

Synopsis of Mesozoic Birds and Early Evolution of Class Aves

Überblick über die mesozoischen Vögel und die Anfänge der Entwicklung der Klasse der Aves

Abstract

The data on the Mesozoic birds have grown tremendously last decade and have fundamentally changed traditional views on the evolution and phylogeny of the class Aves. After 1981 two new infraclasses, seven orders and about 40 species of birds from the Mesozoic were described. Among these finds the major new avian fossils discovered are primitive enantiornithines, the Triassic protobird, Lower Cretaceous true birds, and hesperornithiforms in the Old World. These data demonstrate that origin of the birds should be put early in the Triassic, and that *Archaeopteryx* is not directly ancestral to modern birds. The basal dichotomy of the Aves are the Sauriurae and Ornithurae. In the Cretaceous, birds evolved in parallel in at least five phylogenetic lineages, but the K-T boundary was crossed only by the Palaeognathae and Neognathae. The Enantiornithes, Hesperornithes, and Ichthyornithes disappeared probably no later than the Middle Maastrichtian. The Palaeognathae are a pachyphyletic taxon of monophyletic origin, i.e., they originated from the common ancestor but evolved in parallel lineages for almost all of their existence. The monophyletic Neognathae are also pachyphyletic in that they consist of two major parallel taxa – the Galloanserae and Neoaves.

Zusammenfassung

Fundberichte über mesozoische Vögel haben während der letzten zehn Jahre außerordentlich zugenommen und die traditionellen Ansichten über die Entwicklung und Herkunft der Klasse der Vögel von Grund auf verändert. Nach 1981 wurden aus dem Mesozoikum zwei Unterklassen, sieben Ordnungen und etwa 30 Arten der Vögel neu beschrieben. Die wichtigsten unter diesen Funden sind die urtümlichen Enantiornithines, der »Protovogel« aus der Trias, die echten Vögel der Unteren Kreide und die Hesperornithiformes der Alten Welt. Die Befunde zeigen, daß der Ursprung der Vögel bis in die Trias zurück zu verlagern ist, und daß *Archaeopteryx* kein unmittelbarer Vorfahre der modernen Vögel ist. Die beiden Hauptzweige innerhalb der Vögel sind die Sauriurae und Ornithurae. In der Kreide entwickelten sich Vögel parallel in mindestens fünf phylogenetischen Linien, aber die Kreide-Tertiär-Grenze wurde nur noch von den Palaeognathae und Neognathae überschritten. Die Enantiornithes, Hesperornithes und Ichthyornithes verschwanden wahrscheinlich spätestens im Mittleren Maastrichtium. Die Palaeognathae stellen ein pachyphyletisches Taxon mit monophyletischem Ursprung dar, d.h. sie stammen von einem gemeinsamen Vorfahren ab, haben sich aber schon extrem früh in parallele Linien aufgespalten. Die monophyletischen Neognathae sind ebenfalls pachyphyletisch – sie bestehen aus den parallelen Haupttaxa Galloanserae und Neoaves.

Introduction

An explosive discovery of the Mesozoic birds during last fifteen years characterizes the study of avian evolution and changed drastically the earlier summaries by BRODKORB (1978) and OLSON (1985). It began with the description of the Late Cretaceous Argentinean Enantiornithes as a new subclass of

early birds (WALKER, 1981), and the Early Cretaceous *Ambiortus dementjevi* from Mongolia as the oldest ornithurine birds (Kurochkin 1982), and to date has totaled two new infraclasses, seven orders, and nearly 40 species. These new discoveries of avian fossil birds were entirely surprising and fruitful. At present Mesozoic birds are known from Australia, China, Mongolia, Russia, Uzbekistan, Kazakhstan, Spain, United States, Canada, Mexico, Argentina, Chile, and even Antarctica. Only Africa remains blank for early birds. Among these new findings, the Late Triassic *Protoavis* (CHATTERJEE 1991) and the Late Cretaceous *Mononykus* (PERLE et al., 1993, 1994) have touched off much controversy. Basically the new discoveries of Mesozoic birds resulted in a radically new portrayal of avian evolution from that which has long been accepted in reference and text-books.

Problems in the relationships of *Archaeopteryx*

Discovery in old collections by OSTROM (1972, 1976) in the middle of 1970's of the fourth specimen of *Archaeopteryx*, and finding of the fifth specimen (WELLNHOFER, 1974) stimulated new interest for studying the origin and evolution of birds. Two more specimens of *Archaeopteryx* were subsequently found in Solnhofen and there are unconfirmed reports that isolated bones of *Archaeopteryx* associated with the bones of true birds were found in the earliest Cretaceous of Romania (JURCSÁK & KESSLER, 1986; KESSLER, 1984, 1987; KESSLER & JURCSÁK, 1984, 1986). The taxonomic composition of the Archaeopterygidae is still disputed. Initially the several specimens of this bird were placed in different species or even genera, but by 1985, most workers placed them in *Archaeopteryx lithographica* von Meyer, 1861 (OSTROM, 1992; see BÜHLER and BOCK, in press, for nomenclature). STEPHAN (1987) recognized *Archaeopteryx macrura* Owen [London (first), Maxberg (third), and Haarlem (fourth) specimens], *Archaeornis siemensii* (Dames) [Berlin (second) specimen], and *Jurapteryx recurva* (Howgate) [Eichstätt (fifth) specimen]. The taxon *Archaeopteryx lithographica* is considered uncertain in this scheme because it was not clear whether VON MEYER (1861) applied this name to the isolated feather or to the skeleton (but see BÜHLER and BOCK, in press). The Solnhofen (sixth) specimen belongs to *Archaeopteryx lithographica* von Meyer (WELLNHOFER, 1988, 1992), although the seventh "Solnhofen Aktien-Verein" specimen was described as *Archaeopteryx bavarica* WELLNHOFER, 1993. The morphological differences, including the scapula and coracoid articulation, pes phalangeal formula, presence of a sternum, tooth structure, general size and proportion of the limbs, among the several specimens of *Archaeopteryx* probably do have taxonomic significance, but its resolution is unclear.

Following de Beer (1954), a series of important papers evaluating traditional hypotheses about the position of *Archaeopteryx* in avian evolution terminated in the 1980's by the publishing of three comprehensive volumes: the »Age of birds« (FEDUCCIA, 1980), the transactions of the Eichstätt Conference on *Archaeopteryx* in 1984 (HECHT et al., 1985), and "The Origin of Birds and the Evolution of Flight" edited by PADIAN (1986).

Some workers (e.g., MARTIN, 1985) at the Eichstätt Conference concluded that *Archaeopteryx* was not an immediate ancestor of the birds but rather was a side lineage in avian phylogeny. Later discovery of the sixth and seventh specimens of *Archaeopteryx* (WELLNHOFER, 1988, 1992, 1993) had not stopped discussion on relationships of *Archaeopteryx*, although aspects of its morphology were clarified. Most workers agree on the structure of the maxillary segment, cranial roof, vertebrae, pelvis, shoulder girdle, proximal segments of forelimb and hindlimb, but still disagree on the quadrate and distal segments of the both extremities.

WHETSTONE (1983) reported the reduction or absence of the squamosal and the single-head structure of the quadrate which articulates on the paroccipital process of otic bone in London specimen of *Archaeopteryx*. WALKER (1985) argued for a squamosal articulation of the single-head quadrate. WELLNHOFER (1992, 1993) confirmed the presence of the squamosal, but questioned the nature of the quadrate head. Subsequently, the quadrate of the Eichstätt specimen was shown to be double-headed (HAUBITZ et al., 1988) based on computer tomography. In any case, the squamosal or paroccipital process has only one articular surface for the quadrate which is a principle difference between *Archaeopteryx* and modern birds.

Numbering of manal digits in *Archaeopteryx* is important for determining its relationship within birds or theropods. HINCHLIFF (1985) argued on embryological evidence that the manal digits of modern

birds are II-III-IV of the pectinyl plan. However, ROMER (1966), OSTROM (1976), and TAQUET (1977) have shown that the remaining digits in the theropods are I-II-III. Thus *Archaeopteryx* should have I-II-III digits in its manus if the *Archaeopteryx*-Theropod relationship is accepted without question (OSTROM, 1976, 1991; THULBORN, 1984; GAUTHIER, 1986) which would lead to problems for the relationship of *Archaeopteryx* and the Ornithurae (TARSITANO, 1991).

