

Mesozoic birds of Mongolia and the former USSR

EVGENII N. KUROCHKIN

Introduction

The first Mesozoic avian skeletal remains from Asia were found in Mongolia by the Polish–Mongolian Palaeontological Expedition (Elzanowski, 1974, 1976, 1981). Feathers from the Late Cretaceous of Kazakhstan were described by Bazhanov (1969) and Shilin (1977) and numerous fossil feathers from the Lower Cretaceous of Mongolia and East Siberia were collected by palaeontologists from PIN at the beginning of the 1970s. From the 1970s to the 1990s skeletal remains of various avian fossils were recovered from the Cretaceous of Mongolia by the Joint Russian–Mongolian Palaeontological Expedition and in the Cretaceous of Middle Asia by the late Lev Nesov as a result of his persistent exploration. Further remains of birds were found in recent years in Central Asia by the American–Mongolian expeditions (see Chapter 12) and it now appears that earlier American expeditions in the 1920s also recovered fossil birds, though they were not recognized as such until the 1990s (see Chiappe *et al.*, 1996, and refs therein).

Mesozoic birds from Mongolia and the former Soviet Union (FSU) are rare and usually fragmentary, but they provide some data regarding the early history of the group in this territory. In addition, many Mesozoic birds have recently been found in China (Chiappe, 1995). Together, these records provide the basis for analyses of Mesozoic avian assemblages in Asia (Kurochkin, 1995a). This chapter presents a summary of Mesozoic birds from the FSU and Mongolia, primarily discovered by Russian palaeontologists. Avian macro-taxonomy follows Kurochkin (1995c).

Institutional abbreviations

IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; IZASK, Institute of Zoology of the Kazakh Academy of Sciences, Alma-Aty, Kazakhstan; JRMPE, Joint Russian–Mongolian Palaeontological Expedition; MGI, Geological Institute of the Mongolian Academy of Sciences, Ulaanbaatar; PIN, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia; PO, Collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; TsNIGRI, F.N. Chernyshev Central Museum for Geological Exploration, St. Petersburg, Russia; VPM, Volgograd Provincial Museum, Volgograd, Russia; ZPAL, Institute of Palaeobiology of the Polish Academy of Sciences, Warsaw, Poland.

Systematic description

Class Aves Linnaeus, 1758

Subclass Sauriurae Haeckel, 1866

Infraclass Enantiornithes Walker, 1981

Order Alexornithiformes Brodkorb, 1976

Family Alexornithidae Brodkorb, 1976

Contents. *Gobipteryx* Elzanowski, 1974; *Alexornis* Brodkorb, 1976; *Kizylkumavis* Nesov, 1984; *Zhyraornis* Nesov, 1984 (2 spp.); *Nanantius* Molnar, 1986 (2 spp.); *Sazavis* Nesov and Yarkov, 1989; *Neuquenornis* Chiappe and Calvo, 1994; *Lenesornis* Kurochkin, 1996.

Diagnosis. Cranial half of the synsacrum low and broad; synsacrum convex dorsally; ischium narrow; acrocoracoid and coracoidal process narrow and tapered; shaft of the coracoid strut-like and narrow; shaft of the coracoid with a deep and short depression

on the dorsal side; scapular facet and scapular glenoid fused; ventral epicondyle of the humerus protrudes distad to a striking degree; wing digits clawless; shaft of the tibiotarsus thin; metatarsal III straight; metatarsals II–IV short and gracile.

Kizylkumavis Nesov, 1984

Type species. *Kizylkumavis cretacea* Nesov, 1984.

Diagnosis. Original diagnosis of Nesov (1984): olecranon fossa is narrow and displaced in the direction of the flexor process; flexor process is strongly projected distally; dorsal condyle very narrow and aligned at an angle of 65° to the longitudinal axis of the humeral shaft; ventral condyle is short, aligned almost transversely to the longitudinal axis of the humeral shaft, and only slightly projected in cranial aspect; intercondylar furrow runs slightly on the cranial side; brachial depression is not developed; a small groove is developed distal to a small ventral supracondylar tubercle on the cranial surface of the distal end, and aligned at an angle of 70° to the longitudinal axis of the shaft.

Comments. As I have not seen the specimen recently, the original diagnosis, which includes the generic characters of *Kizylkumavis*, as well as characters of the Enantiornithes and Alexornithiformes is presented here. The following characters form an emended diagnosis for this genus: distal end of the humerus is very wide in the dorsoventral direction; the ventral portion of the distal end of the humerus is remarkably enlarged; the dorsal condyle is broad; the intercondylar furrow is narrow; and the flexor process is strongly projected distally.

The humeri of *Kizylkumavis* and *Alexornis* of Mexico (Brodkorb, 1976) are similar in some respects. For example, they share: a remarkable distal projection of the ventral epicondyle, distal displacement of a shallow olecranon fossa, and an abrupt transition from the distal end to the shaft. However, they also exhibit some differences: the shape of the dorsal condyle (which is broad in *Kizylkumavis* and narrow and olive-shaped in *Alexornis*); a more spacious intercondylar furrow in *Alexornis*, and more distal projection of the flexor process in *Kizylkumavis*.

Kizylkumavis cretacea Nesov, 1984

Holotype. TsNIGRI 51/11915, distal fragment of a right humerus. Dzharakhuduk locality, Navoi District, Bukhara Province, Uzbekistan. Outcrop CBI-5a, Bissekty Svita (Coniacian).

Diagnosis. Same as for genus.

Comments. *K. cretacea* is a very small enantiornithine; the maximum width of the distal end of humerus is 5.1 mm. *K. cretacea* was the first member of the Enantiornithes to be described from the Old World (Nesov, 1984), although in the original description it was assigned to *Aves incertae sedis*. In spite of its fragmentary condition, there are no doubts as to the enantiornithine relationships of *K. cretacea* since it has no fossa for the *M. brachialis*, a transverse position of the dorsal condyle of the humerus, and an inclined position of the ventral condyle.

Zhyraornis Nesov, 1984

Type species. *Zhyraornis kasbkarovi* Nesov, 1984.

Contents. *Z. kasbkarovi* Nesov, 1984; *Z. logunovi* Nesov, 1992.

Diagnosis. Cranial portion of the synsacrum noticeably convex dorsally; cranial end of the synsacrum remarkably broad; synsacrum only slightly broadened across both sacral vertebrae; only one thoracic vertebra precedes two sacral vertebrae; caudal half of the synsacrum long and narrow; the two largest costal processes are inclined caudally; no longitudinal groove on the ventral side of the synsacrum.

Comments. There are four species of bird from Dzharakhuduk that are based on synsacra and assigned to the Ichthyornithiformes (Nesov, 1984, 1986, 1990, 1992b, d; Nesov and Yarkov, 1989; Nesov and Pantelev, 1993). Comparison of these remains with the synsacrum of *Nanantius valifanovi* Kurochkin, 1996 showed that they should be assigned to the Enantiornithes (Kurochkin, 1995c, 1996).

Zhyraornis kasbkarovi Nesov, 1984

Holotype. TsNIGRI 42/11915, incomplete synsacrum, having at least seven coossified vertebrae and lacking the most caudal portion. Dzharakhuduk locality,

Navoi District, Bukhara Province, Uzbekistan. Outcrop CBI-4, Bissekty Svita (Coniacian).

Diagnosis. First vertebra on synsacrum expands gradually in the cranial direction; transverse processes on the second sacral vertebra are slightly marked on the dorsal surface; two pairs of the largest costal processes are slender and distinctly inclined lengthwise; the synsacrum is generally extended and narrow.

Comments. A thoracic vertebra (TsNIGRI 43/11915) from the Khodzhakulsai locality (Khodzhakul settlement, Karakalpakia, Uzbekistan; Khodzhakul Svita, Cenomanian) (Nesov, 1984, 1992b; Nesov and Borkin, 1983), regarded as an indeterminate Mesozoic bird by Nesov (1992d), a left scapula (TsNIGRI 44/11915) and the shaft of a left humerus (TsNIGRI 45/11915) from Dzharakhuduk (Nesov, 1984), were also assigned to *Z. kashkarovi*. The vertebra has a wide neural canal, deep lateral excavations on the centrum, and nearly flat cranial and caudal articular surfaces. It is comparable in size to the vertebrae of the synsacrum of *Z. kashkarovi*. The structure of the glenoid facet on the scapula and its acromion show a certain similarity to that of the enantiornithines, but this is not sufficient evidence for its assignment to *Z. kashkarovi*. The humerus shaft certainly is not enantiornithine, because its nutrient foramen is located in the typical position for neornithine taxa, whereas in the Enantiornithes the nutrient foramen occurs on the opposite side of the shaft.

Zhyraornis logunovi Nesov, 1992

Holotype. PO 4600, incomplete synsacrum, having at least five coossified vertebrae and lacking the most caudal portion. Dzharakhuduk locality, Navoi District, Bukhara Province, Uzbekistan. Outcrop CBI-5a, upper member of the Bissekty Svita (Coniacian).

