase.

The curve of the femur in the dorsal direction is due to counteraction to femur retractors and femorotibiales muscles tending to bend the shaft of the bone ventrally. The ventral curve of the tarsometatarsus is also related to resistance to powerful *m. flexor digitorum longus* (the ratio of the weight of this muscle for the Burrowing Owl is 14.4% as compared to 10.6% for the Little Owl).

Development of ossifications (sesamoids) in terminal tendons of *m. tibialis cranialis*, *m. flexor digitorum longus* is due to increase of jerky movements as they eliminate negative extensibility of the tendons.

Horizontal orientation of the *preacetabular ilium* in the Burrowing Owl moved *m. iliotrochantericus caudalis* ventrolaterally and thus brought it to a more effective position for inward rotation of the hind limb (which compensates the side effect of the outward rotation in femur retractors during locomotive jerk).

Reduction in size of the antitrochanter allowed to strongly abduct the femur and the whole leg. Consequently, the principal role in femur abduction limitation was transferred from the antitrochanter to the additional differentiated ligaments of the caudal part of *capsula articularis* (*lig. ischiofemoralis* and *lig. pubofemoralis*).

Asymmetry of the distal condyles of the femur is connected with greater inward rotation of the shank in the Burrowing Owl, as compared with the Little Owl, during symmetrical terrestrial locomotion, which enables it to make abrupt turns of the body on one leg while running.

Parallel fibrous pattern of *m. popliteus* (in the Little Owl this muscle has pinnate arrangement) allows to increase the amplitude of contractions therefore inwardly rotating the tibiotarsus more effectively. *Lig. transversum genus* has a branch beginning from the medial condyle of the femur and in extended position of knee joint it limits the inward movement of the shank.

Powerful development of *m. gastrocnemius* – the chief intertarsal extensor – should be taken into consideration. It accounts for 12.2% in the Burrowing Owl against 9.6% in the Little Owl.

Shortening of *lig. transversum* – the ligament on the distal end of the tibiotarsus holding the terminal tendon of *m. tibialis cranialis* – reduces the arm of force of the muscle and transfers this system characteristic for owls to despecialised state. This reversion to the initial structure enables to flex the intertarsal joint with greater angular velocity but it is accompanied by reduction of the moment of force on the foot. Therefore the bulk of *m. tibialis cranialis* grows up to 10.2% for the Burrowing Owl vs. 9.3% for the Little Owl.

The lateral process of the proximal end of the tarsometatarsus projects in the lateroproximal direction and brings *m. fibularis brevis* to a more advantageous position for inward rotation of the tarsometatarsus and stabilization of the intertarsal joint (ligament tension in it increases the jerkiness of movements). The terminal tendon of this muscle is ossified.

Some results of the current study might be extrapolated to other avian groups because of the fact, that some adaptations of limb morphology, associated with terrestriality, are universal. On the other hand, level of the morphological modifications is pronouncedly limited by necessity to retain basic functional morphological specificity of the hind limb. Such specification in owls appears to be an effective “tool” for prey capturing. The Little Owl is known for its universality of hunting techniques, which determined opportunity for further morphological experiments in new conditions: either in the absence of terrestrial predators and rivals or with abundance of prey. In the latter case restructuring leading, as a rule, to loss of some morphological features is justified. It can be observed in the example of the Burrowing Owl whose cursorial adaptations gave it an access to enormous food resources.

ASSESSING EARLY FEATHER FOSSILS

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The majority of Mesozoic feather fossils have been identified on the basis of morphology: characteristic attributes of modern avian feathers - calamus, a central rachis with branching barbs, and occasionally barbules – can be discerned. Most of these specimens quite closely resemble the feathers of modern birds, and have generated little controversy. In contrast, many of the specimens associated with nonavian, East Asian dinosaurs lack such unequivocal morphological attributes, but have nevertheless been identified as feathers or protofeathers on the basis of immunohistochemical data and/or the presumed close phylogenetic affinity to birds of the associated skeleton. These specimens figure prominently in recent hypotheses concerning the evolutionary origin of feather structure, and raise a conceptual problem – how to confidently identify the fossilized remains of feather antecedents when they lack the attributes usually associated with (modern) feather form? Here, we evaluate the assertions that these structures are feathers or feather antecedents. We accept that the histochemical approach might ascertain whether preserved materials contain alpha- and/or beta-keratin, and thus imply an epidermal origin. However, the published methodology is not powerful enough to distinguish between the beta-keratins from different sauropsid groups, and therefore cannot distinguish between scales, scutes, and feathers. To evaluate other claims of “feathered” dinosaurs, we used scanning electron microscopy to analyze samples from several of avian and dinosaurian specimens from Liaoning, China. According to Davis and Briggs (1995, Geology 2:783-786), feather fossilization involves autolithification of bacteria associated with beta-keratin decomposition, although it is unknown if these bacteria differentiated between scales, scutes, and feathers. We confirmed the presence of fossilized bacteria in *Confuciusornis* and *Caudipteryx* (Aves), and *Sinornithosaurus* (cf. Dromaeosaurus). However, because bacteria were not found in the dinosaurs *Beipiaosaurus*, *Sinosauropteryx* or the pterosaur *Jeholopterus*, we conclude that the filamentous structures of these specimens may not have an epidermal origin. This lends support to Lingham-Soliar’s interpretation (2003, Naturwissenschaften 90:428-432) of their identity as collagen fibers.

THE TRUTH ABOUT *GOBIPTERYX*

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Gobipteryx minuta was described as a palaeognathous bird from two skull fragments from the late Cretaceous Baruungoyot Formation of Khulsan site, Nemegt Depression, Southern Gobi, Mongolia (Elzanowski, 1974, 1976, 1977). It was assigned to the Enantiornithes (Martin, 1983). Then, avian embryos were described from small elongate eggs from deposits of Baruungoyot, at Hermiin Tsav site, Transaltai Gobi (Elzanowski, 1981); Elzanowski declared the opportunity of assignment of these embryos to *G. minuta*, based on the presence of a lengthened retroarticular process. Based on similarity of geologic age, the embryos of Hermiin Tsav began to be considered as belonging to the same *Gobipteryx* of Khulsan (Martin, 1983, 1995; Elzanowski, 1995), and the eggs were considered those of *Gobipteryx*. Elsewhere, we have shown that skulls of embryos and *G. minuta* are distinct (Kurochkin, 2000), in the form of the external nares, structure of the end of the beak (flat, rounded and wide in embryos and higher, pointed and narrow in *Gobipteryx*), structure of the tomium (wide and flat in embryos and narrow in *Gobipteryx*), etc. Thus, in no way can the embryos be assigned to *Gobipteryx*.

Two types of elongate eggs were found at Khulsan. The shell structure of the small and larger eggs were identical. They were assigned to the parafamily Laevisoolithidae, representing enantiornithine eggs, and named *Gobioolithus minor* and *G. major* (Mikhailov, 1991, 1996). This confirmed the existence of at least two Baruungoyot enantiornithine birds.

A new enantiornithes, *Nanantius valifanovi*, was described from Baruungoyot deposits of Hermiin Tsav on the basis of a fairly complete skeleton (Kurochkin, 1996). *N. valifanovi* appeared similar to *G. minuta* on the basis of two rows of foramina in the mandible, but different in each bird. In addition, jaw bones of *N. valifanovi* differ from those *G. minuta* in general thickness, a thin and sharp tomium (flat in *Gobipteryx*) and an appreciable groove on the dorsal premaxilla (absent in *Gobipteryx*). In the ventral symphysial part of the mandible of *Gobipteryx* there is a low smooth crest, which is absent in *N. valifanovi*.

Chiappe *et al* (Chiappe, Norell, Clark, 2001) described the skull of a new specimen (IGM-100/1011) of enantiornithine bird from the Djadokhta Formation, Ukhaa Tolgod site, Nemegt Depression, which they assigned to *G. minuta*, and *N. valifanovi* was synonymzed with this species. Their analysis utilized more than 49 characters, concluding that all three birds were extremely similar.

Our analysis of their description could not support their conclusions. We added 4 unambiguous characters to the 15 of Chiappe et al (2001), which were preserved in all three forms. *G. minuta* showed no similarity to either specimen 100/1011 or *N. valifanovi* in any of the 19 characters. 14 characters appear common for *N. valifanovi* and specimen 100/1011. *N. valifanovi* and specimen 100/1011 are distinguished on 5 characters. In another 29 characters of Chiappe et al. (2001) and 1 character chosen by us, which are not preserved in *N. valifanovi*, *G. minuta* and specimen 100/1011 are radically different in 21 characters, and have only 9 characters in common. In another 4 characters comparison is complicated owing to unpreserved or uncertain condition in *G. minuta*. However, among these 4 characters, 2 are common to *N. valifanovi* and specimen 100/1011, 1 character differs between them, and 1 character is not preserved in *N. valifanovi*.