The homology of ascending process on the anterior surface of the distal tibia in *Archaeopteryx* is another difficulty. On embryologic evidence, MCGOWAN (1984) claimed that this process is the pre-tibial bone in Carinatae, the separated astragalar process and the pre-tibial bone as part of the calcaneum in the tinamous, and the astragalar process in the Ratitae. MARTIN et al. (1980) and MARTIN (1991) argued that ascending process in *Archaeopteryx* and all birds is the pre-tibial bone, and thus they are homologous. The seventh specimen of *Archaeopteryx* definitely shows that the ascending process is the astragalar process and is not connected with laterally placed calcaneum (WELLNHOFER, 1993). At the same time WELLES & LONG (1974) clearly recognized the ascending process as the astragalar process in different types of theropods. Thus the ascending process of *Archaeopteryx* and birds could not be homologous, and morphology of distal end of the tibiotarsus including two proximal tarsals could be homoplastic with modern birds.

The distal tarsals were considered absent or reduced by STEPHAN (1987), but they are definitely presented in sixth and seventh specimens (WELLNHOFER, 1992, 1993). However, they are small, flat ossifications that do not form a dorsal cap on the metatarsus; therefore the intertarsal articulation exists in *Archaeopteryx* between the proximal tibiotarsus and the distal metatarsals. Consolidation of the metatarsals as a single bone element occurs in *Archaeopteryx* through fusion of the proximal part of the metatarsals. In modern birds the proximal ends of the metatarsals are united by a cap of the distal tarsals, and fusion of the metatarsals begins at the functionally important middle and distal part. Hence the intertarsal joint, the metatarsus and the tarsometatarsus of *Archaeopteryx* and modern birds are also homoplastic.

The Thecodont – Theropod – Crocodylomorph – *Archaeopteryx* – Modern Birds relationship was widely discussed in a number of major papers (BOCK, 1969, 1986; WALKER, 1972, 1985, 1990; OSTROM, 1976; TARSITANO & HECHT, 1980; TATARINOV, 1980; THULBORN & HAMLEY, 1982; THULBORN, 1984; TARSITANO, 1985, 1991; CRACRAFT, 1986, 1988; GAUTHIER 1986; PAUL, 1988; MARTIN, 1983a, 1983b, 1991; WITMER, 1991; ELZANOWSKI & WELLNHOFER, 1992). There are three main hypotheses: thecodont, crocodylomorph, and theropod relationship of birds. The latter is supported by most cladists and paleontologists. GAUTHIER's (1986) constructed a cladogram of the Theropod phylogeny in which the clade Maniraptora contained the Deinonychosauria and all birds including *Archaeopteryx*. But WITMER (1991) clearly argued that the Theropod hypothesis requires considerable refinement. The validity of each hypothesis rests upon differing interpretation of the same characters, different weighing of the morphological evidence, and the method of analysis. At present none of the hypotheses can be rejected or accepted until more fossil material is obtained.

The Late Triassic *Protoavis*

The discovery in 1987 of *Protoavis* from the Late Triassic of Texas was one of the most outstanding recent discoveries in vertebrate paleontology and has affected all hypotheses for the origin of birds. In spite of the three-dimensional preservation of much of the skeleton with many avian features as described by CHATTERJEE (1991; 1995), many workers do not believe its avian relationship. Principal objection appear to center on the 70-80 million years gap from the next avian fossils and the complete contradiction to the theropod hypothesis of avian phylogeny. Nevertheless, the former is not a basis for argument because not long ago an equally large gap existed between *Archaeopteryx* and the true birds. *Protoavis* is represented by a number of disarticulated bones that represent at least three individuals of different ontogenetic ages or different species, but is impossible to suggest that this is a mixed collection of different vertebrates (pers. observ.). It is a magpie-sized creature with a robustly built skeleton, a bony tail, the lightly built and pneumatized skull with a voluminous orbit and an enlarged braincase (CHATTERJEE, 1991). The jaws are practically toothless, just some teeth retained at the tip. The advanced avian affinity are underlined by the morphology of the shoulder girdle, forelimb, and hindlimb with extensive fusion of the distal segments in which *Protoavis* shares a

number of synapomorphies with ornithurine birds (CHATTERJEE, 1991; 1995). These synapomorphies establish a very close (sister-group) relationship of *Protoavis* and ornithurine birds in contrast to *Archaeopteryx*. *Protoavis* was definitely a ground running animal and its flight ability is under discussion. I could not confirm the presence of the quill knobs for primaries on the metacarpals that were pointed out by CHATTERJEE (1991). The morphology of its shoulder girdle and forelegs shows a preadaptation to the next evolutionary change in the wing. I consider the enlargement of forelimb and changes in the wrist joint to encircle tree trunks with the forelimbs as part of the adaptive path linking the ability for climbing trees to flight.

Enantiornithes

In 1981 WALKER described the Enantiornithes as a new subclass of birds based on a large collection of the Late Cretaceous bones from Argentina. The morphology of these birds was so new and curious, that some paleontologists believed that they were erroneously identified as birds. Ensuing findings confirmed WALKER who delineated very accurately the main features of this subclass in his initial, short paper on the enantiornithines and who also noted their similarity to *Alexornis antecedens* from the Campanian of Mexico. Shortly afterwards several other avian fossils were assigned to the Enantiornithes by MARTIN (1983a), including the Late Cretaceous *Alexornis* of Mexico and the Late Cretaceous *Gobipteryx* and avian embryos of Mongolia (ELZANOWSKI, 1981). The Mongolian embryos from the fossil eggs were not definitely assigned to the genus *Gobipteryx* described earlier on partial skulls (ELZANOWSKI, 1974, 1977). NESSOV (1984) and NESSOV & YARKOV (1989) described the new enantiornithines *Kizylkumavis* and *Sazavis* from the Late Cretaceous of Uzbekistan. MOLNAR (1986) described *Nanantius* from the Early Cretaceous of Australia. In the beginnings of 1990's, new enantiornithines were found from the Early Cretaceous of Central Asia and Spain. At present enantiornithines are known throughout the whole world and the entire Cretaceous.

The new Campanian representative of the genus *Nanantius* from Khermeen Tsav in the southern Gobi, Mongolia, is most important because this fossil is an almost complete three-dimensional skeleton. The structure of the articular surfaces of the vertebral centra is important for understanding the limits of the Enantiornithes. These surfaces are not amphicoelous, procoelous, or heterocoelous, but rather slightly convex cranially and almost flat caudally, or opisthocoelous. These features are also found in a new enantiornithine vertebra from the Lower Cretaceous of Australia (MOLNAR & KUROCHKIN, in prep.), partly in *Neuquenornis volans* (CHIAPPE & CALVO, 1994), and were noted in *Iberomesornis* (SANZ & BUSCALIONI, 1992). As MOOKERJEE (1935) has shown the heterocoelous vertebrae of neornithine birds with a cranial socket and caudal convex surface is a modification of the procoelous condition. The slightly opisthocoelous vertebra of the Enantiornithes is the opposing construction from which heterocoelity could not evolve, and thereby supporting the hypothesis that the Enantiornithes are a separate lineage of birds.

The earliest enantiornithines, known from the Early Cretaceous (Valanginian) of Liaoning Province, China, are the genera *Sinornis* and *Cathayornis*, representing small sparrow-sized, arboreal, flying birds with jaws bearing distinctive sharp teeth. Both are represented by larger part of the skeleton on the main slab and counterslab. *Sinornis santensis* was described as a sister taxon to all other Ornithurae with basal position within the Aves because it has such primitive features as a short, snout teeth, flexible clawed manus, pubic foot, gastralia, and not completed ossification at whole skeleton (SERENO & CHENGGANG, 1992). Yet *Sinornis* shares several most important enantiornithine autapomorphies such as a sharp-angled furcula with long hypocleidium, large and long pygostyle, long and caudally projected pubes with pubic foot, globular internal condyle of tibiotarsus, transversely fused proximal metatarsals, abutting of metatarsal I to the medial side of metatarsal II with reverted digit 1; it must be assigned to the Enantiornithes.

Cathayornis yandica was described in the Cathayornithiformes (incertae sedis) from a small specimen on a slab about 10 cm long (ZHOU et al., 1992). Unfortunately almost all bones were lost when the slab was split in the field; but fortunately, an excellent relief cast of the skeletal morphology was obtained from the slab. *Cathayornis* definitely has the main enantiornithine autapomorphies, including a sharp-angled furcula with long hypocleidium, coracoid peg and scapular socket articulation, dorsal head of coracoid with long humeral facet, perpendicular plane of dorsal coracoid to sternal ventral

portion, wide and concave humeral glenoid of scapula, diamond-shaped flat sternum, proximal humerus with pronounced external and internal tuberosities and middle positioned articulated head, unfused distal metacarpals, narrow and sharpened caudal portion of ilium, and globular internal condyle in distal tibiotarsus. The proximal metatarsals in this specimen are lacking, but the distal ones are unfused.