Diagnosis. The first vertebra of the synsacrum expands abruptly in the cranial direction; the transverse processes of the second sacral vertebra are prominently marked on the dorsal surface; two pairs of the largest costal processes are thick; the costal processes of the second sacral vertebra are perpendicular to the sagittal plane; and the synsacrum is generally expanded and broadened.

Lenesornis Kurochkin, 1996

Type species. *Lenesornis malsbevskyi* (Nesov, 1986).

Diagnosis. The cranial portion of the synsacrum is only slightly convex dorsally, the cranial articular surface of the synsacrum is transversely elongated; the third and fourth vertebrae of the synsacrum possess the largest costal processes; the costal processes are at a right angle to the sagittal plane; and the ventral groove is wide and shallow.

Comments. This synsacrum was described as *Ichthyornis malsbevskyi* by Nesov (1986) in the family Ichthyornithidae (see also Nesov, 1992b, d). However, the similarity of this fossil to *Nanantius valifanovi* Kurochkin, 1996, and the abundance of postcranial remains of Enantiornithes at the Dzharakhuduk locality enabled it to be reidentified as an enantiornithine (Kurochkin, 1996). Because of a noticeable difference from *Zhyraornis*, it was assigned to a separate genus.

Lenesornis malsbevskyi (Nesov, 1986)

Holotype. PO 3434, cranial half of the synsacrum. Dzharakhuduk locality, Navoi District, Bukhara Province, Uzbekistan. Outcrop CBI-14, Bissekty Svita (Coniacian).

Diagnosis. Same as for genus.

Sazavis Nesov, 1989

Type species. *Sazavis prisca* Nesov, 1989.

Diagnosis. Small birds; distal end of the tibiotarsus is wide and its large medial condyle has a rounded dorsal margin in cranial aspect; intercondylar furrow is displaced laterally, therefore the lateral condyle is narrow. The diameter of the bone is strongly reduced dorsal to the distal end of the tibiotarsus; the ligamentous tubercle on the cranial surface of the tibiotarsus is weak and located relatively distal.

Comments. As I have not seen the specimen recently, the original diagnosis, which includes the generic characters of *Sazavis*, as well as characters of the Enantiornithes and Alexornithiformes, is presented here. It should also be noted that in the original diagnosis lateral and medial aspects were confused, though these are corrected in the diagnosis given above. The

following characters form an emended diagnosis for this genus: the transition from the shaft to the distal end of the tibiotarsus is abrupt; the medial condyle is nearly circular in cranial view; and the intercondylar fossa is somewhat medially displaced.

Sazavis was assigned, with some doubt, to the Alexornithidae (Nesov and Yarkov, 1989) or to the Enantiornithes (Nesov, 1992b, d). Assignment of *S. prisca* to enantiornithine birds is supported by the presence of a bulbous and enlarged medial condyle of the tibiotarsus, a small and transversely compressed lateral condyle, and a smooth tubercle in the centre of the ascending process.

Sazavis prisca Nesov, 1989

Holotype. PO 3472, distal fragment of the right tibiotarsus. Dzharakhuduk locality, Navoi District, Bukhara Province, Uzbekistan. Outcrop CBI-14, Bissekty Svita (Coniacian).

Diagnosis. Same as for genus.

Comments. *S. prisca* is another very small enantiornithine from the Dzharakhuduk locality. The width of the distal end of the tibiotarsus is 4.5 mm which is comparable in size with *Kizylkumavis cretacea* and a congeneric or conspecific relationship might be supposed. However, this cannot be certainly demonstrated because the remains are non-comparable.

Other alexornithiforms from the Kizylkum Desert

In various papers Nesov described other fragmentary avian fossils from the Dzharakhuduk locality in Bukhara Province, Uzbekistan. Some of these were assigned to the Enantiornithes indet. and some only to Aves indet. The remains of alexornithiforms are listed below.

Alexornithidae gen. indet.

A complete axis, PO 3473, was figured as avian by Nesov (1988, fig. 1: 3, 1992b, fig. 2: O-P) and then cited as similar to Gaviidae (Nesov, 1992d). This specimen shares, with the axis of *N. valifanovi*, a general cranio-caudal elongation, poorly developed cranial articular facets, lateral extensions of the cranial articular facets,

a broad dorsal arch and a flat caudal lamina that is strongly projected caudally, a low dorsal process, and a shallow lateral excavation of the body. These characters allow assignment of PO 3473 to the Alexornithidae (Kurochkin, 1996). This specimen differs from the axis of *N. valifanovi* in being larger: the distance between the cranial and caudal articular surfaces is some 13.5 mm (measured from the figure in Nesov, 1988) but only 6.2 mm in *N. valifanovi*.

Two enantiornithine coracoids were described by Nesov and Panteleev (1993). Specimen PO 4819 is represented by the dorsal half of a coracoid with a narrow shaft, slight projection of the lateral margin, and shallow depression on the dorsal shaft, features characteristic for the Alexornithidae. Specimen PO 4818 is represented by the fragment of a shaft that shows a broadened sternal portion and a deep dorsal depression (Kurochkin, 1996). Because of its very fragmentary condition the family relationships of this bone is uncertain.

Enantiornithidae gen. indet.

The shaft of a right coracoid, TsNIGRI 56/11915, some 15 mm long (measured by the published figure in Nesov and Borkin, 1983), was provisionally assigned to birds (Nesov and Borkin, 1983) and later to the enantiornithines (Nesov and Panteleev, 1993). This specimen clearly belongs to the Enantiornithidae because it shows a distinctive deep dorsal depression, running far dorsally, and a convex lateral margin of the shaft (Kurochkin, 1996).

Alexornithiformes family indet.

'*Ichthyornis*' *minusculus* was based on a single thoracic vertebra, PO 3941 (Nesov, 1990). This specimen shares, with the synsacrum of *I. maltshevskyi*, an elliptical profile of the cranial articular surface and wide vertebral foramen. However, because of its fragmentary nature, '*I. minusculus*' can only be assigned to the Alexornithiformes fam. indet. (Kurochkin, 1996).

The proximal fragment of a left tarsometatarsus, PO 3394, was assigned to the Enantiornithidae by

Nesov and Borkin (1983) or to the Enantiornithes (Nesov, 1984, 1992b). The specimen shows the proximal fusion of the metatarsals and the enlargement of the medial cotyla. The depth of this proximal end is about 4 mm (measured from the figure in Nesov, 1992b). The specimen was correctly identified as an enantiornithine, and should be assigned to the Alexornithiformes on the basis of its very strongly reduced metatarsal IV (Kurochkin, 1996).

Discussion. In total, the Bissekty Svita of the Dzharakhuduk locality has produced 13 enantiornithines all based on fragmentary remains. Seven of them were described under species status here, but it is impossible to compare the other six fragments. Nevertheless, at least three small and two middle-sized enantiornithines might have existed concurrently in the Coniacian of Uzbekistan.

Family Alexornithidae Brodkorb, 1976

Gobipteryx Elzanowski, 1974

Type species. *Gobipteryx minuta* Elzanowski, 1974.

Amended diagnosis. Culmen straight and very thin above the nasal openings; rostral ends of the premaxilla and mandible flattened with rounded tips; mandibula with a low and short symphysis and thin rami; contact surfaces on the ventral margin of the premaxilla and maxilla and dorsal margin of the mandible flat; no distinct grooves on the lateral surface of the rostral portions of the premaxilla and mandible; dorsal mandibular margin distinctly elevated above the level of the lateral mandibular process; and large choanal fenestra located in the rostral area of the palatal shelf.

Comments. Originally, *Gobipteryx* was assigned to the Palaeognathae (Elzanowski, 1976, 1977), but later Martin (1983) attributed it to the Enantiornithes. There are no reliable arguments for assigning the skull portions of *Gobipteryx* to the Enantiornithes, since the skull remains of *Gobipteryx* are not known among undoubted enantiornithines. However, the bipartite mandibular articulation of the quadrate, anterior bifurcation of the pterygoid, the subsidiary palatal fenestra, and a hooked ectopterygoid (Elzanowski,

1976, 1977, 1995) might be features of the Enantiornithes, though at present these features are not known in described skull remains of this group which include the occipital cranium region of *Neuquenornis volans* from the Santonian–Coniacian of Argentina, rostral portions of the mandible and maxillary and palatal apparatus of *N. valifanovi* from the Late Campanian of Mongolia, and rostral portions of the mandible and maxillary and dorsal cranium of embryonic enantiornithines also from the Late Campanian of Mongolia.

Thus, there is only circumstantial evidence that *Gobipteryx* belongs to the Enantiornithes, since it does not have advanced characters in common with known enantiornithine birds. In addition *Gobipteryx* is characterized by some primitive characters of the quadrate, pterygoid and palate which are also unknown in other Enantiornithes.

Gobipteryx minuta Elzanowski, 1974

Holotype. ZPAL MgR-I/12, rostral portion of the skull. Khulsan locality, Nemegt Valley, South Gobi Desert, Mongolia. Baruungoyot Formation (Late Campanian), Late Cretaceous.

Referred material. Rostral portion of a skull, ZPAL MgR-I/32, from the same locality.

Diagnosis. Same as for genus.