Thus, *N. valifanovi* and specimen 100/1011 demonstrate great similarity in 16 characters, differing only in 6 insignificant characters. Together they show substantial differences from *G. minuta*. Only one conclusion is possible: specimen IGM-100/1011 represents a new species of the genus *Nanantius*, and *G. minuta* must retain its generic and specific status. Furthermore, embryos from the elongate eggs from Hermiin Tsav do not belong to *Gobipteryx minuta*, and it is certainly not possible to call these eggs, in which the embryos were discovered, "gobipteryx eggs". They all represent various enantiornithine birds of the family Alexornithidae Brodkorb, 1976. The research was supported by the grant RFBR № 04-04-48829.

NEW FOSSIL BIRDS FROM THE CRETACEOUS OF RUSSIA

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During the last few years, new data have appeared on the isolated findings of Cretaceous birds in Russia. The first early Cretaceous bird in Russia was discovered in 2000 by paleontologists of Tomsk University in Shestakovo-1 site, Kemerovskaya Province, Western Siberia. The alluvial sediments of Shestakovo-1 site belong to the Ilekskaya Svita (Aptian-Albian), with a diversity of some 30 species of terrestrial vertebrates (Alifanov et al., 1999; Leshchinskiy et al., 2000; Averianov et al., 2002). The bird is represented by a small complete metatarsus (length 26.4 mm) of unique morphology. All three metatarsalia are fused in transversal plane along their full length, besides the separated proximal ends of 3d and 4th metatarsals, the cap of the distal tarsalia is absent, the proximal surfaces of each metatarsal has its own concave cotyla, the proximal end of 2d metatarsal is moved distally in respect to the other two, the dorsal surface of 3d metatarsal bears a remarkable ridge in its proximal portion. These characters lead us to recognize this bird as a new order *incertae sedis*. In general, this metatarsus is very gracile with thin and delicate metatarsalia, the distal end of 2d metatarsal is widened and moved far proximally.

The endocast of a primitive bird was obtained by paleontologists of Saratov University in 1993 from the nearshore marine deposits of Melovatskaya Svita (Cenomanian) in Melovatka-3 site, Volgogradskaya Province, Central Russia. The specimen is 20 mm in length, and 13 mm in width. Generally it preserves the principal outlines of the avian skull. The specimen was CT-scanned. The main content of the endocast is presented as phosphorite-substituted brain tissue, and just small portions of the bones are preserved. The brain incorporates the following features: medium-sized cerebral hemispheres, connected by the dorsal dome; prominent olfactory lobes spread forward from the cerebral hemispheres; a shallow epiphiseal pit between the hemispheres on the dorsocaudal side; bulky optic lobes situated caudolaterally and somewhat ventrally to the hemispheres; lateral margins of the hemispheres and optic lobes lie in the same plane; a large enough mesenceplalon placed between the optical lobes and caudally from the hemispheres, only the base of the cerebellum is preserved behind the mesencephalon; the small lobes of the flocculi are seen on the ventrolateral angles of the cerebellum. Thus, this endocast is strongly different from the brain architecture of the modern neornithine birds, and too difficult to correlate with any other primitive feathered creatures. Among the few known brains of Mesozoic birds, our specimen looks more similar to the brain restoration of *Ichthyornis* which was illustrated by Marsh (1888).

The distribution in the eastern hemisphere of the late Cretaceous hesperornithiforms was discovered by Nessov and Borkin (1983) and Kurochkin (1988). These finds were based on isolated fragmentary remains. To date, several genera and species of Hesperornithiformes have been described from the Late Cretaceous in Russia, Kazakhstan, and Sweden as a result of the explorations of the late Lev Nessov (1997). A new site containing hesperornithiforms was discovered in the northern part of Saratovskaya Province, Central Russia, some 400 km to the north of the earlier known sites in the Volga river basin. It is Kariakino site, with the nearshore marine early Campanian deposits (Pervushov et al., 1999). The proximal fragment of the tarsometatarsus of a large hesperornithiform was found there by paleontologists of Saratov University in 1991. The size of this proximal tarsometatarsus (transversal width of the proximal end 40.4 mm) noticeably exceeds all known species and specimens of North American *Hesperornis* and is close to *Hesperornis rossicus* Nessov and Yarkov, 1993, from the early Campanian of Volgogradskaya Province. The new specimen differs from *Hesperornis rossicus* by inverse ratio of the articular cotylas and some other characters. A few characters separate the Kariakino specimen from *H. regalis*, *H. gracilis*, *H. crassipes*, and *H. bairdi*. Hence, the Kariakino *Hesperornis* belongs to a new species of the Old World hesperornithiforms.

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TAPHONOMIC STUDY OF *PYRRHOCORAX GRACULUS* FROM GROTTE VAUFREY (LEVEL VIII): A CASE OF NATURAL DEPOSIT

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Vaufrey cave (Cenac-Saint-Julien, Dordogne, France) contains buried archaeological levels attributable to Acheulean and Mousterian assemblage traditions (Rigaud *et al.*, 1981). One of the Mousterian levels (VIII) has yielded nearly 600 "long" bones of the Alpine chough *Pyrrhocorax graculus*. A detailed taphonomic analysis using several criteria was done in order to determine the origin of the assemblage (Laroulandie, 2000).
According to ethological data, the Alpine chough nests in karst. Thus, the presence of this specie in a cave may be natural. Nevertheless, it cannot be excluded that predators (humans, raptors, carnivores) bring them into their habitats. So, it is necessary to get other arguments in order to interpret such a deposit.
The population is composed of 42 individuals, a third of which are young. Medullary bone was observed inside few bones, testifying that few females died during the breeding period.
The assemblage is highly fragmented. Studies of fracture morphology and oldness testify to post-depositional breakage (in the sediment and during the excavation and/or storage).
Skeletal profiles, expressed in percentage survival, were analysed independently for adults and young. Except for the radius which is the thinnest bone of the limb, anatomical elements of the leg and wing are well represented and preserved for the two age classes. Except for the tibiotarsus, the percentages of survival are higher for adults than for young. This may be a consequence of the high porosity of bones of young individuals which increases area contact with the sediment and so favours dissolution.
Although bone surfaces are well preserved, marks resulting from predator activity are totally absent.
These data allow us to suggest that the Chough accumulation from Vaufrey cave is a natural deposit.

NEW FOSSIL BIRDS FROM THE LATE MIOCENE OF CHAD AND ETHIOPIA, WITH BIOGEOGRAPHICAL IMPLICATIONS

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Since a review of the Tertiary birds of Africa 30 years ago [Rich, P.V. 1974. Significance of the Tertiary avifaunas from Africa (with emphasis on a mid to late Miocene avifauna from Southern Tunisia). *Ann. Geol. Surv. Egypt* 4: 167-210], a great wealth of new data and new interpretations have augmented this fossil record, hitherto still relatively poor when compared with that of the northern continents. A growing amount of new fossils is coming from hominid localities, themselves now extending from as early as the Late Miocene. Data about recently found bird fossils from the Late Miocene of Chad and Ethiopia are presented. They come respectively from Toros Menalla (Chad), dated ca 7 Ma, and several sites of the Western Margin of the Afar Depression (Ethiopia), dated 5.2 to 5.8 Ma. Several taxa are new and are currently being described, or are new to Africa. Some biogeographical implications are drawn, especially on the relations between Africa and Eurasia at that period. A comparison is proposed with the present situation of the living birds of the Ethiopian and Oriental Regions. Finally, the perspective of an integration of the Tertiary records of Africa and Eurasia is introduced. This will be necessary to be able in the future to make relevant comparisons, identifications, and then biogeographical and evolutionary interpretations about the history of African avifaunas.