An unnamed enantiornithine was found in the Lower Cretaceous of China, Ordos Basin, on the bones of shoulder girdle and forelimb (DONG, 1993). This specimen is figured only by a sketchy drawing. It is noticeably larger than all known Early Cretaceous Enantiornithes and presents some features of this group in the general outlines of humerus, but the dorsal head of the coracoid and the coraco-scapular joint look very unusual for the enantiornithines, as do the metacarpals.

Iberomesornis romerali from Las Hoyas in east-central Spain, most probably Barremian rocks (SANZ, pers. com.), is known from a single slab (SANZ et al., 1988) and described extensively in 1992 (SANZ & BONAPARTE, 1992). The slab contains an almost complete skeleton 7-8 cm long without a skull. *Iberomesornis* was put in the monotypic Iberomesornithiformes as a sister-group of the Ornithurae (SANZ & BONAPARTE, 1992) or between *Archaeopteryx* and the Hesperornithiformes (CRACRAFT, 1988). To be noted are traces of opisthocoelity in some cervical vertebrae, the lateral excavation of cervical centra, the high neural arc in trunk vertebrae, the laminar pygostyle of 10-15 vertebrae, the presence of sternum, the strut-like coracoid, sharp-angled furcula with the styloid hypocleidium, the unfused metatarsals, and the reversed hallux. The preservation of specimen is not perfect with the bones crushed and partly eroded; therefore many morphological details are obscured, although excellent ultraviolet photographs revealed some of these. I consider this specimen as a juvenile individual because the metatarsi are totally unfused, ascending astragalar process is short, astragalus and process are not consolidated with the distal tibia, heads of the humerus, femur, and tibia are not molded completely, and sacral vertebrae are unfused. Nevertheless, *Iberomesornis* exhibits some enantiornithine autapomorphies: platycoelic opisthocoelity of vertebrae with laterally depressed centra, enlarged pygostyle, sharp-angled furcula, transversely placed external condyle of the distal humerus more proximal than the pronounced internal condyle. In spite of the metatarsals being unfused, they display clear enantiornithine features such as the rapprochement of proximal ends, proximal plane of three metatarsals lies at the same transversal altitude, pattern of the articular surface is on the proximal surface of the metatarsals, absence of the cap formed by the distal tarsals, and presence of two small separated distal tarsals. Hence *Iberomesornis* has to be assigned to the Enantiornithes. In addition the Las Hoyas site yielded a separate metatarsus with all digits (SANZ & BUSCALIONI, 1994), that has a pes larger than that of *Iberomesornis romerali*, but having the same morphology. However, it is characterized by fusion of the proximal metatarsals. Therefore it could belong to an adult individual of this species (pers. observ.). The fusion of the proximal metatarsals confirms the enantiornithine relationship of *Iberomesornis*.

Another and somewhat larger Las Hoyas bird is represented by the most of postcranial skeleton on a single slab. Some bones are broken but most provide detailed morphological evidence. In spite of good preservation, this fossil, *Concornis lacustris*, was assigned first to a new subclass, the Euornithes, placed on the cladogram between the Archaeornithes and Ornithurae or between *Iberomesornis* and the Enantiornithes (SANZ & BUSCALIONI, 1992). *Concornis* shares indisputable enantiornithine autapomorphies expressed in morphology of the furcula, humerus, ulna, distal tibiotarsus, and proximal metatarsus, and was subsequently placed in the Enantiornithes (SANZ et al., 1993).

Noguerornis gonzalezi, found on a single slab from the Neocomian limestones of Montsec in north-east Spain (LACASA-RUIZ, 1989) and consisting of a partial postcranial skeleton (shoulder girdle, forelimb, vertebrae, tibia) surrounded by some feathers, including primaries and secondaries was first considered as *Aves incertae sedis*. But *Noguerornis* shares the following advanced characters with the Enantiornithes – sharp-angled furcula with hypocleidium, pronounced external and internal tuberosities of the proximal humerus, oblique shaped distal humerus with the distal protrusion of the internal condyle, metacarpals are fused only proximally – and is a member of this group.

The definite enantiornithine *Nanantius eos* was described from a tibiotarsus from the Albian, Lower Cretaceous, of Australia by MOLNAR (1986). An additional new enantiornithine specimen represented

the toothed jaws, hindlimb, and shoulder girdle is from the Lower Cretaceous (Valanginian-Hauterivian) of Kholbotu, Central Mongolia. It looks similar to the described Chinese enantiornithines from the Liaoning Formation. Unfortunately UNWIN (1993) suggested the affinity of the Kholbotu specimen with *Ambiortus* known from the neighboring Khurilt-Ulan-Bulak of the same age. But they have, for example, completely different furculae – sharp-angled with long hypocleidium in the Kholbotu specimen and the rounded without hypocleidium and symphysis in *Ambiortus*.

It is typical that all very early enantiornithines known by almost complete skeletons of small toothed, arboreal birds were deposited in sediments of shallow Early Cretaceous lakes. In Mongolia and in Spain, the sediments of the same lakes produced numerous fossil feathers which can be attributed to small birds but their taxonomic identification is impossible. Late Cretaceous enantiornithines from Mongolia, Uzbekistan, United States, Mexico, and Argentina, are birds of different sizes, from very small to chicken size, and of different ecological types – arboreal, water, and cursorial.

From the Maastrichtian locality El Brete in northwestern Argentina, besides *Enantiornis leali* WALKER, 1981, three new genera and species were described from metatarsi (CHIAPPE, 1991a, b, 1993). One of these is *Lectavis bretincola* with long and thin metatarsus distinguishing by a longitudinal plantar ridge, strengthening this long thin bone, with a hypotarsal prominence on the proximal edge. The true hypotarsus in the Neognathae develops as a distal plantar extension of the metatarsal cap lacking in the enantiornithines; thus the hypotarsi in these two groups is convergent.

Soroavisaurus australis is a sister taxon of *Avisaurus archibaldi* (BRETT-SURMAN & PAUL, 1985) from the Hell Creek Formation (Maastrichtian) of Montana, and of an unnamed avisaurid from the Two Medicine Formation of Montana. Reallocation of the Avisauridae Brett-Surman & Paul, 1985, from the Theropoda to the Enantiornithes was proposed by MARTIN (1991) and confirmed by CHIAPPE (1992). A small enantiornithine from the Rio Colorado Formation (? Coniacian-Santonian) of central western Argentina, placed in the Avisauridae, was described as *Neuquenornis volans* from a nearly complete articulated skeleton (CHIAPPE & CALVO, 1994). Several bones of new enantiornithine were announced from the marine Campanian beds of Alabama (LAMB et al., 1993).

NESSOV (1984, 1988, 1992a, 1992b) and NESSOV & YARKOV (1989) described the small enantiornithines *Kizylkumavis cretacea* and *Sazavis prisca* from the Bissekty Formation (Coniacian) of Dzhyrakuduk in the Kizyl-Koom Desert of Uzbekistan. They are based on the distal portion of the humerus and the tibiotarsus. Fragmentary coracoids of some Enantiornithes from Dzhyrakuduk were mentioned in these papers and some new findings are now known as "*Enantiornis*" *walkeri* and "*Enantiornis*" *martini* (NESSOV & PANTHELEEV, 1993). Some other bones from Dzhyrakuduk such as the proximal metatarsus PO3394 (NESSOV & BORKIN, 1983; NESSOV, 1984, 1992b) and the axis PO3473 (NESSOV, 1992b) also represent enantiornithines in my opinion. Partial synsacrum (two species of *Zhyraornis* and two species of *Ichthyornis*) from the same locality were considered by NESSOV (1984, 1986, 1990, 1992b) as ichthyornithiforms. These fossils demonstrate clear enantiornithine autapomorphies and a similarity with pelvis of genus *Nanantius*. A new representative of this genus occurs from the Campanian beds of South Mongolia. The possibility of *Zhyraornis* belonging to the Enantiornithes was also noted by NESSOV & PANTHELEEV (1993).

Gobipteryx minuta was described on two partial skulls from the Late Cretaceous of Mongolia (ELZANOWSKI, 1974, 1976), and originally put in the Palaeognathae, but MARTIN (1983a;1987) demonstrated that *Gobipteryx* belongs to the Enantiornithes based on comparison of its quadrate and premaxillary with *Archaeopteryx*. The birds embryos reported soon afterwards from the same beds by ELZANOWSKI (1981) were placed by MARTIN (1983a) in the Enantiornithes. New data on the embryos reveal the revised view on composition of these embryonic birds (CHATTERJEE et al., MS). Actually some represent enantiornithines, but different generically from *Gobipteryx*, and others belong to the Palaeognathae.