Comments. *G. minuta* shows a gracile construction of the upper jaw and mandible and large rostral choanal fenestra bordered caudally by the palatines (Elzanowski, 1995). Following additional preparation of the holotype, Elzanowski (1995) discovered a small hooked ectopterygoid that has also been identified in both the Eichstätt and seventh specimen of *Archaeopteryx* (Wellnhofer, 1974; Elzanowski and Wellnhofer, 1996). The ectopterygoid is present in many theropods, and I evaluate this fact as a further confirmation of the relationship between the Enantiornithes and Archaeornithes and their assignment to a phylogenetic lineage separate from ornithurine birds. This and some other cranial synapomorphies support a theropodan origin for Sauriurae, but not all birds.

Nanantius Molnar, 1986

Type species. *Nanantius valifanovi* Kurochkin, 1996.

Contents. *Nanantius eos* Molnar, 1986 (Australia, Albian); *N. valifanovi* Kurochkin, 1997 (Mongolia, Late Campanian); *Nanantius* sp. (Australia, Albian).

Diagnosis. Maxillary and mandible short, high and stout; culmen very straight and thick above the nasal opening; the humerus has a curved shaft with a thin mid-portion; the shaft of the radius is bowed; the proximal phalanx of the major digit has a rectangular top; the tibiotarsus has a long and remarkably thin shaft that is bowed laterally; conspicuous intercotylar prominence on the caudal area of the proximal articular surface of the tibiotarsus; lateral area of the proximal articular surface of the tibiotarsus slopes distad; well-developed fibular crest reaches to the margin of the proximal articular surface; fibular crest located along the cranio-lateral edge of the shaft of the tibiotarsus; proximal origin of the fibular crest and top of the cranial cnemial crest united together; elongate depressions run along the cranial and caudal base of the fibular crest; medial condyle of the tibiotarsus transversely elliptical (not circular) in cranial view; fibula very short, flat and thin; metatarsals II–IV of a similar thickness.

Comments. In spite of the great geographical and temporal gaps between *N. valifanovi* from the Albian of Mongolia and *N. eos* from the Campanian of Australia (Molnar, 1986) it was decided to assign the Mongolian taxon to the same genus because of the great similarity in the derived characters of the tibiotarsus of the two forms.

Nanantius valifanovi Kurochkin, 1996

Holotype. PIN 4492–1, partial skeleton including portions of the skull, vertebrae, synsacrum, all bones of the shoulder girdle, pelvis, and most elements of the forelimb and hind limb (Figures 27.1 and 27.2). Hermin Tsav locality, Trans-Altai Gobi Desert, South Gobi Aimag, Mongolia. Middle layers of the outcrop on the northern slope of Hermin Tsav, Baruungoyot Formation (Late Campanian), Late Cretaceous.

Diagnosis. Shallow longitudinal groove on the ventral

side of the mandible; a shallow, broad axial groove on the ventral side of the synsacrum; a short fibular crest on the tibiotarsus that is approximately five times the transverse width of the proximal articular surface; position of the nutrient foramen on the cranial side of the tibiotarsus close to the distal extremity of the fibular crest; subtriangular cross-section and sharpened caudal edge of the proximal shaft of the tibiotarsus; transversely compressed lateral condyle of the tibiotarsus which projects markedly cranial in distal view; and metatarsal IV is shorter than metatarsal II.

Comments. The Hermin Tsav locality, situated on the western border of the Trans-Altai Gobi Desert in Southern Mongolia, is famous for yielding numerous fossil eggs of birds, some of which contain embryos (Elzanowski, 1981; Chatterjee and Kurochkin, 1994; see below). The nearly complete holotype skeleton of *N. valifanovi* was found on the northern slope of Hermin Tsav, about 4 km east of 'Bird's Hill', a locality for fossil avian eggs at the mouth of Hermin Tsav. Some bones were collected in association including: rostral portions of the mandible and premaxillary; a portion of the palatal apparatus; some cervical vertebrae; part of the pelvis and synsacrum; the proximal end of the first phalanx of the major digit with the carpometacarpus; the distal end of the left femur and pelvis; the tarsometatarsus with some pedal phalanges; and other pedal phalanges. Many pieces of eggshell were also found in association with the bone remains of *N. valifanovi*. The eggshell has a laevisolithid microstructure thus linking this type of eggshell to the Enantiornithes (Kurochkin, 1996; see Chapter 28).

N. valifanovi is distinguished from *N. eos* by the relatively longer fibular crest that extends distally, the greater transverse width of the proximal articular surface of the tibiotarsus, the presence of a nutrient foramen near the end of the fibular crest that is absent in *N. eos*, the sharpened caudal side of the proximal shaft, which is rounded in *N. eos*, a small tubercle at the centre of the ascending process which is located nearer to the top of this process in *N. eos*, greater cranial protrudence of the lateral condyle, a slightly compressed proximodistally medial condyle, which is



Figure 27.1. Holotype skeleton of *Nanantius valifanovi* Kurochkin, 1996 (PIN 4492-1). Scale bar = 20 mm.

more circular in *N. eos*, and a deeper and wider cranial intercondylar fossa. In addition, the tibiotarsus in *N. valifanovi* is about 30% longer than in *N. eos*.

The relationships of *N. valifanovi* to *Gobipteryx minuta* Elzanowski, 1974, need to be discussed here, because they were both found in the Baruungoyot Formation of the South Gobi. *G. minuta* is based on

fragments of two skulls from the Khulsan locality located some 150 km east of Hermin Tsav. This taxon shows some features in common with *N. valifanovi* in the configuration of the maxillary segment and in the presence of conspicuous rows of nutrient foramina in the maxillary and mandible. However, *N. valifanovi* differs from *G. minuta* in having more robust rostral



Figure 27.2. Restoration of the skeleton of *Nanantius valifanovi* Kurochkin, 1996. Scale bar = 10 mm.

portions of the upper jaw and mandible, sharper rostral ends of the upper jaw and mandible, thin and acute contact surfaces of the maxillary and mandible, deep grooves possessing nutrient foramina both in the upper jaw and mandible, nutrient foramina only in the anterior half of the maxillary rostrum, nutrient foramina which become larger caudally, and in the presence of an axial groove on the ventral side of the mandible.

The short tarsometatarsus and relatively short and powerful second and third pedal digits with strong and slightly curved claws of *N. valifanovi* reflect arboreal adaptations. The ungual phalanges are sturdy, similar in size and slightly curved, with symmetrical articular cotyles and well-developed flexor tubercles, signify-

ing the ability for powerful flexion of the digits. This is in contrast to the relatively small size of the trochlea of the left metatarsal I, and the phalanges of digit 1. The powerful anterior second and third toes with curved claws and weak hallux also suggest a climbing adaptation for the foot. The palatal elements and the rostral portions of the mandible and upper jaw have a very powerful and robust construction. This is, apparently, an adaptation for feeding on tough objects, perhaps fruits or seeds.

Family Avisauridae Brett-Surman and Paul, 1985
Contents. *Enantiornis* Walker, 1981; *Avisaurus* Brett-Surman and Paul, 1985; *Soroavisaurus* Chiappe, 1993.
Diagnosis. Deep fossa on the cranial surface of the scapula; scapular facet and scapular glenoid separated; ischium wide; tibiotarsus with a straight and robust shaft; metatarsal III with a strongly convex transversely dorsal surface; medial ridge of the trochlea on the metatarsal III projects markedly on the plantar side.

Enantiornis Walker, 1981

Type species. *Enantiornis leali* Walker, 1981

Contents. *E. leali* Walker, 1981 (Argentina, Maastrichtian); *E. walkeri* Nesov and Panteleev, 1993 (Uzbekistan, Coniacian); *E. martini* Nesov and Panteleev, 1993 (Uzbekistan, Coniacian).

Diagnosis. Shoulder end of the coracoid robust and short; shaft of the coracoid wide; acrocoracoid and coracoidal process stout; scapular acromion broad with an obtuse top; fossa or foramen on the cranial surface of the shoulder end of the scapula; scapular facet and glenoid facet of the scapula are separated; dorsal portion of the humeral head longer than the ventral portion; distinct cranial fossa in the cranial surface of the proximal end of the humerus; deltopectoral crest with a thin proximal base; distinct depression in the caudal surface of the proximal end of the humerus.

Comments. In the present state of knowledge of the Enantiornithes it is a difficult task to develop a generic diagnosis for *Enantiornis*, since almost all authors analyzed either the characters of the Enantiornithes or

separate species of this infraclass, beginning with Walker (1981) and including many other recent papers on the enantiornithines. In the diagnosis given above I attempted to select the advanced characters of *Enantiornis* which distinguish it from other enantiornithines also represented by the humerus and bones of the shoulder girdle.

Enantiornis walkeri Nesov and Panteleev, 1993

Holotype. PO 4825, dorsal fragment of the left coracoid. Dzharakhuduk locality, Navoi District, Bukhara Province, Uzbekistan. Outcrop CBI-5a, Bissekty Svita (Coniacian).

Diagnosis. Coracoidal process is stout, proximal portion of the shaft is gracile.