HOMOLOGY OF WINGS AND FEATHERS: INTRODUCTION, GOALS AND GROUND RULES

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Possession of a highly derived forelimb form and feathers are features that unequivocally distinguish living birds from all other tetrapods. Their evolutionary origin and subsequent history have been subjects of interest since the 1860s and it might have been hoped that the plethora of recent new fossils would have helped resolve the attendant debate to the satisfaction of all evolutionary biologists. Regrettably, for reasons perhaps unique in the history of biological thought, not only has such a resolution not yet been reached, there exists a polarization of opinion – the "dino-bird controversy" - that has thus far defied attempts at mutual understanding. This polarization, while reasonably designated by different descriptors of research programs – "paleontological versus neontological" or "systematic versus non-systematic", but *not* "cladist versus non-cladist", derives fundamentally from different methodological approaches. The polarization is not even a simple dichotomy. For avian limb and skin, favored model systems in developmental biology for more than half a century, there exists a wealth of data that, to many, seems to be misunderstood or even ignored, by paleontologists. Equally, other scholars, rightly impressed by the inherent rigor of analysis of the tree of life through phylogenetic systematics, and justifiably skeptical of "evolutionary fairy stories", are frustrated by criticisms of their schemae for avian evolution that come from neontologists. Using the generalizing theme that problems of interpretation of avian limb and skin evolution are fundamentally related to the issue of "homology" and how it is defined, "interested" developmental biologists, with no published stances on the "dino-bird" controversy, meet with representatives of the two opposing camps, in the hope that free exchange of facts and ideas will facilitate future understanding.

AMNIOTE SKIN DEVELOPMENT: ITS RELEVANCE TO MODELS OF FEATHER ORIGINS.

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A summary of various features reveals the many similarities in skin development between living reptiles and birds and shows that Vertical Alternation of Keratinization (VAK), observable in feathers, is a synapomorphy for sauropsid amniotes (Maderson and Alibardi [2000] Amer Zool). This and many other features of adult feathers are ignored in the Prum-Brush "developmental model" (PBDM) for feather origins (see refs in Prum and Dyck [2003] J Exp Zool/MDE). The PBDM, rooted in ill-defined – perhaps indefinable – notions of "hierarchical organization" invokes a speculative morphogenetic mechanism from the early 1930s that was later disproven experimentally. Furthermore, allusions in the PBDM to a myriad of features said to reflect "structural complexity" and "uniqueness" of avian feathers detracts from an understanding of the role of patterned regions of loss of adhesion between mature cells as the basis for barb and rachis formation. A new scheme of feather development permits an evolutionary model requiring only one "novel mechanism" to produce this "splitting" – unique among all known epidermal appendages. The scheme facilitates a refinement of the "elongate scale model" favored by many classical workers. This refinement accommodates all available neontologic and paleontologic data.

ORIGINS OF FLIGHT - A NEW PERSPECTIVE

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New fossil discoveries in China appear to give a definitive resolution to the controversy between ground up and trees down models for the origin of avian flight. Beebe's postulated tetrapteryx stage seems to be vindicated and the ancestral bird was an arboreal glider. *Microraptor* and *Caudipteryx* are not sister groups on the outside of this radiation, but are imbedded within it, as was suggested by Paul. The origin of feathers is best understood within the context of the new model for the origin of flight that is emerging from the fossil record. Evidence is presented that argues that feathers originated from folded scales.

HIGHER-LEVEL PHYLOGENY OF BIRDS - WHEN MORPHOLOGY, MOLECULES, AND FOSSILS COINCIDE

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Although higher-level relationships of modern birds are generally regarded as poorly resolved, some clades result from recent cladistic analysis of both morphological and molecular data, and are further in agreement with the mosaic character distribution in early Tertiary fossil taxa: (1) Sister group relationship between landfowl (Galliformes) and waterfowl (Anseriformes) resulted from almost all recent phylogenetic analyses of morphological and molecular data, and is supported by the morphology of early Tertiary stem group Galliformes, that exhibit plesiomorphic, distinctively "anseriform", features. (2) Sister group relationship between flamingos (Phoenicopteriformes) and grebes (Podicipediformes) was recently shown by analyses of molecular data and is also supported by derived morphological characters; the Tertiary phoenicopteriform Palaelodidae exhibit an osteology that is strikingly similar to that of grebes. (3) Sister group relationship between hummingbirds (Trochilidae) and swifts (Apodidae and Hemiprocnidae) results from all recent analyses of molecular and morphological data, and early Tertiary stem group hummingbirds still exhibit a very "swiftlike" osteology. (4) Sister group relationship between owlet nightjars (Aegothelidae) and apodiform birds was first proposed after study of morphological characters and subsequently also retained in analyses of molecular data; the Middle Eocene stem group hummingbird *Parargornis* exhibits a - presumably plesiomorphic - owlet nightjar-like feathering. (5) Sister group relationship between jacamars/puffbirds (Galbulae) and woodpeckers and allies (Pici) also received support from both, morphological and molecular, data; the early Tertiary piciform Sylphornithidae exhibit a mosaic of plesiomorphic and apomorphic features of both taxa. (6) Sister group relationship between parrots (Psittaciformes) and mousebirds (Coliiformes), finally, is supported by some morphological and at least one molecular study, and by the osteology of early Tertiary stem group Coliiformes and Psittaciformes.

PLIO-PLEISTOCENE AVIFAUNA AND TAPHONOMY OF FOSSIL LAKE, OREGON

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The paleontological locality at Fossil Lake, Oregon, has long been known for the abundance and diversity of its avian fossils, which include hundreds of specimens representing approximately 70 species. Previous workers have disagreed on the age of the deposit, limiting its usefulness in biogeographic and other studies. A new and extensive collection from the locality has been made by the South Dakota School of Mines and Technology (SDSM&T) Museum of Geology, with particular attention to the occurrence of the fossils within lithologically distinct units. In addition to fossil birds, the SDSM&T collection includes small and large terrestrial mammals, fish, aquatic invertebrates, rare amphibians, and a few aquatic plants.

The fossils at Fossil Lake were accumulated in a number of different environments of deposition associated with a maar formed by a volcanic eruption, a new interpretation based on the current work. The conventional interpretation of the deposit as hosted in lacustrine beds with the fossils subsequently exposed and concentrated by eolian deflation is contradicted by taphonomic analyses. In addition, the new interpretation is supported by a number of lines of faunal and geologic evidence.

The Fossil Lake locality is located within the Fort Rock Maar Field, among other maars and tuff rings of probable Pliocene age. The Fossil Lake diatreme erupted through diatomaceous Pliocene lakebeds and formed a crater rim of tuffaceous material surrounding a broad, shallow crater floored with large downdropped blocks of Pliocene diatomite. The central crater depression provided a sedimentary basin in which remains could be covered and preserved. At times, the crater rim projected above the lake surface forming an island and attracting colony-nesting birds such as cormorants (*Phalacrocorax macropus* Cope). Adult bones of this bird are found in the same lithologic unit with juvenile bones also identifiable as *P. macropus* and numerous eggshell fragments. As the Pliocene lake receded, and as Pleistocene pluvial Fort Rock Lake filled and emptied, the crater rim was eroded by wave action at intermediate lake levels. At progressively lower levels of the Pleistocene pluvial lake and water table, the maar crater hosted marshes, ponds, and flowing springs. These environments are represented by a great diversity of migratory and water birds, including a sandpiper (*cf. Calidris bairdii* (Coues)) not previously known from Fossil Lake. Taphonomic analysis suggests some of the remains may have originally been accumulated beneath raptor roosts. A period of forestation at Fossil Lake is also postulated, supported by the occurrence of a nearby disjunct stand of Ponderosa pine and identification of two fossil passerines not previously known from the locality.

Clarification of the mechanisms of formation of the Fossil Lake locality has brought about a better understanding of the paleoenvironments and paleogeography of the deposit.

Further work to more precisely date the time periods represented within the deposit will result in fulfillment of the early promise of the locality as an important benchmark for biogeographical and other studies of the fossil birds of North America.

THE STRUTHIONIDAE AND PELAGORNITHIDAE (AVES: STRUTHIONIFORMES AND PELECANIFORMES) FROM THE LATE PLIOCENE OF AHL AL OUGHLAM, MOROCCO

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The Pliocene locality of Ahl al Oughlam is situated at the southeastern limit of the city of Casablanca, in Morocco, on an ancient seashore of the Atlantic Ocean. It has yielded a very rich vertebrate fauna (macro- and micromammals, birds, reptiles, amphibians and fishes) including both terrestrial and marine forms. On the basis of biostratigraphy, the fauna has been dated at about 2.5 Ma, which corresponds to the latest Pliocene.

The avifauna is very diversified and includes birds belonging to twelve different orders. In this paper we only describe the Struthionidae and the Pelagornithidae. Ostriches are represented by a large-sized form, referred to the extinct species *Struthio asiaticus* Milne-Edwards, and its eggshells, of struthioid type, are comparable to those of the recent species *Struthio camelus*. The Pelagornithidae, giant birds with bony pseudoteeth, are represented by an extinct species of the genus *Pelagornis*. As far as we know, this species was the latest representative of the family Pelagornithidae.