One new specimen of small arboreal enantiornithine was discovered from the Campanian of Mongolia in Khermeen Tsav where bird embryos were found also in the same beds. This disarticulated three-dimensional specimen exhibits most of the skeleton including some skull bones (Pers. Obs). It belongs to *Nanantius* and provides much new understanding of the cranium, vertebrae, and pelvis of enantiornithine birds.

At present the Enantiornithes contain several distinct taxonomic lineages and diverse ecological modes of the large terrestrial, water, and small arboreal birds. The Enantiornithes are a most diverse group of the Cretaceous birds which disappeared at the end of the Cretaceous. They share a number of autapomorphic characters, and also possess specific primitive characters in comparison to the Ornithurae such as construction of skull-mandibular articulation, pattern of vertebrae, some morphological details in the structure of shoulder girdle, pelvis, forelimb, and hindlimb, many of them are common with the Archaeornithes and suggesting that the Enantiornithes are a very primitive taxon. Simultaneously the Enantiornithes share some important derived characters with the Archaeornithes such as a single-headed quadrate with latero-caudal condyle, a pubic peduncle articulation of pubis with ilium, a fusion of metacarpals in proximal heads, reduction of fourth and fifth manual digits, a peculiar fossa on the distal surface of external condyle of femur, transverse fusion of proximal metatarsals, anterior posterior compression of proximal metatarsals, intertarsal articulation between of distal tibiotarsus (including proximal tarsals) and proximal metatarsus, and prominent longitudinal grooves on the both sides of unguis pedal phalanges. I concur with MARTIN's (1983a, 1991) proposed relationship of the Enantiornithes with *Archaeopteryx* which is strongly supported by this list of synapomorphies, and consider the combined group (subclass Sauriurae) to be a separate primitive lineage in the evolution of birds.

Hesperornithes

Not long ago the hesperornithiforms were known only as large flightless birds from the Late Cretaceous of central North America, which were highly specialized for foot-propelled diving and possessed teeth in maxillary and dental grooves. Their range has now been extended north to Alaska and to Europe and Asia. Small and probably flying hesperornithiforms were discovered in the Late Cretaceous of North America and Central Asia. Chinese workers (S.A.P.E., 1992) announced the discovery of hesperornithiforms from the Lower Cretaceous of Antarctica. The Enaliornithidae, known since the middle of last century from the Albian of England and until recently believed to be loons (BRODKORB, 1963), are now treated as the earliest known hesperornithiforms by MARTIN & TATE (1976). MARTIN (1983a) also discussed the *Enaliornis*-like bird from the Cenomanian of Kansas. Two species of *Enaliornis* known from fragments of the hindlimb elements and other bones, including partial skulls, were discovered recently; their taxonomic composition and relation with other birds still must be studied in detail (ELZANOWSKI & GALTON, 1991). Late Cretaceous North American hesperornithiforms belong to the genera *Hesperornis* (4 species), *Parahesperornis*, and *Baptornis*, and are distributed from Kansas to the Arctic coast of Alaska and Canada. Their occurrence parallels the shoreline of the Late Cretaceous American Western Interior Seaway. Flightless *Hesperornis*, *Asiahesperornis*, and *Parascaniornis* were described by NESSOV & PRIZEMLIN (1991) and NESSOV & YARKOV (1993) from the Santonian-Maastrichtian (?) of Kazakhstan, Central Russia, and South Sweden. They represent large and very large species recognized from fragmentary tibiae, tarsometatarsi, and vertebrae. Interestingly, *Hesperornis rossica* Nesson & Yarkov, 1993, is found from the Don River region in Russia as well from Scone in Sweden. These new Eurasian hesperornithiforms inhabited the Late Cretaceous Turgaj and Fenno-Scandian sea straits (NESSOV, 1992c). The first Asian hesperornithiform *Judinornis* (Baptornithidae) was discovered from a single vertebra in the Nemegt Formation, Maastrichtian, of Mongolia (NESSOV & BORKIN, 1983; NESSOV, 1986). A hesperornithiform distal tibiotarsus found in the same beds from another locality (KUROCHKIN, 1988), was first identified as *Baptornis* sp., and finally shown to be closely related to *Parahesperornis*. With the exception of one occurrence of *Hesperornis* in the non-marine rocks of Alberta (FOX, 1974), the first-known hesperornithiforms came from marine beds. Later discovered thin-walled and highly pneumatic vertebra and tarsometatarsi of the noticeably smaller and probably flying representatives of new hesperornithiform families were recorded from the Maastrichtian sites of continental beds in the United States, Canada, and Mongolia (MARTIN & KUROCHKIN, in prep).

All hesperornithiforms have a number of the primitive characters in the postcranial and cranial morphology. They also have a set of autapomorphies, some of which are clearly connected with diving specialization of these birds, but other are not. Some advanced characters in the morphology of the vertebrae, jaw apparatus, and histostructure of the bones (HOUDE, 1987) are shared with

neornithine birds. This complicated combination of characters suggests placement of the hesperornithiforms in a high category taxon of ornithurine birds.

Ichthyornithes

The Ichthyornithiformes are another group of Mesozoic toothed birds described by O. MARSH. In contrast to the Hesperornithiformes, they bear teeth in alveoli; however, both groups have in common an intramandibular articulation and a prementary bone. In other respects, these groups are very different in both cranial and postcranial morphology. Three known species of the genus *Ichthyornis* occurred in the Late Cretaceous from the Early Turonian to the Late Campanian, in marine rocks of North America from Alabama to Manitoba (MARTIN & STEWART, 1982; FOX, 1984; OLSON, 1985; PARRIS & ECHOLS, 1992). The toothed Ichthyornithiformes display a very complicated mosaic of primitive and advanced characters in their skeletal morphology and share a number of the advanced characters with neornithine birds. Hence they should be placed in the Ornithurae as a separate high category taxon.

Apatornis of the Late Cretaceous Niobrara Chalk of Kansas had been placed in the Ichthyornithiformes by O. MARSH and until recently has been traditionally retained in this order although in its own family. Differences between *Apatornis* and *Ichthyornis* were shown by HOWARD (1955), OLSON (1985) and MARTIN (1987), with the affinity of the former to *Telmabates* or *Ambiortus*. The neornithine relationship of *Apatornis* remains unclarified, but obviously it should be excluded from the Ichthyornithiformes.

Several Late Cretaceous (Coniacian) ichthyornithiform birds from Uzbekistan were described on fragmentary synsacra by NESSOV (1986, 1990, 1992a) in *Zhyraornis* and *Ichthyornis*. The flatness of the general shape of synsacra in these fossils, the conspicuous ventral longitudinal groove, lateral excavations on the vertebral centra, and their small size prevent their assignment to the Ichthyornithiformes. At the same time these characters are shared with the enantiornithine birds; therefore I concluded that they belong to the Enantiornithes (see above).

Palaeognathae

The modern Palaeognathae – the Ratitae and Tinamiformes – lacked fossil roots until HOUDE and OLSON (1981) published on the Paleogene flying paleognaths. Later HOUDE (1988) placed new Paleogene paleognaths in the Lithornithiformes, and the Eocene European *Palaeotis* in the Ratitae (HOUDE & HAUBOLD, 1987; PETERS, 1988). These discoveries opened the possibility of identifying fragmentary postcranial remains of Paleogene and the Cretaceous paleognaths (KUROCHKIN, 1995). At present the Palaeognathae are found in the Paleogene of Europe, Africa, Australia, and South America, as the genera *Emuarius*, *Stromeria*, *Eremopezus*, *Proceriavis*, *Eleutherornis*, *Palaeotis*, *Pseudocrypturus*, *Paracathartes*, *Lithornis*, *Diogenornis*, and *Remiornis* (KUROCHKIN, 1995). The Late Cretaceous paleognaths are represented only by some embryos from fossil eggs among those described by ELZANOWSKI (1981) and new ones (CHATTERJEE et al., MS). They occur from the same rocks of the Campanian locality Khermeen Tsav where the embryos of the Enantiornithes are also found. The Early Cretaceous genera *Ambiortus*, *Gansus*, *Wyleyia*, and *Palaeocursoris* represent paleognaths from Central Asia and Western Europe.