Enantiornis martini Nesov and Panteleev, 1993

Holotype. PO 4609, shoulder fragment of the right coracoid. Dzharakhuduk locality, Navoi District, Bukhara Province, Uzbekistan. Outcrop CBI-14, middle member of the Bissekty Svita (Coniacian).

Diagnosis. Coracoidal process is narrow latero-medially and the proximal portion of the shaft is stout.

Comments. The two shoulder portions of the coracoid, upon which the two species listed above are based, are of a very similar size (approximately 10 mm between the top of the acrocoracoid and the top of the coracoidal process: measured from published figures). However, they differ in the structures mentioned in the diagnoses. *E. walkeri* and *E. martini* are distinguished from *E. leali* by their much smaller size, narrower coracoidal process, shorter acrocoracoid, distal broadening of the proximal shaft, and by the narrower and more elongated coracoidal nerve foramen.

Enantiornithidae

Gurilynia Kurochkin, 1999a

Gurilynia nessovi Kurochkin, 1999a

Several wing and shoulder girdle bones of a large enantiornithid, *Gurilynia nessovi*, were collected by the JRMPE in South Mongolia in 1994 at the Guriliin Tsav locality, which is situated in the Bügiin Tsav depression, some 15 km to north of Altan Uul mountain, in the South Gobi Aimag. The sediments of this

locality belong to the Late Cretaceous (Late Campanian–Early Maastrichtian) Nemegt Formation.

Gurilynia nessovi is characterized by the almost equal length of the ventral and dorsal portions of the humeral articular head, a very shallow cranial fossa in the middle of the proximal area of the cranial surface of the proximal end of the humerus, the thick base of the deltopectoral crest, a very shallow caudal depression in the caudal surface of the proximal end of the humerus, the pointed ventral termination of the processus coracoideus, and a remarkably thin coracoidal neck between the shoulder end and the shaft (Figure 27.3). The humerus also shows other specific characters, including the oval shape of the dorsal ligamental impression near the proximal base of the deltopectoral crest, the very wide and open angle between the ventral and dorsal portions of the articular head, a very stout, wide base that is not perforated by the axial foramen ventral tubercle, and the proximal end of the humerus is large and possesses a deep circular ventral ligamental impression on the ventrocranial angle of the ventral side (Kurochkin, 1999a)

The distal ends of a humerus and probably an ulna, radius and carpometacarpus also belong to this new form. It is a large bird, the width of the proximal end of the humerus being 26.2 mm and thus distinctly larger than *E. leali*.

The discovery of this large flying representative of the Enantiornithes increases their known diversity in the Late Cretaceous of Central Asia and shows that large enantiornithids inhabited Mongolia at the end of the Cretaceous, as well as North and South America.

Enantiornithine embryos from Mongolia

Elzanowski (1981) described embryonic avian skeletons in small elongate eggs from Hermin Tsav which had previously been thought to be turtle or crocodile eggs. In all probability he assigned these embryos to *Gobipteryx minuta* Elzanowski, 1974, which was described from Khulsan. Martin (1983, 1995a), and later Elzanowski (1995) recognized all the fossil embryos as *G. minuta* and assigned them to the Enantiornithes. Later, two types of elongate avian fossil eggs, small and large, were found at Khulsan by

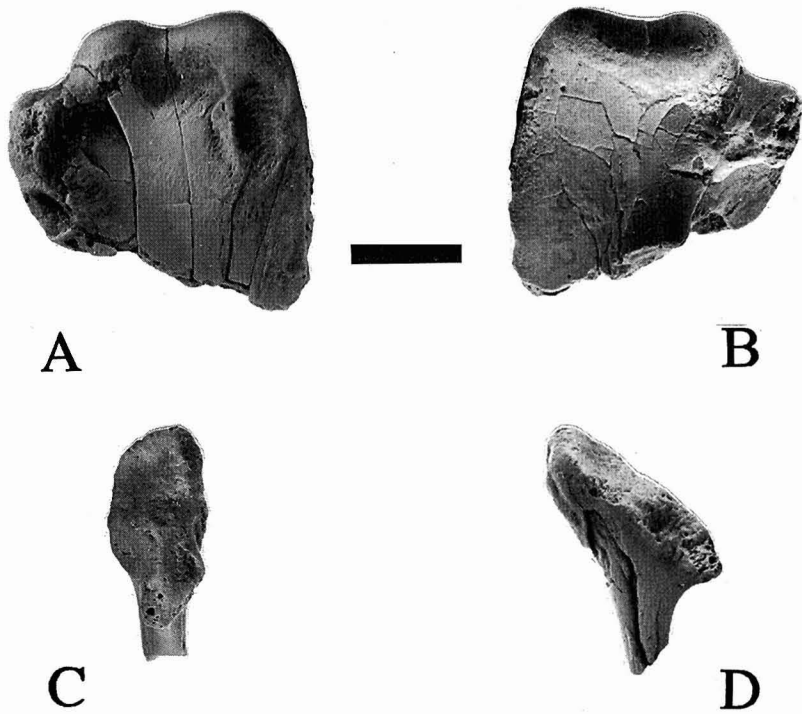


Figure 27.3. *Gurilynia nessovi* Kurochkin, 1999a, Nemegt Formation (Late Cretaceous) of Guriliin Tsav, Ömnögov' Aimag, Mongolia. Holotype PIN 4499-14, proximal end of the right humerus in (A) cranial and (B) caudal view. Paratype PIN 4499-13, shoulder end of the left coracoid in (C) dorsal and (D) lateral view. Scale bar = 10 mm.

the JRMPE. The small egg type is the same as that found at Hermiin Tsav (Mikhailov, 1995, 1996), but fossil embryos have not yet discovered in eggs from Khulsan.

The avian embryos from Hermiin Tsav, now in the collections of ZPAL and PIN (Figure 27.4), are beautifully preserved and show even the smallest ossified elements including, for example, the most proximal wing phalanges. This characteristic, as well as the complete ossification of the bones, from the ends across the shafts, differs fundamentally from the embryos of recent birds. In the latter case the process of ossification begins from centres in the ends of bones and in the shaft, so that cartilaginous insertions between these ossifications exist some weeks after hatching.

In earlier papers I concluded that two groups of birds were represented among the Hermiin Tsav

embryos (Kurochkin, 1995a, c, 1996). However, after study of fossil material in the ZPAL collections I now agree that only one taxon is present and that it belongs to the enantiornithines as originally proposed by Martin (1995a). Differences among the embryos (Kurochkin, 1996) represent different age stages, as was first noted by Elzanowski (1981). The structure of the eggshell is an important piece of evidence supporting the identification of the embryos as enantiornithine. The ratio between the spongy and mammillary layers, the ultrastructure, absence of asymmetry, and the greater thickness of the eggshell are all characters of enantiornithine eggs (Mikhailov, 1991, 1996). By contrast, the possible absence of the external layer of vertical crystals distinguishes the Hermiin Tsav eggshell from that of the Ratitae, Galliformes, and Anseriformes.

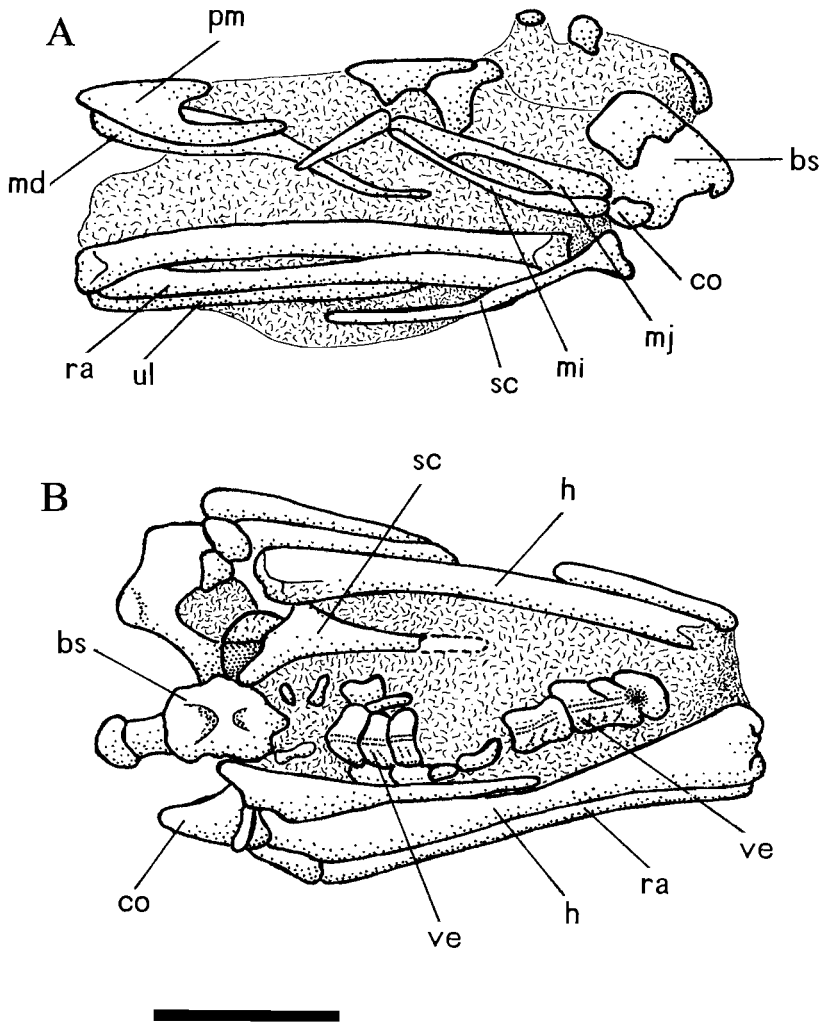


Figure 27.4. Fossil avian embryo (PIN 4492-3) from the Baruungoyot Formation (Late Cretaceous) of Hermin Tsav, Ömnögov' Aimag, Mongolia. Left side (A) and posterior (B) view. Abbreviations: bs, basisphenoid; co, coracoid; h, humerus; md, mandible; mi, minor metacarpal; mj, major metacarpal; pm, premaxillary; ra, radius; sc, scapula; ul, ulna; ve, vertebrae. Scale bar = 5 mm.