MANDIBULAR KINESIS IN HESPERORNIS

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Some aspects of mandibular morphology are known for three hesperornithiform genera: *Hesperornis, Parahesperornis* and *Baptornis.* All share a distinctive intermandibular joint between the angular and the splenial. This joint is bridged by a special process of the surangular extending between the splenial and the dentary. The symphysis appears to have been elongate and unfused joining anteriorly with a short intersymphysial bone. It appears that the mandibles could spread posteriorly allowing the swallowing of larger prey. The mandible is very slender anteriorly resembling the mandible in some cetaceans and seems highly adapted for the capture of fish. The discovery of fish remains in a preserved stomach cast of *Baptornis* gives direct support for this interpretation.

FIRST RECORD OF LEPTOPTILINI (CICONIIFORMES: CICONIIDAE) IN THE NEOGENE OF SOUTH AMERICA

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The stork family (Ciconiidae) is a well-defined group of waterbirds, traditionally divided into the tribes Mycterini, Ciconiini and Leptoptilini. They were already differentiated at the beginning of the Tertiary, the first record coming from the early Oligocene of Egypt. However, most of the fossil storks known from the Tertiary of Europe, Asia, the Americas, and Africa, are based on isolated and fragmentary remains which make it difficult to analyse the relations among the Ciconiidae. The oldest South American fossil stork, *Ciconiopsis antarctica*, was described from the early Oligocene of Santa Cruz (Argentina), but its ordinal assignment has been questioned. More recently, isolated fragments of tarsometatarsi undoubtly referable to the Mycterini appeared in the late Miocene of the same country in the Entre Ríos Province. In this contribution we report the finding of a large stork referable to the Leptoptilini which comes from Punta Buenos Aires, northwestern extreme of the Valdés Península, in the Chubut Province of Argentina. It was excavated from lower levels of the Puerto Madryn Formation, informally known as "Entrerriense" unit and assigned to the Late Miocene. The specimen consists mainly in associated wing (humerus, ulnae, radii, carpometacarpi, and cuneiform) and leg (tibiotarsus) bones, pelvis, sternum, cervical vertebrae and a few fragments of the skull (tip of the mandible; fragments of the ramus mandibulae and the articular) which represent a single individual. It belongs to the collections of the Museo Paleontológico Egidio Feruglio of Trelew (MEF 1363). We adopt provisionally the traditional systematic scheme into tribes, referring the specimen to the Leptoptilini by showing phenetic similarities mainly with extant genera of the tribe. The Leptoptilini comprises three living genera (*Ephippiorhynchus*, *Jabiru*, and *Leptoptilos*) with six species distributed on all continents with the exception of Antarctica, *Jabiru mycteria* being the only extant resident species of Leptoptilini in the Neotropical region. MEF 1363 resembles in overall morphology and size the compared species of Leptoptilini, but it also exhibits several characters of the pelvis shared with *Ciconia* (Ciconiini). Additionally, its wing proportions are different from those of any living taxon, making it prudent to avoid a generic assignment at the moment. Fossils assignable to this tribe had previously been absent in Tertiary deposits of South America.

A NEW GIANT DARTER (PELECANIFORMES: ANHINGIDAE) FROM THE UPPER MIOCENE OF ARGENTINA

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Darters, also known as anhingas or snakebirds, are fairly large fresh waterbirds presently distributed in tropical regions on all continents. Until recently, fossil darters were mainly known from North America, Europe, and Africa. In the last decade, descriptions of various paleospecies in three different genera (*Meganhinga*, *Macranhinga*, and *Giganhinga*) revealed a radiation of large-bodied darters in the Tertiary of South America. Two of the largest species, *Macranhinga paranensis* and *M. ranzii*, came from upper Miocene and upper Miocene-lower Pliocene localities of Argentina and Brazil, respectively. A third one, *Giganhinga kiyuensis*, was recorded in upper Pliocene-lower Pleistocene geologic unit in Uruguay. In this contribution, we report the finding of the largest specimen of Anhingidae known to date. This specimen comes from the basal part of the Ituzaingó Formation, informally known as the "Mesopotamian", which outcrops discontinuosly along the eastern cliffs of the Paraná River in Entre Ríos Province at Argentina. These beds are biochronologically assigned to the Late Miocene (Huayquerian Land-Mammal Age). The material, housed in the collections of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia of Buenos Aires (MACN 12179), consists on a well preserved distal fragment of shaft of a femur with its distal end. It clearly separates from the Phalacrocoracidae by having the distal portion of the shaft straighter; fibular condyle less protruded laterally; posterior intercondylar fossa not as deep; crista supracondylaris medialis more developed and sharper. MACN 12179 can be distinguished from the genus *Anhinga* and resembles *Macranhinga* by presenting some characters with an intermediate condition between those observed in cormorants (Phalacrocoracidae) and those typical of living darters: shaft more robust; distal end wider and more produced posteriorly; origin of the external head (Pars lateralis) of M. gastrocnemius located more proximally, with the presence of the tuberculum M. gastrocnemialis lateralis correspondingly greater and located more proximal. The specimen cannot be directly compared with *Giganhinga kiyuensis* because the latter is known only by a pelvis with its fused synsacrum. However, the possible fit of this femur with the pelvis of *G. kiyuensis* can be inferred by analyzing the proportions between both elements: if the head of the former is supposed to measure approximately half the length of its preserved distal end, then it would be congruent with the size of the acetabulum of *G. kiyuensis*. The most striking feature of the femur herein described is its large size, much greater than in all other known fossil or extant anhingas. A quantitative approach in estimating the body mass of this bird by using Campbell & Marcus's scaling model, throws a result of 17.7 kg which is 30% larger than that of *G.*

kiyuensis (reestimated on 12.8 kg) and 300 % larger than in *Macranhinga paranensis* (5.4 kg). Due to the lack of well defined diagnostic features at a generic level in the fragment of femur herein described we avoid to make a more accurate assignment.

WING-BONE MORPHOLOGY AND THE EVOLUTION OF FLIGHTLESSNESS.

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Previous work has suggested that taxa containing flightless species have shorter wings for a given body mass than their sister taxa containing no flightless species. Shorter wings in taxa containing flightless species is perhaps not unexpected, because it is well known that the wing-bones of flightless species, particularly the radius/ulna and hand-wing, are regressed relative to those of species that are capable of flight. A shorter overall wing-length, however, does not tell us anything about the order in which components of the wing reduce in length. The pattern of wing-morphology change in taxa containing flightless species may provide an insight into the key selection pressures driving the evolution of flightlessness.

A comparative analysis of a large data set containing wing-bone measurements for more than 1000 bird species was performed. The results show taxa containing flightless species to have relatively shorter total wing-bone lengths (humerus + ulna + hand-wing) than their sister taxa containing no flightless species. Furthermore, all the individual wing-bones are shorter in taxa containing flightless species when compared with their sister taxa. It therefore appears that during the early stages of the evolutionary transition to flightlessness all wing-skeletal elements reduce relative to body mass. Perhaps regression of the hand-wing and ulna occur late on in the evolutionary transition to flightlessness or do not occur until flight ability is completely lost.

ENANTIORNITHINE BIRD REMAINS FROM THE LATE CRETACEOUS OF HUNGARY

Attila Ősi

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The recently documented (Ősi et al. 2003) fauna from the Santonian Csehbánya Formation of Iharkút, (Bakony Mts, Hungary) provided the first evidence for the peculiar, extinct avian group, Enantiornithes Walker, 1981 from the Upper Cretaceous of central Europe. These bird remains were discovered in a rich assemblage of separated bones of turtles, crocodiles, lizards, dinosaurs and pterosaurs.

A nearly complete left femur, a distal fragment of a subadult left femur, a nearly complete right tarsometatarsus, and a metatarsus III identified as enantiornithine bird remains, represent the earliest known avian fauna from Hungary.

The femoral head of the well-preserved 2.2 cm long femur is a slightly damaged, but is separated from the shaft by a distinct groove similar to the enantiornithine femur from southern France (Buffetaut 1998). The characteristic trochanteric crest spreads over slightly dorsally above the level of the femoral head. The posterior trochanter is very prominent and borders ventrally the deep lateral wall of the trochanteric crest as in other enantiornithine birds. Three intermuscular lines are recognizable on the surface of the shaft and have positions similar to those of *Vorona berivotrensis* (Forster et al. 2002).

The second specimen, the distal end of a left femur, is preserved only with a small portion of the hollow shaft. The surrounding suture on the epiphysis indicates a subadult specimen.

The nearly complete right tarsometatarsus has a long shaft (5,1 cm) with coplanar orientation of metatarsals II-IV. Only the proximal ends of the tarsometatarsus are fused. No distinct tubercle is visible on the dorsal surface of metatarsal II.