Ambiortus is represented by a partial articulated skeleton from the Lower Cretaceous (Berriasian-Valanginian, see SINITZA, 1993) of Central Mongolia (KUROCHKIN, 1982, 1985). The position of *Ambiortus* with the Palaeognathae is based on absence of the bicipital crest, proximal beginning of the pectoral crest, dorsal displacement of the humeral articular glenoid along the coracoid head, short and wide configuration of acrocoracoid, long acromial process of scapulae, and absence of the hypocleidium. There are suggestions that *Ambiortus* is related to the Ichthyornithiformes (MARTIN, 1987) or to the Lithornithiformes (HOUDE, 1988). Comparison of *Ambiortus* with *Lithornis*, *Paracathartes*, and *Ichthyornis* leads to the conclusion that it is not closely related to them; the affinities of *Apatornis* within the Palaeognathae must still be resolved.

Gansus from the middle of the Lower Cretaceous, the Xiagou Formation, of Gansu Province, China, was described on the articulated distal tibiotarsus, tarsometatarsus, and digits (HOU & LIU, 1984). This specimen belongs to the paleognathous birds because the supratendinal bridge is absent,

foramens in the proximal tarsometatarsus, knob for *M. tibialis anticus*, perforation of the hypotarsus, and symmetric trochlea for third digit. *Gansus* appears to be a diving bird because of its laterally compressed tarsometatarsus, longest fourth digit, distinctly asymmetric distal tibia, and proximal elevation of the internal cotyla (the later features suggests foot-propulsion).

Wyleyia is known on the partial humerus from the Barremian of England (HARRISON & WALKER, 1973). Based on the absence of the bicipital crest, the proximal beginning of the pectoral crest, and the pneumatic fossa, it has to be placed in the Palaeognathae.

Palaeocursornis corneti from the Wealdian continental rocks of Romania (KESSLER & JURCSÁK, 1986; see BOCK and BÜHLER, in press) is represented by the distal femur. It has paleognathous characters such as narrowness of the articular surface of medial condyle, wide cranial ridge, and unexpressed crest on the internal supracondyle.

Whether the Palaeognathae are monophyletic (BOCK, 1963; BOCK & BÜHLER, 1990; PRAGER et al., 1976; FEDUCCIA, 1985; CRACRAFT, 1986, 1988; ELZANOWSKI, 1988; SIBLEY & AHLQUIST, 1990; KUROCHKIN, 1988, 1995) or polyphyletic (MCDOWELL, 1948; MARTIN, 1983a; OLSON, 1985; HOUDE, 1988) has been widely discussed. Principal palaeognathous characters include lack of a joint articulation of the palatine with the pterygoid, gliding articulation of the vomer with the parasphenoid rostrum, posterior position of the joint of the elongated basipterygoid process with the pterygoid, and fusion of the interorbital and internasal septas. Whether these are primitive or advanced condition is open to discussion, but monophyly of the Palaeognathae is supported by an extensive set autapomorphies such as the undivided supraoccipital, unpaired frontal process of the premaxillary, secondarily single-headed quadrate, lack of the hemipterygoid, extensive articulation of the vomer and pterygoid, far posterior extension of the nasal relative to the posterior border of the premaxillary, lateral opening of the eustachian tubes, microstructure of feathers and bone, anatomy of the circulatory and nervous systems, anatomy of the tongue, histology of primary osteons, system of reproduction and social behavior, protein composition of blood and egg, DNA-DNA hybridization (SIBLEY & AHLQUIST, 1990) and fossil eggshells (MIKHAILOV, 1991). I consider the Palaeognathae to be an old pachyphyletic taxon of monophyletic origin. They appeared at least in the earliest Cretaceous and were most diverse during the first $\frac{2}{3}$ of their history, after which they lost in competition with the neognathous birds, almost disappeared, and exist today mainly on the southern continents. The Palaeognathae and Neognathae are two sister-groups within the Neornithes.

Neognathae

The most ancient present-day neognathous birds are known from the Early Cretaceous, namely: *Gallornis* from the Neocomian of France, *Eurolimnornis corneti* from Romania (KESSLER & JURCSÁK, 1984, 1986; see BOCK and BÜHLER, in press) and *Horezmavis* from the Albian of Uzbekistan (NESSOV & BORKIN, 1983). These records are most important in spite of the fragmentary nature of the fossils and impossibility to determine their affinity with any modern birds, because they establish the presence of the Neognathae and their simultaneous existence with the Palaeognathae in the Early Cretaceous. The next occurrence of the Neognathae is from the Campanian and Maastrichtian of the Late Cretaceous, when representatives of 4 modern orders of birds – the Gaviiformes, Procellariiformes, Pelecaniformes and Charadriiformes – are found. Cretaceous loons were found in Chile [*Neogaeornis* transferred by OLSON (1992) from the Hesperornithiformes to the Gaviiformes] and in Uzbekistan [NESSOV's (1992a) report of a very probable loon's vertebra in the Coniacian of Dzhyrakuduk]. The Maastrichtian albatross *Tyttostonyx* is from New Jersey (OLSON & PARRIS, 1987). Another record of a Maastrichtian albatross is from the Nemegt Formation of Mongolia. Early reports of Cretaceous Pelecaniformes proved to be incorrect. ANDREWS (1913) based the pelecaniform *Elopteryx nopcsai* on the epiphyses of a femur and tibiotarsi from the Maastrichtian of Romania. The tibiotarsi were redescribed by HARRISON & WALKER (1975) as the owl family Bradycnemidae. Subsequently, BRODKORB (1978), ELZANOWSKI (1983), MARTIN (1983a), and OLSON (1985) decided that these bones are those of small dinosaurs. However, GRIGORESCU & KESSLER (1980), KESSLER (1987), and JURCSÁK & KESSLER (1986) published new finds of epiphyseal remains and a well preserved cranium of *Elopteryx* from the same Cretaceous rocks of Hateg Basin. The supposed limnofregatid *Volgavis marina* was described on a mandible from the Maastrichtian or Danian of

Central Russia (NESSOV & JARKOV, 1989). I have a cormorant-like scapula from the Nemegt rocks, Maastrichtian, of South Mongolia, which will be described in the near future. The best known Late Cretaceous neognathous birds belong to the Graculavidae – “transitional charadriiforms” as determined by OLSON (1985). All formerly described pelecaniforms, phoenicopteriforms, gruiforms and charadriiforms (*Graculavus*, *Telmatornis*, *Laopteryx*, *Palaeotringa*, and *Cimolopteryx*) from the Maastrichtian of the United States belong to 5 genera of the Graculavidae (OLSON & PARRIS, 1987). Several new graculavids come from the Nemegt Formation of Mongolia. One presbyornithid is recorded from the Barun-Goyot Formation, Campanian, of Mongolia (KUROCHKIN, 1988). A Late Cretaceous loon-like bird and presbyornithid-like bird from Antarctica were announced recently (CHATTERJEE, 1989; TAMBUSSI & NORIEGA, 1993). I expect that neognathous birds were much more diverse in the Cretaceous, and they are not known because of poor preservation of their remains. Monophyly of the Neognathae is supported by autapomorphies such as a palatine- pterygoid articulation, loss of broad vomer-maxillary contact, separation of two otic condyles of the quadrate by the pneumatic recess, three quadrate cotylas to articulate with the lower jaw, medial opening of the eustachian tubes, caudal fusion of ilium and ischium, development of the bicipital crest, obliteration of all braincase sutures, and advanced microstructure of the eggshell.

Incertae sedis Mesozoic avian

Several new Cretaceous birds were described over the past years whose relationships remain unclarified. CHIAPPE & CALVO (1989) and CHIAPPE (1990) described the partial skeleton of a medium-sized flightless bird from the Coniacian of Patagonia described as *Patagopteryx deferrariisi* (ALVARENGA & BONAPARTE, 1992) in the new order Patagopterygiformes. The cervical vertebrae of *Patagopteryx* are heterocoelous and thoracic ones are transitional to heterocoelity or are procoelous, proximal tibiotarsus possesses lateral and cranial cnemial crests, distal metatarsals are completely fused, hallux has two phalanges, ischia, ilia and pubes do not fuse caudally. These characters suggest that *Patagopteryx* has uncertain relationships within the Ratitae.

Kuszholia mengi was established on two caudal portions of the synsacri from the Coniacian of Uzbekistan and put in the family Kuszholiidae incertae sedis (NESSOV, 1992b; NESSOV & PANTHELEEV, 1993). In a later paper the Kuszholiidae were assigned to the Patagopterygiformes.

Chaoyangia beishanensis, from the Jiufotang Formation (Neocomian, Early Cretaceous) of Liaoning Province in China, is known on the elements of hindlimb, pelvis, ribs and thoracic vertebrae (HOU & ZHANG, 1993). The mosaic of the advanced (uncinate processes, 8 sacral vertebrae, absence of fourth trochanter of femur) and archaic features (non-heterocoelous thoracic, unfused sacral vertebrae, separation of ischium from ilium and pubis, pubic foot) prevent determination of the relationships of *Chaoyangia* within birds.