However, the question still remains as to whether the Hermin Tsav embryos can be assigned to *Gobipteryx minuta* from Khulsan. Specimen ZPAL MgR-1/34 (Elzanowski, 1981) is clearly enantiornithine, since it exhibits the boss and socket articulation between the coracoid and scapula, and other specialized postcranial characters of enantiornithines. In

addition, this specimen has a long retroarticular process in the mandible, which is also found in *G. minuta* from Khulsan and appears to be characteristic for the Enantiornithes. However, a long retroarticular process is the only common feature for *Gobipteryx* and embryos. Elzanowski (1981) argued that the premaxillary of *Gobipteryx* and the embryo specimens were

similar and that the latter probably belonged to *G. minuta*. Certainly, the embryonic specimen ZPAL MgR-1/88 is somewhat similar in its general outlines to the premaxillary of *G. minuta*, but differs in the larger and more cranially concave nasal aperture and in the sharper angle between the lateral surfaces of the premaxillary. The principal difference between them is the structure of the rostral end of the beak. It is thin and sharp in *Gobipteryx* from Khulsan, but flat and rounded in the embryos from Hermin Tsav. Moreover, the exterior contact areas between the premaxilla and mandible in *Gobipteryx* are narrow while they are wide and flat in embryos. The embryos also show a double-headed quadrate with orbital process; a ventral flange on the rostral edge of the mesethmoid, a lateral groove on the mandible, a very elongated scapular acromion with a medioventral projection, no scapular labrum, a short and wide acrocoracoid, incorporation of the scapular glenoid and coracoid glenoid for the glenoid facet of the humerus, a merged scapulo-coracoid construction, a proximal origin for the deltopectoral crest, a major metacarpal that is longer than the minor metacarpal, a manual phalangeal formula of 1-1-0, and a notarium composed of two thoracic vertebrae. They also exhibit distinctive features such as a small nasal aperture, a broad and dorsoventrally compressed rostral portion of the premaxillary, a long basal phalanx of the first digit, a very short cranial part of the ilium, a stout fibula which is of similar length to the tibia, and the absence of fusion of the proximal tarsalia (astragalo-calcaneus complex) to the tibia.

Thus, I consider, in contrast to Martin (1995a) and Elzanowski (1995), that assignment of the embryonic specimens ZPAL MgR-1/34, MgR-1/33, and MgR-1/88 to *Gobipteryx* or even to *G. minuta* cannot be justified and they together with the specimens in the PIN collections (Figure 27.7) must be assigned to a new taxon (Chatterjee and Kurochkin, 1994).

Order Euornithiformes Kurochkin, 1996

Family nov.

The partial skeleton of a small vertebrate was collected by the JRMPE at Kholboot in the Eastern area of the Mongolian Altai in the Bayankhongor Aimag.

Kholboot is located just 10 km west of the Khurilt Ulaan Bulag locality where *Ambiortus* was found and the sediments at these localities, which are currently assigned to the Bööntsagaan Gorizont (possibly Neocomian – see Chapter 14) are of similar age, though Kholboot may be slightly younger (Sinitsa, 1993).

The Kholboot specimen consists of portions of the skull and some shoulder, wing and hind limb bones. Initially, it was erroneously identified as a pterosaur because of teeth on the jaws (Kurochkin, 1991), but was later recognized as avian (Unwin, 1993; Kurochkin, 1993; Bakhurina and Unwin, 1995), though suggestions of a relationship with *Ambiortus* (Unwin, 1993) are incorrect. The Kholboot specimen has clear enantiornithine characters including a V-shaped furcula with a long hypocleideum and metatarsals that are only fused proximally, and is similar, for example, in respect of the toothed jaws, to Lower Cretaceous Chinese enantiornithines, but distinguished from them by the very long tarsometatarsus.

Subclass Ornithurae

Infraclass Odontornithes Forbes, 1884

Order Hesperornithiformes Fürbringer, 1888

Diagnosis. See Martin (1984, p. 147).

Contents. Hesperornithidae Marsh, 1872; Baptornithidae American Ornithologists' Union, 1910.

Comments. Hesperornithidae and the genus *Hesperornis* have never really been diagnosed. Martin (1984) attempted to diagnose Hesperornithiformes and to this list one important character can be added: location of teeth in grooves.

Family Hesperornithidae Marsh, 1872

Contents. *Hesperornis* Marsh, 1872; *Parahesperornis* Martin, 1984; *Asiabesperornis* Nesov and Prizemlin, 1991.

Hesperornis Marsh, 1872

Type species. *Hesperornis regalis* Marsh, 1872.

Contents. *Hesperornis regalis* Marsh, 1872; *Hesperornis crassipes* Marsh, 1876; *Hesperornis gracilis* Marsh, 1976; *Hesperornis rossicus* Nesov and Yarkov, 1993.

Hesperornis rossicus Nesov and Yarkov, 1993

Holotype. VPM 26306/2, proximal portion of the right tarsometatarsus. Right shore of the Tzimlyanskoe Reservoir, Don river, between Rychkovo and the 278 km Station, Surovikinskii District, in the south-west of Volgograd Province, Central South Russia. Marine beds, *Belemuellocamax mamillatus* zone, upper zone of the Early Campanian.

Referred material. The shaft of a tarsometatarsus, an intermediate phalanx of the fourth pedal digit, a fragment of a thoracic vertebra, and a fragment of a cervical vertebra were all recovered from the same locality (Nesov and Yarkov, 1993). A fragment of the proximal end of a right tarsometatarsus from the Early Campanian of Ivö-Klack, Scone, Southern Sweden has also been assigned to this species (Nesov and Yarkov, 1993).

Diagnosis. The proximal articular surface of the tarsometatarsus has a very large transverse width and small dorsoplantar depth, the diagonal slant is strongly expressed, the lateral edge of the lateral cotyla exceeds the intercotylar prominence in proximal direction and the medial cotyla is located more distal in respect to the lateral cotyla.

Comments. *Hesperornis* is of the masculine gender, thus according to the *International Code of Zoological Nomenclature* (1985, article 32d, 33 (II), 34b) the original epithet *rossica* (Nesov and Yarkov, 1993) must be changed to *rossicus*.

H. rossicus is clearly hesperornithiform, but differs from *Hesperornis regalis* Marsh, 1880, from North America in the larger depth of the proximal articular surface, more proximal projection of the lateral cotyla and approximately 20% larger size of the tarsometatarsus.

Because of the proposed presence (see below) of a second species (*Hesperornis* sp.) in the same locality, the inclusion of the two vertebrae and the pedal phalanx in the referred material of *H. rossicus* is entirely arbitrary.

Hesperornis sp.

A fragment of the proximal end of a left tarsometatarsus from the same locality and same beds as the holo-

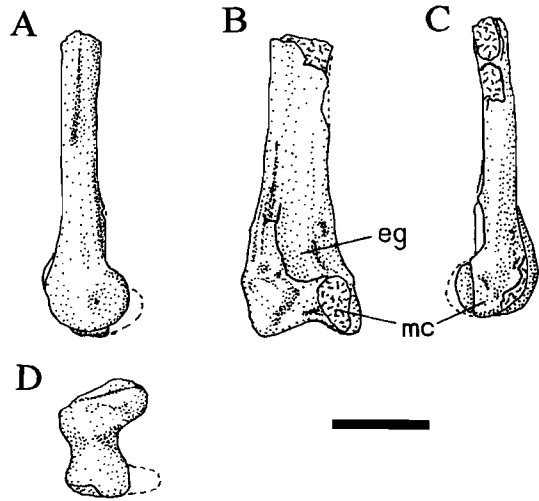


Figure 27.5. Right distal tibiotarsus of a small hesperornithiform from the Nemegt Formation (Late Cretaceous) of Tsagaan Khushuu, Ömnögov' Aimag, Mongolia. Lateral (A), cranial (B), medial (C), and distal (D) views. Abbreviations: eg, extensor groove; mc, medial condyle. Scale bar = 10 mm.

type of *H. rossicus* was assigned to *Hesperornis* sp. (Nesov and Yarkov, 1993). This specimen differs from *H. rossicus* in the more medial location of the intercotylar prominence and a larger ridge in the dorsal base of the intercotylar prominence (Nesov and Yarkov, 1993).