The fourth specimen, a metatarsus III is crushed from the complete tarsometatarsus. The trochlea is little angled from the shaft of the metatarsus, similar to *Avisaurus archibaldi* (Chiappe and Walker 2001). The long shaft of the bone shows that only the proximal part of the metatarsus was fused.

These first three separated bird bones indicate the presence of very small (size of a thrush) terrestrial birds in the Santonian of Europe, and document that some members of the Hungarian enantiornithines retained the small size of their Early Cretaceous ancestors. The large tarsometatarsus is a clear evidence for the existing of other larger enantiornithine birds in the area.

REVISION OF THE FOSSIL BIRD ASSOCIATION OF THE NEOGENE OF THE GARGANO (APULIA, SE ITALY)

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The Gargano area (Apulia, SE Italy) has been known for a long time for its vertebrate assemblages found in fissure fillings in the numerous limestone quarries of the Apricena area, on the West edge of the Gargano promontory. The vertebrate assemblage, particularly the mammals, are well studied (Abbazzi et al., 1996, Revision of the Neogene and Pleistocene of the Gargano region (Apulia, Italy). The marine and continental successions and the mammal fauna assemblages occur in an area between Apricena and Poggio Imperiale (Foggia). *Mem. Soc. Geologica It.*, 51: 383-402) and they can be separated in two different associations, one of the Neogene (MN 13-15) (Freudenthal, 1971, Neogene vertebrate from the Gargano Peninsula, Italy. *Scripta Geologica*, 14: 1-10) and the other one of the Early Pleistocene (De Giuli, Masini, Torre, 1987, The latest Villafranchian faunas in Italy: the Pirro Nord fauna. *Paleontographia Italica*, 74: 51-62).
Fossil bird remains have been found in both associations. The present analysis deals with that found in the Neogene fissure fillings. It has already been studied by Ballmann (1973, Fossile Vogel aus dem Neogen der Halbinsel Gargano (Italien). *Scripta Geologica*, 17: 1-75; 1976, Fossile Vogel aus dem Neogen der Halbinsel Gargano (Italein), zweiter Teil. *Scripta Geologica*, 38: 1-59). Here we present the revision of the material, already presented by Ballmann, but also new and unpublished bird material. The new material comes from the collections of the Nationaal Naturhistorische Museum of Leiden (The Nederlands), the Dipartimento di Scienze della Terra of Firenze University (Italy), the Museo di Geologia e Paleontologia of the Torino University (Italy) and the Naturmuseum Augsburg (Germany). Following Ballmann, (1973, 1976, opp. citt.), the bird association of the Neogene of Gargano contains 16 taxa, in particular *Garganoaetus freudenthali*, *G. murivorus*, *Palaeortyx grivensis*, *Tyto sanctialbani*, *T. robusta*, *T. gigantea*, *Strix? perpasta*, *Columba omnisanctorum*, *Apus wetmorei* and a few other taxa not determined at specific level. These analyses of Ballmann revealed the presence of several new endemic extinct species, testifying the high degree of isolation of the Gargano area during the Late Miocene and Early Pliocene.
The present analysis of the new material confirms the species described by Ballmann, but in some cases, the new material allows an amelioration of the description of their osteological characteristics, and new taxa can be added to the bird association. In particular, the present analysis reveals 12 new taxa, here presented in a preliminary way: Treskiornithidae indet., *Anas* cf. *A. velox*, a small sized Accipitridae, two species of Rallidae, Otitidae n. gen. et n. sp., two species of Charadriiformes, *Athene* sp., *Strix* n. sp., Coliidae indet. and Corvidae indet.; some of these taxa have already been found, but not

determined by Ballmann. Our study also changes some of his determinations, in particular the remains formerly attributed to *Palaeortyx grivensis* actually represent a new species of *Palaeortyx*, and *Tyto sanctialbani* actually belongs to *Tyto balearica*, as previously suggested by Mlíkovský (1998, A new Barn Owl from the early Miocene of Germany, with comments on the fossil history of the Tytoninae. *Journal für Ornithologie*, 139: 247-261). The new material also gives the opportunity to better the osteological description of both *Tyto robusta* and *Tyto gigantea* and to confirm their taxonomic validity as separate species, and not a single one under *T. gigantea*, as suggested by Mlíkovský (1998, op. cit.).

A NEW PENGUIN-LIKE BIRD (PELECANIFORMES: PLOTOPTERIDAE) FROM THE LATE OLIGOCENE TOKORO FORMATION, NORTHEASTERN HOKKAIDO, JAPAN

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The fossil skeleton of a large bird from shallow-marine strata near Abashiri City in northeastern Hokkaido, Japan, represents a new genus and species of the extinct pelecaniform family Plotopteridae. The rocks that yielded the Abashiri specimen were exposed along the Ubaranai River and are between 24 to 29 Ma, or Late Oligocene, in age and are mapped as part of the Tokoro Formation. Initially, the Abashiri plotopterid (Ashoro Museum of Paleontology specimen no. 44) was assumed to be a new specimen of *Copepteryx hexeris* Olson and Hasegawa because of its age, size, and other observed similarities to some of the paratype specimens. However, differences observed in some of the other parts of the skeleton, especially the coracoids preserved in the holotype of *C. hexeris*, made it apparent that the Abashiri specimen represented a new taxon, revealing an unexpected diversity within the larger Late Oligocene Plotopteridae. The sternal end of the coracoid is very different from that of *C. hexeris,* and also from that tentatively referred to *Tonsala* sp. [Olson and Hasegawa, 1996, Jour. Vert. Paleo. 16:742-751, fig. 1b] in having a more angular sterno-coracoidal process. The humerus of the Abashiri specimen has a distal end that is different from that of all other plotopterids in shape and arrangement of condyles, with the shaft more sinuous than that of *C. hexeris* and appearing more elongate than that of *Tonsala hildegardae* Olson. The leg bones of the Abashiri specimen and *C. hexeris* are nearly identical, and if found isolated, probably would be deemed congeneric/conspecific. Thus, the identity of some of the paratypical specimens of *C. hexeris* must now be regarded as tentative until the discovery of material from the posterior part of the skeleton that can be unequivocally assigned to that species.

SKULL SHAPE ANALYSIS AND DIET OF SOUTH AMERICAN FOSSIL PENGUINS (SPHENISCIFORMES)

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The form and function of the skull of Recent and fossil genera of available Spheniscidae are analyzed so that the possible dietary behaviors might be inferred for extinct penguins.
Skull and mandible shapes were compared using the Procrustean method Resistant-Fit Theta-Rho-Analysis (RFTRA). Procrustes methods allow the analysis of morphology through the superimposition of one morphology onto another using landmarks. RFTRA (software made by R. Chapman 1989) was developed to identify and measure the homologous regions of change in shape by establishing congruence among those that have not changed. Due to the availability and quality of the material, this study was based on six living species belonging to five genera (*Spheniscus*, *Eudyptula*, *Eudyptes*, *Pygoscelis*, and *Aptenodytes*) and two Miocene species: *Paraptenodytes antarticus* (Moreno and Mercerat, 1891) and a second specimen (currently under study) that undoubtedly corresponds to a new species and subfamily, different from that in which *Paraptenodytes* belongs.
Comparisons between dorsal and lateral views of the skulls and mandibles were made. Fifteen landmarks of the skull and five of the mandible were chosen, including homologous and geometrical points. Morphological similarities among RFTRA distances are depicted using the resulting dendrograms for UPGMA (unweighted pair-group method using arithmetic average) using cluster analysis.
This shape analysis allows the assessment of similarities and differences in the skulls and jaws of penguins within a more comprehensive ecomorphological and phylogenetic analysis. Even though the food of penguins is not well known, there is a relative wealth of knowledge supporting that *Spheniscus* + *Eudyptes* penguins specialise on fish and all other taxa are plankton-eating or fish and crustaceans-eating. We compared representative species of both ecomorphological groups with the available fossil materials to evaluate its feeding strategies. Penguins are the most abundant birds, indeed the most abundant aquatic tetrapods in Cenozoic marine sediments of South America. The results that arise from this study will be of singular importance in the reconstruction of those marine ecosystems.

THE EXTENT AND CAUSES OF NEW ZEALAND'S RECENT AVIFAUNAL EXTINCTION EVENT

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The New Zealand archipelago has an excellent Holocene terrestrial vertebrate fossil history preserved. Evidence from new fossil finds, combined with historical data, continues to improve our understanding of the extent and causes of New Zealand's recent avifaunal extinction event. Enough detail is now known to reconstruct what each species looked like and how it lived.