Platanavis nana was recognized on the middle portion of a tiny synsacrum from the same Coniacian Dzhyrakuduk site in Uzbekistan (NESSOV, 1992b), but cannot be placed in the system of early birds.

Problematic avian

Mononykus olecranus from the Maastrichtian of Mongolia (NORELL et al., 1993; PERLE et al., 1993, 1994) was assigned to Avialae (= birds) sensu GAUTHIER (1986) based a such derived characters as a sternum, sternal carina, antitrochanter on the ilium, undivided large trochanter of the femur, and the short fibula. The isolated numerical analysis of these characters led to the conclusion of position of *Mononykus* as an advanced member of the Avialae. But a detailed examination of its morphology, including articulation of cervical ribs on the same level as cranial zygapophyses and transverse processes, biconvex posterior dorsal vertebrae and opisthocoelous thoracic and cervical, obtuse apex of the scapula that should be directed dorsad in natural articulation to the coracoid [therefore the position of the scapula had to be vertical, not horizontally longitudinal as it was figured in the original reconstructions in PERLE et al. (1993, 1994; pers. comm. of A. KARHU)], single distal condyle of the humerus, composition of the metatarsus with the metatarsal III attenuated proximad, proximal articular surface of the metatarsus formed only by the metatarsals II and IV, are not in accordance with position of *Mononykus* within the Avialae. On the derived condition of these features, *Mononykus*

is an obvious maniraptoran theropod demonstrating some independent trends toward avian features, but without any close relationship to birds.

Higher taxa of class Aves

There were a several attempts to postulate and discuss the major clades of the Aves (MARTIN, 1983a; THULBORN, 1984; GAUTHIER, 1986; CRACRAFT, 1988). Recent data from Mesozoic birds show a more complicated picture of the early evolution of birds than it was believed earlier. The basic conclusions from these data are the appearance of ornithurine ancestors in the Triassic (*Protoavis*) and parallel evolution of the Sauriurae and Ornithurae. I will try to define the major taxa of birds using all available characters, but make no attempt to identify the reptilian origins of birds. Currently delimitation of the class Aves, including *Protoavis*, *Archaeopteryx* and all later birds, encounters many difficulties because several major features formally characterizing birds (furcula, sternum, etc.) are also found in the Theropod. Nevertheless, the set of the derived anatomical and system morphological features designates the monophyly of class Aves (node 1) by the following diagnosis:

Diagnosis A: (1) premaxillary elongate; (2) maxillary process of premaxillary reduced; (3) fenestra pseudorotunda developed; (4) dentary thinned and elongated; (5) postorbital are reduced; (6) cervical thinned and elongated; (7) pronounced scapular acromion; (8) tapered scapula; (9) coracoid narrowed and reverted antero-posteriorly; (10) metacarpals fused with distal carpals; (11) metacarpals are fused at least proximally; (12) ischium compressed and dorso-ventrally deep; (13) axis of femoral head perpendicular to shaft; (14) first pedal digit reversed; (15) olfactory lobe reduced; (16) advanced cephalization index; (17) orbits enlarged; (18) position of forelimb with flexion-extension of wrist joint at the plane of manus; (19) feathers. These autapomorphies suggest that the basal dichotomy of birds into the Sauriurae and Ornithurae has to be extended well into the Triassic.

The infraclasses Archaeornithes and Enantiornithes were united in the subclass Sauriurae by MARTIN (1983a, 1985, 1991). The Sauriurae (node 2) is supported by the combination of primitive characters and autapomorphies of the following diagnosis, including some primitive characters, too:

Diagnosis S: (1) single-headed quadrate with latero-caudal condyle; (2) adjacent quadrate-quadratojugal joint; (3) broad scapular glenoid forms the main articulation to humeral head; (4) bicipital crest not developed; (5) proximal fusion of metacarpals; (6) reduction of fourth and fifth manual digits; (7) large dorsal ischiadic ridge; (8) elongation of preacetabular portion of ilium; (9) absence of antitrochanter; (10) pubic peduncle articulation of pubis with ilium; (11) pubes thin and long; (12) peculiar fossa on the distal surface of external condyle of femur; (13) femoral fibular condyle not developed; (14) intertarsal articulation between distal tibiotarsus (including proximal tarsals) and proximal metatarsus; (15) distal tarsals strongly reduced; (16) metatarsal cap absent; (17) three proximal metatarsals fuse in transverse row; (18) proximal metatarsals compressed anterior posterior; (19) prominent longitudinal grooves on the both sides of unguis pedal phalanges. Characters 3, 6-8, 10-12, 14, 15, and 17-19 are postulated to be derived.

One important criterion demonstrates similarity of the physiological system of the Archaeornithes and Enantiornithes. As concluded by WELLNHOFER (1992), observing different specimens of *Archaeopteryx*, its hindlimb and tail show a positive reptilian growth allometry rather than an avian growth pattern. Different species of the Enantiornithes also demonstrate the absence of epiphyseal sutures in the long bones as distinctive for neornithine birds. Moreover, some specimens of the Enantiornithes have incompletely molded long bone heads that look like those of typical lizard's bones from Cretaceous rocks.

GAUTHIER & PADIAN (1985:191) claim that: "We can find no apomorphies of *Archaeopteryx*, based on known evidence, and so there is no obstacle to considering it 'ancestral' to other birds, were that the objective". But the Archaeornithes (*Archaeopteryx*) are supported by the following autapomorphs: Diagnosis A¹: (1) reduced slender quadrate; (2) enlarged paroccipital process; (3) quadrate articulates at the posterior base of the parocciput; (4) coracoid somewhat enlarged and inflected postero-medially; (5) pubis reverts ventrally; (6) ischium bipartite caudad; (6) free tail vertebrae reduced to 23; (7) metacarpal II longer relative to shortened metacarpal III.

The Enantiornithes are based on the following combination of characters:

Diagnosis E: (1) pterygoid bifurcated rostrad; (2) long retroarticular process of mandible; (3) axis stretched cranio-caudally and with broad neural arc; (4) caudal articular surface of axis body nearly globular; (5) articular surfaces of cervical centra opisthocoelous; (6) thoracic vertebral centra possess lateral excavations; (7) synsacrum includes 7-12 fused vertebrae; (8) 8-12 unfused tail vertebrae have lengthened centra; (9) long pygostyle includes 4-14 vertebrae; (10) neural vertebral canal vast; (11) plane of shoulder coracoid extremity lies perpendicularly to plane of sternal extremity; (12) acrocoracoid stretched; (13) distinct scapular process, projecting caudo-ventrally, develops on caudal side of coracoid head; (14) articulation of acrocoracoid and scapular acromion forms the roof of diosseal canal for ligament of M. supracoracoideus; (15) coracoid peg and scapular socket articulation; (16) wide scapular glenoid forms principal articular surface to humerus; (17) each head of furcula attaches to acrocoracoids on cranial side; (18) heads of furcula very delicate and flat; (19) furcula V-shaped with sharp (45-60°) branching angle; (20) long hypocleidium bears a laterally compressed crest along caudal side; (21) sternal plate short, wide, and with long lateral trabeculas; (22) caput humeri locates at midline of proximal head; (23) ventral and dorsal humeral tuberosities well developed and directed proximad; (24) distal end of humerus remarkably compressed cranio-caudally; (25) external condyle of distal humerus almost transversely oriented; (26) shaft of radius with a longitudinal groove along ventro-caudal surface; (27) remarkable oblong hole developed in front of the acetabular ventro-cranial edge of ilium; (28) opistopubic pelvis with long and narrow pubes, fusing by their caudal ends in the elongated pubic symphysis; (29) tibiotarsus with large globular internal condyle and small laterally compressed external condyle; (30) hypotarsus not developed; (31) metatarsal I abuts to medial facet of metatarsal II; (32) digit 1 reverted. The characters 2, 3, 6-12, 15, 18-29, and 32 show autapomorphies generally characteristic for the Enantiornithes.