Hesperornithidae gen.

The distal portion of a tibiotarsus from the Nemegt beds of the Tsagaan Khushuu locality in the South Gobi Desert was announced as *Baptornis* sp. (Kurochkin, 1988). After comparison with all known hesperornithiforms in the collections of the Natural History Museum of Kansas University it was reidentified as representing a bird more closely related to *Parahesperornis*, on the grounds that it shows few differences between the lateral and medial condyles, no distal projection of the medial condyle, and the remarkable medial position of the extensor groove. The transverse width of the distal end of the tibiotarsus (Figure 27.5) is 11.7 mm, thus this was a small bird.

Subfamily Asiahesperornithinae Nesov and Prizemlin, 1991

Asiabesperornis Nesov and Prizemlin, 1991

Type species. Asiabesperornis bazbanovi Nesov and Prizemlin, 1991.

Diagnosis. Medial condyle of the tibiotarsus markedly mediolaterally compressed, cranial intercondylar furrow comparatively deep. The tarsometatarsus is comparatively gracile and has parallel lateral and medial sides. Both the lateral and medial crest on the plantar side of the tarsometatarsus have a sharp plantar margin and the flexor groove is shallow. The dorsal facet in the middle of the tarsometatarsal shaft is deep and narrow, and covered by a high dorsolateral crest and the separate medial facet is developed on the distal portion of the shaft. The base of the trochlea of the fourth digit is much larger than the base of the trochlea of the third digit and the fossa for metatarsal I is very small and short.

Comments. The diagnosis given above is abstracted from the author's original diagnosis and omits some characters which appear to be characteristic for hesperornithiforms. However, further evaluation, via direct comparison with remains of *Hesperornis* is required to identify those characters that are derived for this new taxon, especially in the context of some of Nesov's remarks that several remains of *Asiabesperornis* can be assigned to other taxa (see below). The following characters show that in any case the Kushmurun remains are those of hesperornithiforms: the bones are heavily constructed with well-expressed pachyostosis, a transversely compressed tarsometatarsus, and a strongly developed fourth trochlea.

Asiabesperornis bazbanovi Nesov and Prizemlin, 1991

Holotype. IZASK 5/287/86a, shaft of a left tarsometatarsus. Priezernyi Quarry, Kushmurun locality, near the settlement of Kushmurun, Kustanaiskaya Province, North Kazakhstan. Eginsai Svita (Latest Santonian–Early Campanian).

Diagnosis. Same as for the genus.

Referred material. IZASK 5/287/86: shaft of a right tarsometatarsus, two thoracic vertebrae and a fragmentary distal portion of the tibiotarsus from the same

locality (Nesov, 1992c; Nesov and Prizemlin, 1991). *Comments.* The distal portion of the right tibiotarsus and the thoracic vertebra previously assigned to *A. bazbanovi* were later illustrated as 'hesperornithiforms' (see caption to fig. 5 of Nesov and Yarkov, 1993) and, in the same caption, the proximal portion of the left tarsometatarsus was provisionally assigned to another species.

The shaft of the tarsometatarsus of *Asiabesperornis bazbanovi* exhibits a distinct transverse compression, an acute medial plantar ridge, a strongly reduced facet for metatarsal I, and a markedly craniocaudally compressed distal end of the tibiotarsus. The restored length of the tarsometatarsus is 122 mm (Nesov and Prizemlin, 1991). The hesperornithiform from Kushmurun inhabited the Campanian Turgai Inferior Seaway which ran from the Polar Ocean to the Southern Ocean between Fennoscandia and Eurasia, and was in some ways analogous to the Western Inferior Seaway which divided North America in the Campanian (Nesov and Prizemlin, 1991; Nesov, 1992a, c).

Family Baptornithidae American Ornithologists' Union, 1910

Diagnosis. See Martin and Tate (1976).

Contents. *Baptornis* Marsh, 1877 (Coniacian, USA) and *Judinornis* (Maastrichtian, Mongolia).

Comments. *Judinornis* Nesov and Borkin, 1983 does not exhibit any of the characters listed in the diagnosis given by Martin and Tate (1976). However, Martin and Tate (1976) noted a small pit lying directly anterior to the diapophysis in the trunk vertebra of *Baptornis advenus* and this is also present in *Judinornis nogontsavensis* Nesov and Borkin, 1983. The flat ventral side of the body is another character which might also be apomorphic for the Baptornithidae and circular pits in the articular surfaces of the centra of the thoracic vertebrae are also found in both *Baptornis* and *Judinornis*.

Judinornis Nesov and Borkin, 1983

Type species. Judinornis nogontsavensis Nesov and Borkin, 1983.

Diagnosis. The articular surfaces of the centrum of the thoracic vertebra are trapezoid-shaped and extend transversely. The ventral side of the centrum is distinctly narrowed in the middle but very broad caudally and the cranial zygapophyses are located close together on the centerline.

Contents. Type species only.

Judinornis nogontsavenensis Nesov and Borkin, 1983

Holotype. PO 3389, incomplete thoracic vertebra. Nogoön Tsav locality, western area of the Trans-Altai Gobi, Bayankhongor Aimag, Southern Mongolia. Nemegt Formation, Late Cretaceous.

Diagnosis. Same as for genus.

Comments. Based on a single thoracic vertebra, *Judinornis nogontsavenensis* was originally referred to the Charadriiformes (Nesov and Borkin, 1983). Later, it was referred to the Baptonithidae (Nesov, 1986, 1992a, b), but without any character evidence. *Judinornis nogontsavenensis* is the first hesperornithiform to be recorded from the Old World. It is a middle-sized bird, the vertebral body of the type thoracic vertebra measuring 14.1 mm in length between the articular surfaces. The vertebra shows a very expanded caudal ventral surface of the body, narrow cranial zygapophyses, very deep pleurocoels, and transversely expanded cranial and caudal articular surfaces which are characteristic of hesperornithiforms.

Hesperornithiformes

Family nov.

Further evidence of the presence of small Hesperornithiformes in the interior water basins of the Mongolian Cretaceous was obtained from the Nemegt (Maastrichtian) beds of Bügiin Tsav in South Gobi. The fossil material consists of a large portion of a small tarsometatarsus, PIN 4491-8 (Figure 27.6). This specimen shows derived characters of the Hesperornithiformes, including an inclined cross-section of the tarsometatarsal shaft, the high proximal position of the second trochlea, and the proximal position of a facet for metatarsal I. In general, the tarsometatarsus is stout and short and the metatarsal shaft is transversely expanded. These characters distinguish

this bird as a separate taxon of small hesperornithiform. Two further remains (a cervical vertebra and the portion of a mandible) representing small hesperornithiforms were collected by the JRMPE in the Nemegt beds of Guriliin Tsav and Tsagaan Khushuu in 'Ömnögov' (South Gobi) Aimag. These fossils are also somewhat different from known representatives of this order.

The existence of small, possibly volant hesperornithiforms was first claimed by Nesov (1992a). This conclusion was based on his discovery, in North American museum collections, of several small bones of hesperornithiforms from the Late Campanian and Maastrichtian beds of Canada and the USA. Further records of small hesperornithiforms, from the Eginsai Svita (Latest Santonian–Early Campanian) of Kushmurun locality, in Kustanaiskaya Province, North Kazakhstan (see above), were subsequently published by Nesov (1992a, c).

Thus, small hesperornithiforms are found in the continental Maastrichtian of Mongolia and North America. The small, lightly constructed pneumatized bones of the hind limb support the possibility that they were volant.

Infraclass Neornithes Gadow, 1893

Parvclass Palaeognathae Pycraft, 1900

The monophyly of the Palaeognathae is supported by various morphological and molecular characters, as well as behavior and eggshell microstructure (Bock, 1963; Cracraft, 1986, 1988; Kurochkin, 1995b). At present, there is good evidence that the Palaeognathae radiated in the Paleocene and Eocene and evidence for this group has also been found in the Cretaceous of Central Asia and Europe (Kurochkin, 1995a, b).