Fifty-nine bird species are known to have become extinct since human colonisation of New Zealand in the 13th century. These are 49 (83%) land birds, 9 (15%) water birds and 1 (2%) seabird. In total, the 59 extinctions represent 26% of the original breeding avifauna of 226 species. The surviving avifauna consists of 167 species, including 86 (52%) seabirds, 59 (35%) land birds and 22 (13%) water birds, so seabirds have now replaced land birds as the most diverse element of the avifauna.

This extinction event was mainly due to predation by alien mammals. The primary contributors to the extinctions, in order of decreasing importance, were: human-hunting, Pacific Rat *Rattus exulans*, Cat *Felis catus*, Ship Rat *Rattus rattus*, Stoat *Mustela erminea*, Norway Rat *Rattus norvegicus* and Weka *Gallirallus australis*.

New Zealand conservation managers now lead the world in their ability to control and eradicate introduced mammals (most recently having eliminated Norway Rats from 11,331 ha subantarctic Campbell Island), and offer new hope for the large number of species still under threat of extinction.

LATE PLEISTOCENE AVIAN EXTINCTIONS – HUMAN BLITZKRIEG, CLIMATE CHANGE OR OTHER CAUSES?

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This paper is an effort to review and analyze the considerable but widely scattered data on Late Pleistocene avian extinctions, with emphasis on the possible causes of the extinction. The focus is exclusively on the avifaunas of the five main continental landmasses, since there is little doubt that the, largely Holocene, extinctions of island birds are due to humans. Since the fact that a number of birds also became extinct at the end of the pleistocene have been used as an argument against the "blitzkrieg" hypothesis for the late Pleistocene megafaunal extinctions, the characteristics of the avian extinctions is directly relevant to the ongoing debate on the reasons for the megafaunal extinctions.

The analysis shows that timing and severity of avian extinctions in North and South Americas, northern Eurasia and Australia correlate well with the megafaunal extinction in the same areas, though the poorness of the avian fossil record in the Afrotropic and Indomalayan regions makes it uncertain whether the apparent absence of Late Pleistocene avian extinctions in these areas is real or due to insufficient data.

A study of the extinct species show that these are a far from random sample of the avifaunas. Large scavengers and other species that were probably directly or indirectly dependent on the megafauna make up a very large part of the extinct species. These extinctions were probably a consequence of the disappearance of the megafauna, and therefore not directly related to the original cause of the megafaunal extinction.

Of the remaining extinct species a large proportion had were large and/or flightless and/or colonial breeders. All these characteristics would tend to make the species vulnerable to human predation.

The climatic changes at the end of the glaciation, often claimed as the main reason for the disappearance of the megafauna, are unlikely to cause extinctions in such mobile organisms as birds, while alternative causes which have been postulated for the megafaunal extinctions, such as infertility caused by rising temperatures and hyperdisease are even more unlikely to be applicable to birds.

It is therefore concluded that characteristics of the Late Pleistocene avian extinction on the whole strengthens rather than weakens the "blitzkrieg" hypothesis.

ITERATIVE USE OF MOLECULAR CLOCKS AND FOSSILS IN INFERRING TEMPO AND MODE OF NEORNITHINE EVOLUTION

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Partnership between paleontology and neontology is perhaps greatest in the study of dating the branches on the Tree of Life, yet debate in this area is also strongest regarding the relative merits of fossils and modern genetic records. This debate is fueled by major discrepancies observed in the evolutionary time of first appearance of well-known groups such as birds. Unfortunately, all too often, paleontologists and molecular biologists have stagnated into concluding that either clocks or fossils must be severely biased, which has not helped in further developing the interface between paleontology and genetics.

Here I highlight available avenues for future collaborative efforts in dating the avian tree through investigation of which branches show congruence between fossils and clocks based on available data. This framework points out that the following are needed for legitimate comparison between fossil and molecular timescales: (1) a cladistic scaffold combining extant and extinct lineages, (2) more comprehensive taxon sampling in DNA sequence studies, (3) use of multiple fossil tie points to calibrate molecular clocks, (4) consistent use of stem-crown concept, and (5) representation of uncertainties intrinsic to both bird fossil and genetic records.

ANALYSIS OF SPHENISCID TARSOMETATARSUS AND HUMERUS MORPHOLOGICAL VARIABILITY USING DAISY AUTOMATED DIGITAL IMAGE RECOGNITION.

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Despite a fossil record of more than 55 million years the phylogenetic status of the Spheniscidae remains poorly known. One reason for this is that most fossil species have been based on isolated elements. Normally these are the robust humerus and tarsometatarsus that provide comparatively little phylogenetic information, and in extant taxa show a high degree of intraspecies variability. So, how reliable are identifications of fossil taxa based on these elements? Distance-based morphometric approaches (e.g., Livezey, B. C. (1989) Morphometric patterns in Recent and fossil penguins (Aves, Sphenisciformes). *Jour. Zool. Soc. Lond*, **219**, 269-307; Myrcha, A. P. Jadwiszczak, C. P. Tambussi, J. I Noriega, A. Gaździcki, A. Tatur and R. del Valle (2002) Taxonomic revision of Eocene Antarctic penguins based on tarsometatarsal morphology. *Polish Polar Res.*, **23**, 5-46) have provided good results, but are time consuming and are subject to variability from inconsistent measuring. As an alternative approach, artificial neural net (ANN) systems approximate human cognitive ability in image recognition tasks, potentially providing a more consistent and speedy technique to group images of selected elements in a discriminant species space. The Digital Automated Identification System (DAISY) ANN incorporates a variant of the Lucas *n*-tuple nearest neighbour classifier and plastic self-organising mapping, effectively making DAISY a self-learning system. DAISY has been tested on a variety of object types at the Natural History Museum, London, and has provided excellent results particularly using insect wings and modern planktonic foraminifera. Effectively, the system analyses only tonal information about the specimen outline and internal patterns (e.g. tubercle size, shape and spacing), and ignores original specimen size. Identifications are made by assessing the 8-fold nearest-neighbour coordination between each unknown image and the training set ordination; where the system cannot make a positive identification it can often suggest which other species are a close match. The aim of the present study is to determine whether DAISY can provide reliable identifications of a training set of spheniscid humerus and tarsometatarsus images from 17 extant species. The confidence at which identifications are made or species suggested as alternatives provides a measure of the distance between inter- and intra-species groups, and therefore the how much information/variability these elements provide for species identification purposes.

NEW PENGUIN REMAINS FROM THE NEOGENE OF CHILE.

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The Middle Miocene to Early Pliocene marine sediments of the Bahía Inglesa Formation, northern Chile, have yielded a diverse assemblage of seabirds including *Phalacrocorax* sp, *Sula* sp, Pelagornithidae indet. (probably *Pelagornis* sp.), *Diomedea* sp and a penguin closely related to *Spheniscus* (Walsh, S. A. and J. P. Hume (2001) A new Neogene marine avian assemblage from north-central Chile. *Jour. Vert. Pal.*, **21**, 484-491). In addition, Acosta Hospitaleche *et al*. (Acosta Hospitaleche, C., O. Fritis, C. P. Tambussi, & A. Quinzio, (2002) Nuevos restos de pingüinos (Aves Spheniscidae) en la Formación Bahía Inglesa (Mioceno superior-Plioceno inferior) de Chile. pp. 16 *In* Abs. 1st Cong. Lat. Am. Pal. Vert., Chile) reported at least four spheniscid species from the formation, including *Palaeospheniscus*, *Paraptenodytes robustus*, *P. antarctica* and a new species close to *Pygoscelis*.