Protoavis, all other avian fossils (excluding the Sauriurae), and the extant birds are united into an unnamed taxon (node 3) diagnosed by the following set of features:

Diagnosis U: (1) double-headed quadrate; (2) quadrate pneumatized; (3) peg and socket articulation between quadrate and quadratojugal; (4) presence of the quadrate orbital process; (5) narrow anteriorly frontal bones; (6) strongly enlarged the brain hemispheres and cerebellum; (7) heterocoelity of cervical vertebrae; (8) scapular peg and coracoid socket articulation; (9) strut-like coracoid, flattening cranio-caudad; (10) pronounced acrocoracoid; (11) developed procoracoid process; (12) triosseal canal; (13) two condyles in distal humerus; (14) developing epicondyle on distal humerus; (15) fusion of third and fourth metacarpals by the proximal and distal ends; (16) reduction of first and fifth metacarpals; (17) pelvis fused; (18) postacetabular ilium broad; (19) fusion of ilium and ischium enclosing an ilioischadic fenestra; (20) deep renal fossa; (21) pubes without caudal symphysis and with cranial prepubic process; (22) fibular condyle in distal femur; (23) plantar protrusion of middle (third) metatarsal in proximal portion of metatarsus. The condition of some of these characters (1, 9, 10, 19) in the Palaeognathae is secondary primitive or unclarified.

I suggest a new subclass Praeornithurae (*Protoaves*) as a sister-group to the Ornithurae based on the following autapomorphies:

Diagnosis P: (1) triangle-shaped quadrate; (2) expanded temporal area; (3) highly reduced pterygoid; (4) partial fusion of metacarpals; (5) beginning of reduction of first and fifth metacarpals; (6) foramen at base of astragalar ascending process; (7) number of free tail vertebrae somewhat reduced; as well as the overall primitive condition of robust skeleton. The Praeornithurae share the 23 synapomorphies of Diagnosis U with the Ornithurae.

The monophyly of the subclass Ornithurae (node 4), which includes all other fossil and extant birds, is supported by the following diagnosis:

Diagnosis O: (1) premaxillary fused; (2) premaxillary toothless; (3) nasal process of premaxillary overlies nasal; (4) free caudal vertebrae reduced at least to 15; (5) pygostyle; (6) ossified uncinat process; (7) ossified ventral ribs attached to sternum; (8) lack of gastralia; (9) triosseal canal; (10) monolithic sternal plate; (11) antitrochanter; (12) pelvis opened ventrally; (13) distal tarsals form cap fully fused with metatarsals; (14) intertarsal articulation between proximal tarsals and distal tarsals; (15) ossification of metatarsals begins from middle portion of bone and extends proximad and distad.

Ossification of the metatarsals is one of the most important characters separating the Sauriurae and Ornithurae. Transverse fusion of the proximal metatarsals in *Archaeopteryx* and the Enantiornithes was stressed by many workers. Two individuals of *Iberomesornis* (see above) confirm such fusion in the postnatal development of enantiornithine birds. Most workers claim erroneously that the ornithuraen metatarsals begin to consolidate from their distal end. As was shown by JOLLIE (1977), fusion of the metatarsals starts at their middle and extends proximally and distally. Later the ossified mass of distal tarsals (a cap) fuses with the proximal end of the metatarsus forming the consolidated tarsometatarsus of ornithurine birds.

The Hesperornithiformes and Ichthyornithiformes definitely share the synapomorphies of Diagnosis O, consequently they are members of the Ornithurae. At the same time, their position on the cladogram is problematic because they possess some very primitive characters that are apparently inherited from early avian evolution. Therefore these two taxa do not have a transitional place on the cladogram. Based on only derived characters, the Hesperornithiformes and Ichthyornithiformes occupy positions at the base of the Neornithes. However, such plesiomorphic characters as thecodontian teeth, morphology of shoulder girdle and palate apparatus in the Hesperornithiformes, and the amphicoelous vertebrae, absence of bicipital crest, toothed jaws, etc. in the Ichthyornithiformes suggests their placement as separate clades at the base of the Ornithurae as sister-groups of the Neornithes. Another possibility is to consider the Ichthyornithiformes as members of the Neognathae (= Carinatae; MARTIN, 1983a, 1991; CRACRAFT, 1988).

The hesperornithiforms are united in the infraclass Hesperornithes based on the combination of derived and primitive characters in the following diagnosis:

Diagnosis H: (1) prokinesis; (2) intramandibular articulation; (3) long retroarticular process; (4) short robust pterygoid; (5) long delicate palatine; (6) bipartite unfused vomer; (7) teeth in a longitudinal groove; (8) prementary bone; (9) cervical vertebrae dorsoventrally high with wide wing-like postzygapophyses; (10) heterocoelous trunk vertebrae; (11) uncinatous process ossified and unfused; (12) short coracoid lacking acrocoracoid; (13) delicate unfused clavicles; (14) reduced wing bones; (15) pelvic bones not fused caudad; (16) patellar foramen for tendon of *M. ambiens*; (17) absence of hypotarsus; (18) distinct lateral ridge on plantar tarsometatarsus; (19) metatarsal IV enlarged and longest. The characters 1, 3-6, 9-14, 16, and 18-19 are postulated to be derived. The reticular pattern of the vascular canals in the primary osteon is an important synapomorphy shared by the Hesperornithes and the Neognathae (HOUDE, 1987).

The Ichthyornithes form an unnamed taxon (node 5) with the Neornithes supported by the following diagnosis of synapomorphies:

Diagnosis I: (1) coracoid elongated and flattened cranio-caudally; (2) scapular socket on coracoid; (3) scapular articulation placed well below the head of coracoid; (4) procoracoid process; (5) pneumatized acrocoracoid; (6) peg-like coracoidal articulation of scapulae; (7) keeled sternum; (8) dorsad located head of humerus; (9) ball-shaped internal and olive-shaped external (locating oblique to long axis of bone) condyles of distal humerus; (10) developing brachial depression of humerus; (11) true fused carpometacarpus with intermetacarpal space.

The infraclass Ichthyornithes can be established as a separate clade based on the following diagnosis:

Diagnosis I': (1) prementary bone; (2) teeth in individual alveolus; (3) intramandibular articulation; (4) absence of retroarticular process; (5) amphicoelous cervical; (6) thoracic centra strongly laterally excavated; (7) enlarged pygostyle; (8) short wide acrocoracoid; (9) absence of acromial process in scapula; (10) thin heads of furcula; (11) strongly projecting internal humeral tuberosity; (12) indistinct capital groove; (13) conspicuously long and high delto-pectoral crest in the plane of epiphysis; (14) absence of bicipital crest; (15) flattened proximal articular surface of carpal trochlea; (16) robust rectangular-like shape of proximal carpometacarpus; (17) pelvic bones unfused caudad; (18) absence of supratendinal bridge; (19) developing external foramen in proximal tarsometatarsus; (20) smooth unperforated hypotarsal prominence. Characters 6-9, 11, 13, 19, and 20 are derived. The Palaeognathae and Neognathae are sister-groups forming the infraclass Neornithes (node 6) which is based on the following diagnosis:

Diagnosis N: (1) loss of teeth on maxillary and dentary; (2) bony mandibular symphysis; (3) loss of mandibular coronoid bone; (4) dentary forked posteriorly; (5) rynchokinesis; (6) palatine possesses a long maxillary process; (7) bony eustachian tubes; (8) loss of gastralia; (9) fused uncinat process; (10) prominent scapular acromion; (11) elongated ilium overlaps the most of thoracic ribs; (12) appearance of obturator foramen; (13) delto-pectoral crest is deflected cranially; (14) development of proximal pneumatic humeral fossa.

The monophyletic, but pachyphyletic Palaeognathae are recognizing by the next combination of characters:

Diagnosis PG: (1) undivided pterygopalatine bar; (2) gliding articulation of vomer and parasphenoid rostrum; (3) extensive articulation of vomer and pterygoid; (4) articulation of elongated basipterygoid process and pterygoid; (5) otic head of quadrate undivided (single condyle); (6) interorbital and internasal septa fused; (7) undivided supraoccipital; (8) unpaired frontal process of premaxillary; (9) far posterior extension of nasal relative to posterior border of premaxillary; (10) lateral opening of eustachian tubes; (11) long acromial process of scapulae; (12) absence of hypocleidium; (13) absence of bicapital crest; (14) olecranal fossa reduced; (15) olecranon obtuse; (16) ilium not fused with ischium caudad; (17) projected anterior iliac crest; (18) lack of supratendinal bridge; (19) hypotarsus unperforated and raised proximad; (20) lack of knob for *M. tibialis anticus*; (21) symmetrical trochlea for third digit; (22) pygostyle reduced. Characters 3, 5, 7-9, 11, 12, 14, 15, and 22 are derived.

The monophyletic and pachyphyletic Neognathae are diagnosed by the following complex of autapomorphies:

Diagnosis NG: (1) obliteration of all brain case sutures; (2) loss of broad vomer-maxillary contact; (3) pterygo-palatine joint; (4) separation of two dorsal condyles of the quadrate by the pneumatic recess; (5) medial opening of the eustachian tubes; (6) caudal fusion of ilium and ischium; (7) beginning of delto-pectoral crest distad from external tuberosity; (8) development of bicapital crest; (9) development of supratendinal bridge; (10) foramina in the proximal tarsometatarsus; (11) knob for *M. tibialis anticus*; (12) true perforated or grooved hypotarsus.