Order Ambiortiformes Kurochkin, 1982

Family Ambiortidae Kurochkin, 1982

Amended diagnosis. Small flying birds; cervical vertebrae heterocoelous; sternum with a keel; a wide procoracoid process perpendicular to the shaft; scapular blade long and thin; ventral edge of the proximal end of the humerus strongly developed and with a distinct tubercle on its cranial surface; transverse groove is

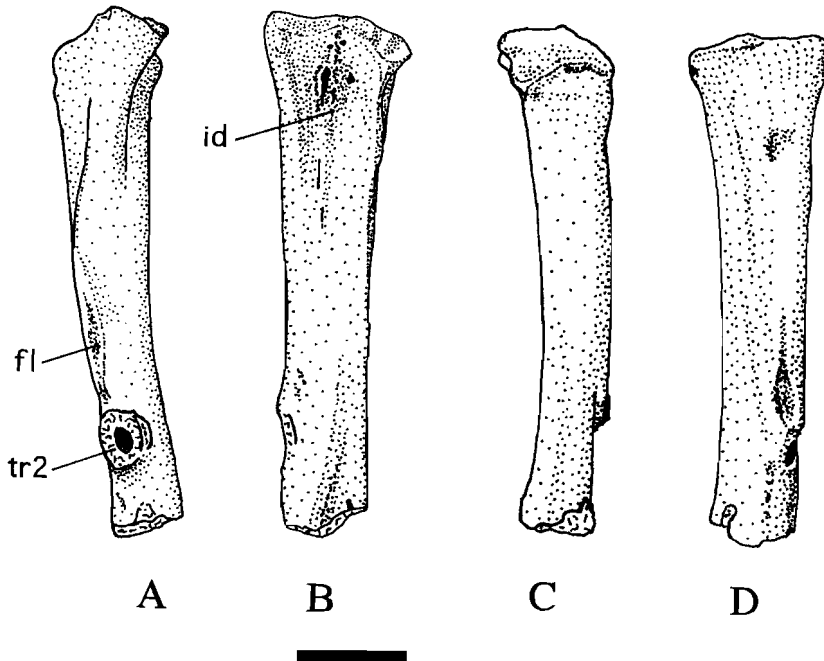


Figure 27.6. Left tarsometatarsus of a small, possibly volant hesperornithiform from the Nemegt Formation (Late Cretaceous) of Bügiin Tsav locality, Ömnögov' Aimag, Mongolia. Medial (A), cranial (B), lateral (C), and plantar (D) views. Abbreviations: fl, facet for metatarsal I; id, infracotyler depression; tr2, base of trochlea for digit 2. Scale bar = 10 mm.

short, fossa-like, and runs dorsoventrally; pneumotricipital fossa of the humerus not developed.

Contents. *Ambiortus* Kurochkin, 1982 (Neocomian, Mongolia) and *Otogornis* Hou, 1994 (Neocomian, China).

Comments. *Otogornis gengbisi* Hou, 1994 is based on associated elements of the forelimb and shoulder girdle (holotype IVPP V 9607), together with some flight feathers, from the locality of Chabu Sumu, Otog Qi, Yikezhao-meng, in the Ordos Basin of Inner Mongolia, China. The mudstones which yielded the specimen belong to the Yijinhuoluo Formation of the Zidan Group and are earliest Cretaceous or possibly even Late Jurassic in age. *Otogornis* was first identified as an enantiornithid (Dong, 1993), but later assigned to *Aves incertae sedis* (Hou, 1994).

In 1995 I had an opportunity to investigate the holotype of *Otogornis gengbisi* through the courtesy of Dr

L. Hou and Z. Zhou. I found that *Ambiortus* and *Otogornis* shared a number of derived characters including: a thickened, three-edged acrocoracoid with an acute top; flat, wide humeral articular facet of the scapula; ventral position of a small, short, and oval articular head of the humerus; and a thin and long intermediate phalanx of the major wing digit. These characters provide evidence for a close relationship between *Ambiortus* and *Otogornis*, and for the assignment of *Otogornis* to the Ambiortidae (Kurochkin, 1999b).

The heterocoelous cervical vertebrae, U-shaped furcula, convex coracoidal cotyla in the scapula, and concave scapular cotyla in the coracoid are clear evidence that Ambiortidae belongs in Neornithes. Assignment of this family to Palaeognathae is based on the advanced condition of the strong ventrocaudal transverse processes of the cervical vertebrae; the well

developed, dorsoventrally compressed scapular acromion with the tubercle or prominence on its dorsal side, and the projecting ventral edge of the proximal end of the humerus which bears a remarkable cranial tubercle with a centre pit on its cranial surface.

Ambiortus Kurochkin, 1982

Type species. *Ambiortus dementjevi* Kurochkin, 1982.

Diagnosis. Procoracoid process wide and long; scapular acromion long and dorsoventrally compressed; deep groove along lateral side of the scapula; scapular blade narrow; short, fossa-like groove cranial to the tubercle on the projecting ventral edge of the proximal end of the humerus; undivided capital groove in the proximal end of the humerus; metacarpals fused at the proximal end; intermediate phalanx of the major digit dorsoventrally compressed.

Comments. *Ambiortus* represents the earliest known stage in the evolution of neornithine birds. It indicates that early palaeognaths were keeled birds and good fliers. Comparison with the Lithornithiformes and the Ichthyornithiformes does not support the opinion of Martin (1991) and Elzanowski (1995) regarding the close relationships of *Ambiortus* to the Ichthyornithiformes.

Ambiortus dementjevi Kurochkin, 1982

Holotype. PIN 3790–271+, 3790–271–, and 3790–272, portion of the articulated left shoulder girdle, the left forelimb, and cervical and thoracic vertebrae (Figures 27.7 and 27.8). Khurilt Ulaan Bulag locality, Central Mongolian Altai Mountains, Bayankhongor Aimag. Bööntsagaan Gorizont, Neocomian, Lower Cretaceous. (The age of the Cretaceous shales and sandstones at Khurilt is disputed. According to the latest analysis (Sinitza, 1993) the Khurilt beds were deposited between the Dundargalant Gorizont (Latest Jurassic) and the upper member of the Bööntsagaan Gorizont, which is of uncertain age, although, in places, the Khurilt beds are overlapped by the Khulsangol Svita (Aptian–Albian). The dating of the latter is based on lithofacies data, fossil fish, mollusks, and ostracods, thus the age of the Khurilt beds must be at least older than the Aptian. Palaeoentomologists

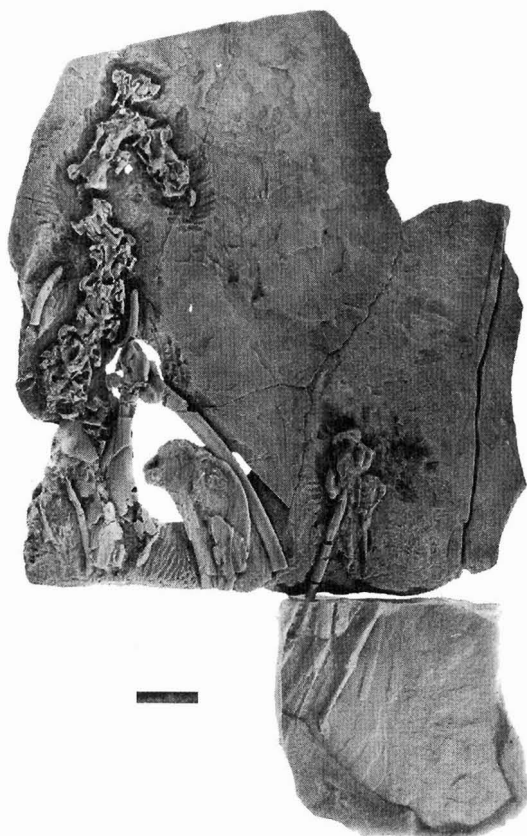


Figure 27.7. *Ambiortus dementjevi* Kurochkin, 1982. Holotype PIN 3790–271+ combined with a mould of PIN 3790–272. Scale bar = 10 mm.

and palaeobotanists consider the Khurilt beds as Late Neocomian (Zherikhin, 1978), Aptian (Krasilov, 1980, 1982; Dmitriev and Zherikhin, 1988), or just as the youngest insect assemblage among the three Lower Cretaceous assemblages of Central Mongolia (Ponomarenko, 1990). Based on geological data, Shuvalov (1982, and this volume) assigned the Khurilt and Kholboot beds to the Andaikhudag Formation that he dated as Hauterivian–Barremian. Kurochkin (1999b) further discusses the age of the Khurilt and Kholboot beds and possible correlations with the Chinese Jiufotang Formation, aged on the basis of absolute dates.

Diagnosis. Same as for the genus.