Recent discoveries at a new Pliocene vertebrate-bearing locality at the Bahía Inglesa site has led to a revision of the Bahía Inglesa spheniscid fauna. Much of the material referred to cf. *Spheniscus* by Walsh and Hume (2001) is now referred to *Spheniscus urbinai* Stucchi 2002, with a single isolated rostrum tentatively referred to *S. megaramphus* Stucchi, Urbina and Giraldo 2003, both taxa known from coeval sediments of the Pisco Formation, Peru. An isolated humerus from Pliocene sediments is also tentatively referred to *S. chilensis* Emslie and Correo 2003, recovered from the Caleta Herradura de Mejillones Formation of Antofagasta, Chile. Two new species are also present. Material referred to the first comes from Middle to Late Miocene levels and consists of two right coracoidea, proximal right radius, distal left tibiotarsus, fibula and left tarsometatarsus. These elements indicate that this new taxon is a small species of *Spheniscus* slightly larger than *S. mendiculus*. The second new species is represented by an incomplete but associated skeleton that was recovered from the same Pliocene beds as the new small *Spheniscus* species, and also from a Late Miocene horizon. These remains are referable to a new species of *Pygoscelis* based on characters present in the best-preserved elements. Comparison of these remains with living species indicates that this species was around the size of *Aptenodytes patagonicus*, and is therefore clearly separate from the material of Acosta-Hospitaleche *et al*. (2002), which is within the size range of living species of *Pygoscelis*. Preliminary phylogenetic analysis was conducted on PAUP 4.0 b10 using 39 osteological characters coded for 15 extant species and the five fossil species from the Bahía Inglesa and Pisco Formations. The heuristic analysis (run with unweighted and unordered characters) recovered 9024 most parsimonious trees, the best of which took 96 steps and confirmed placement of the new large *Pygoscelis* within *Pygoscelis*, and the two Pisco Formation *Spheniscus* species within a *Spheniscus* clade. The tree topology does not agree with published molecular and integumentary results, and placed *Eudyptula* and *Megadyptes* as sister taxa to (*Spheniscus* (*Eudyptes* (*Pygoscelis* + *Aptenodytes*))).

The presence of two species of *Pygoscelis* almost within the tropics raises questions regarding the climate during the Late Miocene and Pliocene, and indicates that the northerly range of the genus was formerly much greater than at present. The Neogene diversity of *Spheniscus* species on the South American Pacific coast is in marked contrast to the contemporary spheniscid assemblage of the Atlantic coast, and of New Zealand, suggesting a possible Miocene Pacific centre of origin for the genus.

ANALYSIS OF SPHENISCID TARSOMETATARSUS AND HUMERUS MORPHOLOGICAL VARIABILITY USING DAISY AUTOMATED DIGITAL IMAGE RECOGNITION.

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Despite a fossil record of more than 55 million years the phylogenetic status of the Spheniscidae remains poorly known. One reason for this is that most fossil species have been based on isolated elements. Usually these are the humerus and tarsometatarsus, which provide comparatively little phylogenetic information and, in extant taxa, appear to show a high degree of intraspecies variability. So, how reliable are identifications of fossil taxa based on these elements? Distance-based morphometric approaches (e.g., Livezey, B. C. (1989) Morphometric patterns in Recent and fossil penguins (Aves, Sphenisciformes). *Jour. Zool. Soc. Lond*, 219, 269-307; Myrcha, A. P. Jadwiszczak, C. P. Tambussi, J. I Noriega, A. Gaździcki, A. Tatur and R. del Valle (2002) Taxonomic revision of Eocene Antarctic penguins based on tarsometatarsal morphology. *Polish Polar Res.*, 23, 5-46) have provided good results, but are time consuming and are subject to variability from inconsistent measuring. As an alternative approach, artificial neural net (ANN) systems approximate human cognitive ability in image recognition tasks, potentially providing a more consistent and speedy technique to group images of selected elements in a discriminant species space.

The Digital Automated Identification System (DAISY) ANN incorporates a variant of the Lucas *n*-tuple nearest neighbour classifier and plastic self-organising mapping, effectively making DAISY a self-learning system. DAISY has been tested on a variety of object types at the Natural History Museum, London, and has provided excellent results particularly using insect wings and modern planktonic foraminifera. Effectively, the system analyses only tonal information about the specimen outline and internal patterns (e.g. tubercle size, shape and spacing), and ignores original specimen size. Identifications are made by assessing the 8-fold nearest-neighbour coordination between each unknown image and the training set ordination; where the system cannot make a positive identification it can often suggest which other species are a close match. The main aim of the present study is to determine the level of intraspecific variation in spheniscid tarsometatarsi and humeri by testing whether DAISY can provide reliable identifications of a training set of 296 images from 13 extant species in the two standard views (cranial and caudal for humerus, dorsal and plantar for tarsometatarsus. Failure of the system would indicate that the images lack distinctive characteristics for taxonomic cluster separation, and would suggest that use of these elements for fossil species diagnosis is dubious.

Our preliminary results show that DAISY achieved 100% accuracy in identifications and found discrete taxonomic groupings at the specific (46% pass) and generic (68% pass) levels. However, although well separated generically, species of *Spheniscus* were poorly supported. We found that the tarsometatarsus is generally a better element for identification purposes than the humerus, and that the plantar view of the element contains more useful information than the dorsal view. These results suggest that identification of spheniscid species is justified using these elements, but we urge caution where specific level identifications of *Spheniscus* are required. Further testing of variability using DAISY, superposed landmark and eigenshape multivariate morphometric analysis is in progress.

THE STERNUM OF *ARCHAEOPTERYX* REVISITED – AN ALTERNATIVE RESTORATION

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The sternum of *Archaeopteryx* from the Late Jurassic Solnhofen limestone is documented in only one out of seven skeletal specimens known so far. And even in that individual, the Munich specimen, *Archaeopteryx bavarica* Wellnhofer 1993, the sternum is only partly preserved. Based on the available evidence the author had originally offered a tentative restoration resulting in a relatively small, short, transversely expanded sternal plate.
After 1993 an increasing number of basal birds, in particular *Confuciusornis sanctus* Hou et al. 1995, with well preserved sterna have been discovered from the Early Cretaceous of China. A comparison of the sternal remains in both taxa has led to an alternative reconstruction of the sternum of *Archaeopteryx bavarica*. It is especially one character, a semicircular notch in the lateral margin of the sternum which is strikingly similar in both, *Confuciusornis sanctus* and *Archaeopteryx bavarica.* If this feature is homologous in these taxa, the sternal margin as exposed in *Archaeopteryx bavarica* should be identified as the lateral margin rather than the rostral one as proposed by the author in 1993. It is interesting that this character, a lateral sternal notch, is not only present in *Confuciusornis* and the long-tailed contemporary bird *Jeholornis,* but also in some non-avian theropods, namely dromaeosaurids and oviraptorids.
All this favours an alternative reconstruction of the sternum of *Archaeopteryx bavarica*. Considering the close phylogenetic relationship of *Archaeopteryx* and *Confuciusornis* it is supposed that in its general morphology it could have been similar to the sternum of *Confuciusornis sanctus*, but was of relatively smaller size. It was probably composed of a single, thin bony plate providing sufficient area for the origin of effective flight muscles. This confirms some other indications for advanced flight capabilities of *Archaeopteryx* proposed by different authors elsewhere.

Addendum:

In November 2004 after further preparation of the specimen of *Archaeopteryx bavarica* and investigations under ultraviolet light it became obvious that the bone which hitherto had been kept for the sternal plate is in fact part of the left coracoid. At several places at the boundary between the two components a continuous bony connection can be observed. What before seemed to be two distinct elements of the shoulder girdle, coracoid and sternum, turned out to belong to a single bone, the left coracoid. The alleged sternal plate is clearly the medial part of the coracoid blade. The “lateral notch” at the exposed margin can now be interpreted as the “incisura inferior” (sensu PETRONIEVICS 1921) at the medial margin of the coracoid blade. Although a reliable reconstruction of the coracoid of

Archaeopteryx is not possible on the basis of the structures preserved, it can be concluded that in its general morphology it was neither avian, i. e. long and pillar-like, nor theropodan, i. e. short and semicircular expanded in one plane, but rather intermediate and extending in two planes.

For more details see: WELLNHOFER, P. & TISCHLINGER, H. (2004). Das "Brustbein" von *Archaeopteryx bavarica* WELLNHOFER 1993 – eine Revision. The „sternum" of *Archaeopteryx bavarica* WELLNHOFER 1993 – a revision. – Archaeopteryx **22** (in press).

GENE EXPRESSION AND DIGIT HOMOLOGY IN THE CHICKEN EMBRYO WING

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The bird wing is of special interest to students of homology and avian evolution. Morphological signs of a vestigial digit I are seen in bird embryos, but no digit-like structure develops. To examine the developmental mechanisms of digit loss in chicken wings, we studied the expression of the high mobility group box containing Sox9 gene, and bone morphogenetic protein receptor 1b (BMPR1b) (markers for pre-condensation and pre-chondrogenic cells, respectively). We find expression of Sox9, but not BMPR1b, anterior to digit II. We interpret this as a digit I domain that reaches the pre-condensation, but not condensation or pre-cartilage stages. It develops late, when the tissue in which it is lodged is being remodelled. Expression of Sox9 is also seen in the elusive 'element X' that lies proximally and ventrally in relation to digit V. Our study provides the first evidence that birds have five distinct domains of digital gene expression. No evidence was seen for budding or branching of elements. Our data cannot distinguish between frame-shift and reduction models. However, any model still needs to consider possible anomalies of the primary axis in some archosaurs, in which that axis appears to pass through 'digit III'. Another problem I shall discuss is the identity of element 'X' in the chick.