The relationship of the many orders within the Neognathae is poorly studied. However, some evidence supports a basic dichotomy of this taxon, demonstrating that the orders Anseriformes, Galliformes and Gastornithiformes are distinct from the other Neognathae (but see OLSON, 1985). This was shown by analysis of the jaw apparatus (DZERZHINSKY, 1988; ANDORS, 1991, 1992; WEBER, 1993), DNA hybridization data (SIBLEY et al., 1988; SIBLEY & AHLQUIST, 1990), amino acid sequences (STAPEL et al., 1984), immunological distances (HO et al., 1976), and microstructure of the eggshell (MIKHAILOV, 1993). Initially, SIBLEY et al. (1988) established the Galloanserae (Galliformes + Anseriformes) as the sister-group of the Ratitae into the infraclass Eoaves. Later (SIBLEY & AHLQUIST, 1990:256) transferred the Galloanserae to the Neoaves, although in their cladogram (p. 838) the Galloanserae were retained in the Eoaves. The monophyly of the Galloanserae is supported by the autapomorphies in the following diagnosis:

Diagnosis GA: (1) pterygo-parasphenoid articulation (rostrompterygoid joint after WEBER); (2) articulation of undivided pterygoid with palatine; (3) palatine long and thin; (4) squamosal and otic quadrate condyles are close together; (5) development of originating process for *M. adductor mandibulae externus*; (6) two mandibular condyles of quadrate; (7) lateral mandibular condyle of quadrate larger than medial condyle; (8) mandibular articular surface possesses longitudinal intercotylar ridge; (9) development of medial mandibular process; (10) development of long and flat retroarticular process.

The others Neognathae were united in the infraclass Neoaves by SIBLEY et al. (1988; see SIBLEY & AHLQUIST, 1990:838), but divided into five parvclasses within an expanded infraclass Neoaves by SIBLEY & AHLQUIST (1990:258-264); I accept their original infraclass Neoaves as a monophyletic superorder although almost no autapomorphs support this conclusion. I can cite only (1) splitting of the pterygoid into two segments with the appearance of the intrapterygoid joint; (2) reduction of the basipterygoid articulation, and (3) tricondylar mandibular articulation of the quadrate. The above-mentioned molecular data and eggshell structure also confirm the unity of the Neoaves.

The evidence and conclusions presented above results in the following classification of the major subdivisions for the class Aves (see Fig. 1 for a cladogram):

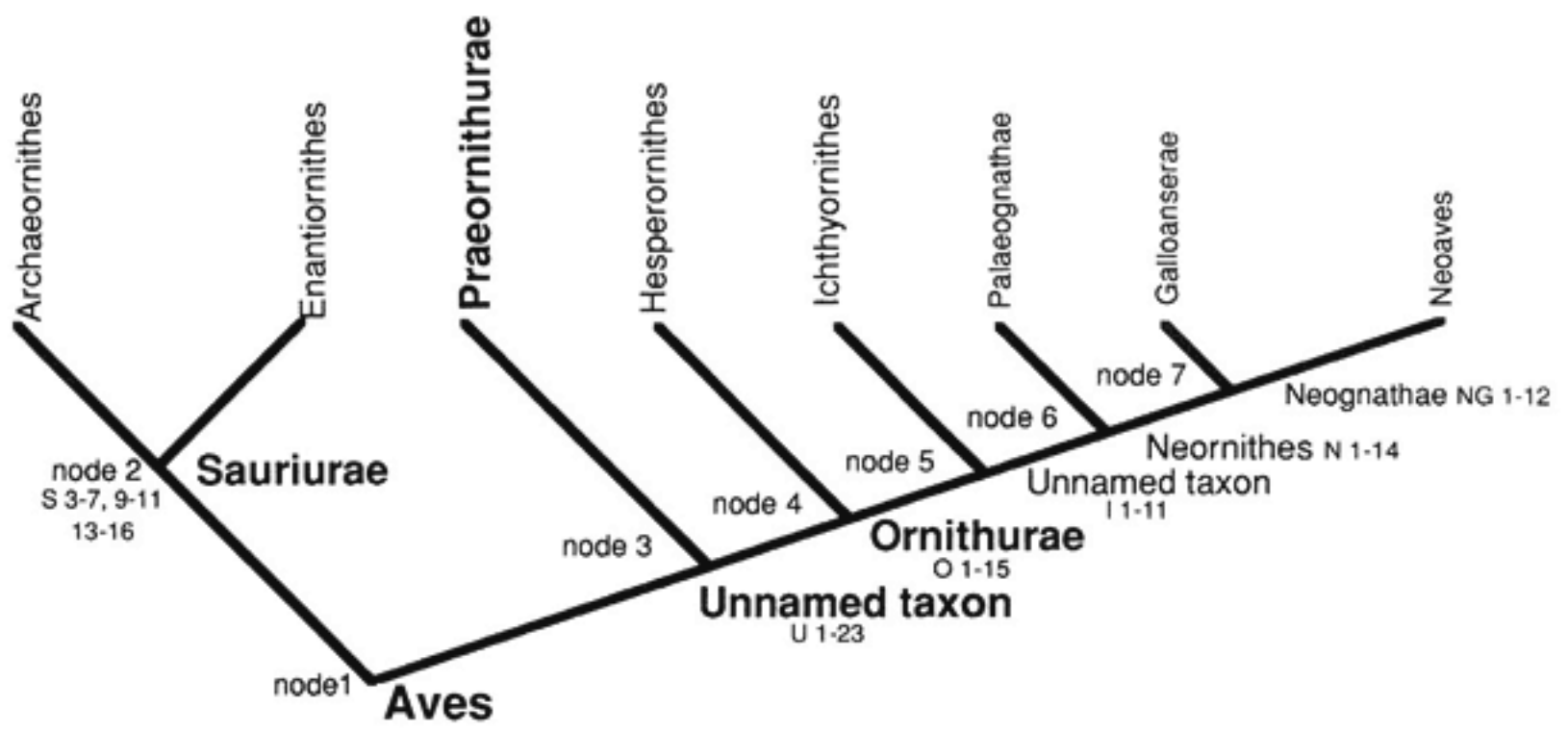


Fig. 1. Cladogram of the class Aves, based on the data of the Mesozoic avian record. The numbers of characters for the principal nodes are in agreement with the enumerated Synapomorphies in the corresponding diagnoses.

- Class Aves
 - Subclass Sauriurae
 - Infraclass Archaeornithes
 - Infraclass Enantiornithes
 - Subclass Praeornithurae
 - Infraclass Protoaviornithes
 - Subclass Ornithurae
 - Infraclass Hesperornithes
 - Infraclass Ichthyornithes
 - Infraclass Neornithes
 - Parvclass Palaeognathae
 - Parvclass Neognathae
 - Superorder Galloanserae
 - Superorder Neoaves

Conclusion

At the present state of knowledge about fossil birds, it appears that several major evolutionary lineages co-existed during the Mesozoic with broad geographical distribution and adaptive parallelism as known for mammals and fishes. For birds, this parallelism was especially characteristic for the evolution of the forelimb and hindlimb. The present data suggests that the keeled sternum, furcula, humerus with two distal condyles, carpometacarpus, cnemial crests of the tibia, and metatarsus or tarsometatarsus have originated at least twice. But it appears unlikely that feathers evolved independently several times, especially if their origin was associated with thermo-regulation. Fossil feathers and bird tracks are known even more extensively throughout the Jurassic and Cretaceous than fossil avian bones. They provide strong support for the conclusion of a world-wide distribution of the birds during the Mesozoic. In spite of the extensive new data on Mesozoic birds, analysis of the origin and early radiation of birds remains controversial, and even more so because *Protoavis* and the large infraclass Enantiornithes which must be included in any discussion. Moreover, this new information has changed fundamentally the traditional idea that avian history is just a simple branch from some group of reptiles via *Archaeopteryx* to the known diversity of birds. This advance has occurred during last decade owing to greatly increased activity of avian paleontologists. At the

present time, analyses of avian origins, the evolution of feathers and avian flight, and all other avian features based mainly on the study of *Archaeopteryx* will continue to be uncertain. With the exceptions of *Archaeopteryx* and *Protoavis*, all known Mesozoic avian fossils are Cretaceous in age. What is needed now are additional avian fossils from the Jurassic and Triassic as the major questions about the evolutionary history of birds can be resolved only with the discovery of such new avian fossil material.

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