THE ANATID FAUNA OF THE LOWER-MIDDLE MIOCENE OF THE MANUHERIKIA GROUP, NEW ZEALAND.

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A diverse anatid fauna is established from the lacustrine Manuherikia Group, early-middle Miocene 16-19 Ma, of New Zealand. A minimum of six taxa are present. Most numerous, with hundreds of specimens, are two species of Dendrocheninae established in a new genus that is close to *Mionetta*. Largest is a new genus and species in Tadorninae indicating a long history of shelducks in Australasia. Within Anatinae, two further genera and species are indicated. One, in some ways morphologically similar to the eider ducks and probably a diver, cannot yet be assigned to any known subfamily. It is known from bones of a single individual. The other taxon is a possible anatine with some similarities to *Chenonetta* known from rare humeri in two sites. A sixth taxon is represented by a single coracoid larger than those of the tadornid and possibly of anserine affinity. No modern anatid genera are represented and anserine taxa, especially swans Cygnini, are absent.

BIRDS OF THE PALAEOLITHIC SITE DYUKTAI CAVE, EAST SIBERIA

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The Late Palaeolithic site Dyuktai Cave is located on the Aldan river (Lena river basin, Eastern Siberia). The Cave was inhabited several times by early man during the period of 15000 – 740 years B.P. The remains of “mammoth fauna” are abundant (Mochanov, 1977). The avian remains from Dyuktai Cave, collected by Mochanov at the end of 1960s, are represented by more than 700 birds bones and fragments. 66 species, from 10 recent orders, have been identified. The remains of the Willow Grouse (*Lagopus lagopus*) – 117 bones and fragments -, and Ptarmigan (*L. mutus*) – 38 remains - are the most abundant. The next are ducks (Anatidae) – 143 bones and fragments from 12 species, waders (Scolopacidae) – 100 remains from 14 species, and thrushes (*Turdus spp*.) – 87 remains from at least 5 species. With a few exceptions, all bird species represent a fauna of open-land habitats. This includes the thrushes, which frequently use meadows and open countries for feeding. The fauna of woodland habitats is represented only by *Tetrastes bonasia, Tetrao parvirostris, Perisoreus infaustas, Zoothera dauma* and *Fringilla montifringilla*, but remains of these species are rare. In our times, *Anas strepera* and *Otis tarda* are inhabitants of the steppe landscape and are absent in the Aldan basin. The presence of these species indicates that a steppe landscape was to be found near the cave in the Late Pleistocene. *Clangula hyemalis, Buteo lagopus, Phalaropus spp*., and *Philomachus pugnax* might have reached the place during the period of migration. *Lyrurus tetrix, Limosa limosa* and *Gallinago megala* are also found outside of their recent breeding range.

In the collection two new species are documented. One is a goose, which is slightly larger than recent *Anser anser*, and the other is a Sawbill, which is smaller than modern *Mergellus albellus*. Further species determined within the material include a crane (*Grus sp.*), loons (*Gavia stellata, G. arctica*), 4 species of grebes (*Podiceps* spp.), black kite (*Milvus migrans*), sparrowhawk (*Accipiter nisus*), buzzard (*Buteo buteo*), golden eagle (*Aquila chrysaetus*), falcons (*Falco tinnunculus, F. subbuteo*), turtle dove (*Streptopelia orientalis*), and owls (*Asio otus, A. flammeus, Strix nebulosa, S. uralensis*). Some anseriform bones show cut-marks made by early man though most bones have none. However, the type of selection represented mainly by ptarmigans and waterfowl leads us to the conclusion that the accumulation of avian remains is the result of human activity. The research was supported by the program of the RAS “Origin and evolution of biosphere. Sub-Programme II” and the Leading Scientific School SSc-1840.2003.4.

LEG FEATHERS IN EARLY BIRDS AND THEIR IMPLICATIONS

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Although a tetrapteryx or four-winged hypothesis was originally proposed about the origin of the flight of birds nearly a century ago, the recent discovery of long and asymmetric feathers associated with the femur, tibia and metatarsus in the basal dromaeosaur *Microraptor gui* has, for the first time, provided fossil evidence in support of the hypothesis that there probably existed a tetrapteryx, gliding stage before the appearance of active, flapping-flight in birds.

It has been well known that feathers can be attached to the lower leg in some extant birds. With the discovery of a four-winged theropod, the question of whether the early birds also possess pennaceous leg feathers has become more intriguing and important for understanding the origin of avian flight. The presence of contour feathers attached to the tibia in the oldest bird *Archaeopteryx* has recently been confirmed, which appears to lend further support for the tetrapteryx hypothesis concerning the origin of avian flight.

Reexamining the Early Cretaceous fossils from China, we have recognized a new enantiornithine bird, which preserved fairly long pennaceous feathers attached to the tibiotarsus of the leg. Leg feathers have also been found to be associated with the leg of *Confuciusornis* and several other enantiornithine specimens. Based on these observations and newly reported information, we conclude that the leg feathers could be divided into the following 4 categories in birds and dinosaurs: 1) long, remix-like feathers, 2) short, remix-like feathers, 3) contour feathers, and 4) open-vaned or plumulaceous feathers.

The aerodynamic function of the leg feathers is strong in “long, remix-like feathers”, and becomes reduced in “short, remix-like feathers”, further reduced in “contour feathers”, and finally lost in “open-vaned or plumulaceous feathers”. The evolutionary scenario of the aerodynamic function of the leg feathers appears to be consistent with the phylogenetic framework, i.e., the aerodynamic function of leg feathers has progressively decreased from the “four-winged” *Microraptor*, through *Archaeopteryx*, and other early birds such as *Confuciusornis* and enantiornithines, to modern volant birds.

Although the aerodynamic function of the pennaceous feathers in *Confuciusornis* and the new enantiornithine is more reduced than that of *Microraptor*, their long, curved, and orderly arranged pennaceous characteristics suggest that 1) there was a four-winged stage during the origin of the flight of birds, and 2) some early birds with active, flapping flight ability, such as *Archaeopteryx*, *Confuciusornis* and this new enantiornithine, could use their long, pennaceous leg feathers to assist in flight. Using leg structure to assist flight can also be found in some modern birds. For instance, the kittiwake (*Rissa tridactyla*) spreads webbed feet as an effective airbrake, and the lappet-faced vulture (*Torgos tracheliotus*) extends its legs and feet fully as it descends steeply on to a kill.

RECENT PROGRESS IN THE STUDY OF MESOZOIC BIRDS AND THEIR ASSOCIATED BIOTA IN CHINA

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Since 2000, newly discovered Mesozoic in China have ranged from some of the most basal avian forms such as *Sapeornis* (Zhou and Zhang, 2002, 2003) and *Jeholornis* (Zhou and Zhang, 2002, 2003), to some enantiornithines with unusual feeding adaptations such as *Longipteryx* (Zhang et al., 2001) and *Longirostravis* (Hou et al., 2004), and to much more derived ornithurine birds such as *Yanornis* and *Yixianornis* (Zhou and Zhang, 2001). These forms not only represent three major evolutionary steps towards the origin of living birds, but also document the first major evolutionary radiation in avian history.

The temporal distribution of the Mesozoic birds in China is now better known thanks to the collecting of more material and the precise dating of the fossil-bearing deposits in the Jehol Group. The dating of the Jiufotang Formation (120 Ma) provided the minimum age for the first appearance of *Sapeornis*, *Jeholornis*, and *Yanornis*. *Confuciusornis*, which has been found in both the Yixian (125 Ma) and Jiufotang formations, had existed for at least 5 million years (He et al., 2004) while most other birds had probably lived for a shorter geological time.

The studies of Mesozoic birds in China have been accompanied by the discoveries of a variety of other important vertebrates such as dinosaurs (Xu et al., 2003), pterosaurs (Wang and Zhou, 2004) mammals (Luo et al., 2003) and flowering plants (Leng et al., 2003).

The Jehol vertebrate radiations are highlighted by the presence of many arboreal and scansorial species, or vertebrates with herbivorous diets, which can probably be explained by the presence of the flourishing forest environment in the Early Cretaceous of this region against the global geological background of high rates of sea floor spreading, volcanism, excess atmospheric CO_2, and high surface temperature in the Early Cretaceous (Zhou, 2004). The appearance of arboreal dinosaurs has not only been critical to the radiation of dinosaurs but also to the origin of birds and their flight. Although early birds in the Jehol Biota mainly lived an arboreal life, ornithurine birds had exploited new niches outside the forest and became successful in the near-shore environment.