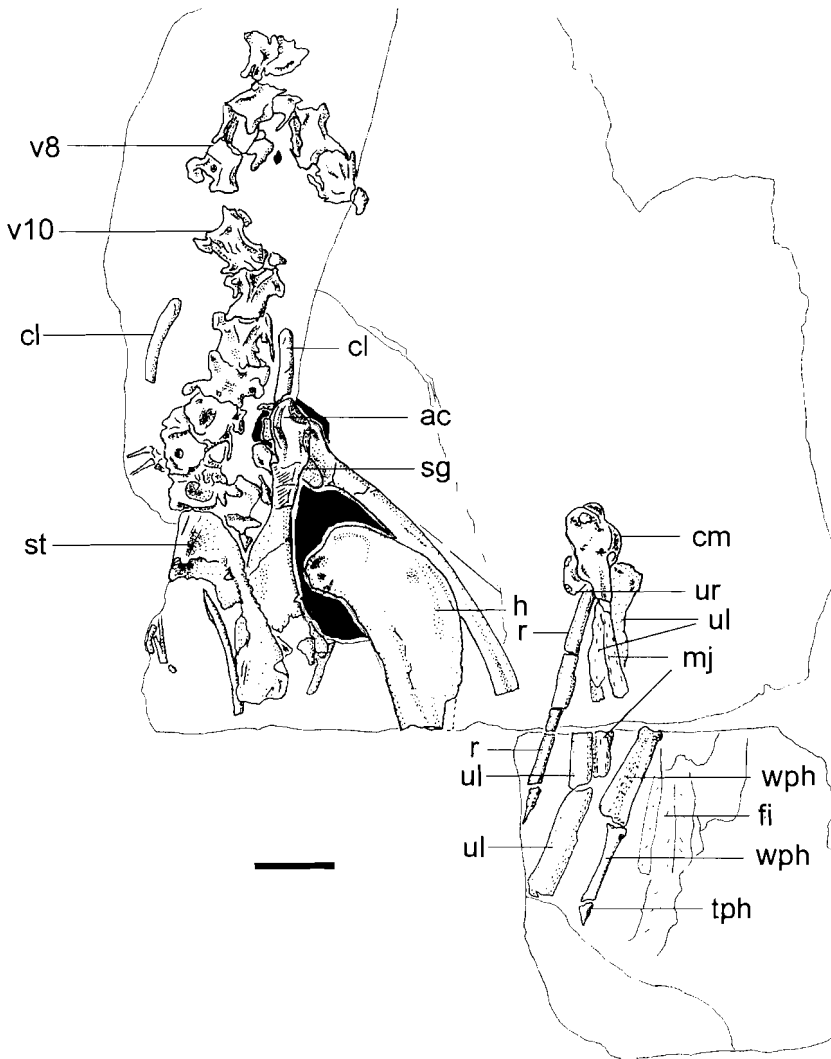


Figure 27.8. *Ambliortus dementjevi* Kurochkin, 1982. Holotype PIN 3790–271+ combined with a mold of PIN 3790–272. Abbreviations: ac, acrocoracoid; cl, clavicle; cm, carpometacarpus; fi, feather imprints; h, humerus; mj, major metacarpal; r, radius; sg, scapular glenoid; st, sternum; tph, terminal (ungual) phalanx of major digit; v8, eighth cervical vertebra; v10, tenth cervical vertebra; ul, ulna; ur, ulnare; wph, proximal and intermediate phalanges of major digit. Scale bar = 10 mm.

Comments. New preparation of *A. dementjevi* shows that the eight and tenth cervical vertebrae have heterocoelous not amphicoelous articular surfaces as previously reported (Kurochkin, 1985a, b). Further investigation also led to the discovery of a contact between the

broken edges of the counterslab (PIN 3790–271) and the slab bearing the distal portion of the forelimb (PIN 3790–272). Thus the carpometacarpus, radius, and ulna on the main slab (PIN 3790–271+) extend to specimen PIN 3790–272. *Ambliortus dementjevi* shows

some characters that confirm the primitive condition of this bird. The articular head of the humerus is oval and short, the bicipital crest and intumescence are absent, the pneumatic foramen and fossa are absent; the shaft of the radius is rounded in cross-section, the major and minor metacarpals are long, of the same length, and of similar thickness, the intermediate phalanx of the major digit is long and the major wing digit bears an ungual phalanx.

Parvclass Neognathae Pycraft, 1900

There are a few neognathous birds from the Cretaceous of Mongolia, Uzbekistan, and Russia. They are mainly represented by fragmentary remains and most have not yet been described. However, they provide important data on the distribution of neognaths in the Cretaceous and on the existence of some extant orders of birds at that time.

Order ? Gruiformes Bonaparte, 1854

Family indet.

Horezmavis Nesov, 1983

Type species. *Horezmavis eocretacea* Nesov, 1983.

Diagnosis. Medial cotyla of the tarsometatarsus inclined dorsally and located markedly more proximal than the lateral cotyla; intercotylar prominence low; dorsal infracotylar fossa deep and elongate; dorsomedial margin sharpened; tuberosity for insertion of *M. tibialis cranialis* short, high, and located in the proximal region of the fossa; the large vascular foramen on the lateral side and the impression for the ligamental attachment on the medial side are almost symmetrical with respect to the tuberosity; retinacula attachment located proximal to the ligamental attachment mentioned above, close to the dorsomedial margin; plantar crest relatively weak (Nesov and Borkin, 1983).

Horezmavis eocretacea Nesov, 1983

Holotype. PO 3390, proximal end of a left tarsometatarsus. Khodzshakul locality, outcrop CX-20, near to the north-western end of the Sultan-Uvais mountain ridge, Karakalpakia, Uzbekistan. Middle member of the Khodzshakul Svita (Late Albian).

Diagnosis. Same as for the genus.

Comments. *H. eocretacea* was assigned to the Gruiformes *sensu lato*, based on some (?) characters of the Ralli (Nesov and Borkin, 1983; Nesov, 1992d), but this needs to be confirmed. More recently, this taxon was erroneously assigned to the Enantiornithes by Martin (1995a). *Horezmavis* shows such characters of neognathous birds as a completely fused tarsometatarsus with dorsal infracotylar depression and an intercotylar prominence on the proximal articular surface. Relationships to any extant birds are difficult to establish because of the fragmentary condition of the material. However, *Horezmavis*, which was about the size of the extant *Gallinula chloropus* provides good evidence of the existence of neognathous birds in the latest Early Cretaceous.

Order Anseriformes Bechstein, 1804

Family Presbyornithidae Wetmore, 1926

Genus and species nov.

Unnamed taxon

There is a somewhat damaged, but complete tarsometatarsus of a presbyornithid from the Baruungoyot Formation at Üiden Sair, Ömnögov', Bulgan Sum, Mongolia (Kurochkin, 1988). This very small form, with a tarsometatarsus length of only 40.3 mm, is the only avian from the locality where the maniraptoran dinosaur *Avimimus* and the marsupial *Asiatherium* were discovered.

Order ? Pelecaniformes Sharpe, 1891

Family ? Fregatidae Garrod, 1891

Subfamily ? Limnofregatinae Olson, 1977

Volgavis Nesov and Yarkov, 1989

Type species. *Volgavis marina* Nesov and Yarkov, 1989.

Diagnosis. Tip of the mandible strongly ventrally deflected.

Comments. *Volgavis* was originally assigned, though with some doubt, to the Charadriiformes, then later determined as a member of the Limnofregatinae which belongs in the Pelecaniformes (Nesov, 1992d). This conclusion remains to be confirmed.

Volgavis marina Nesov and Yarkov, 1989

Holotype. PO 3638, rostral portion of the lower jaw

with both rami and a fragment of the surangular. Malaya Ivanovka locality, Dubovskii District, Volgograd Province, South Central Russia. Quartz-glaucanite sands of Latest Maastrichtian or Danian.

Diagnosis. Same as for the genus.

Comments. The lower jaw fragment of *V. marina* is about 27 mm, as measured from figure 1–1a of Nesov and Yarkov (1989), and thus it was a small bird. The mandibular ramus exhibits the opening of the neurovascular canal on the medial side and some neurovascular foramina in a shallow groove on the lateral side. A ventrally deflected tip of the mandible also suggests a strongly hooked end of the upper jaw.

The beds that yielded this fossil, greenish, quartz-glaucanite sands were originally considered to be Latest Maastrichtian (Nesov and Yarkov, 1989; Nesov, 1992b), but are now thought to be Danian (Palaeocene) (Nesov, 1988, 1992c).

Aves incertae sedis

Platanavis Nesov, 1992

Type species. *Platanavis nana* Nesov, 1992.

Diagnosis. Middle vertebrae of synsacrum heavily dorsoventrally compressed; vertebral foramen very spacious in the middle portion of the synsacrum; double ridge along ventral side of the synsacrum; pleurocoels very low and short; dorsal area of the middle vertebrae of the synsacrum broadened (Nesov 1992).

Platanavis nana Nesov, 1992

Holotype. PO 4601, fragment of the synsacrum consisting of two or three vertebrae. Dzharakhuduk locality, Navoi District, Bukhara Province, Uzbekistan. Outcrop CBI-5a, upper member of the Bissekty Svita (Coniacian).

Diagnosis. Same as for the genus.

Comments. *P. nana* represents a small bird with the following unique characters: the vertebrae of the synsacrum are strongly dorsoventrally compressed, the pleurocoels are deep and there is a doubled ridge on the ventral side of the synsacrum.

Family Kuszholiidae Nesov, 1992

Kuszbolia Nesov, 1992

Type species. *Kuszbolia mengi* Nesov, 1992.

Contents. Only the type species.

Diagnosis. Synsacrum wide; transverse process of the next to last vertebra on synsacrum strongly developed and stout; caudal pleurocoels small-sized, but deep; caudal articular surface large, wide and dorsoventrally compressed; postzygapophyses of the last vertebra on synsacrum very large; ventral groove especially deep in articulated areas of the centra; centrum of the third vertebra from caudal end heavily dorsoventrally compressed (Nesov, 1992).

Kuszbolia mengi Nesov, 1992

Holotype. PO 4602, caudal portion of the synsacrum. Outcrop CBI-52, Dzharakhuduk locality, Navoi District, Bukhara Province, Uzbekistan. Upper member of the Bissekty Svita (Coniacian).

Referred material. Cranial portion of the synsacrum, PO 4623, from the same outcrop (Nesov, 1992d, plate IV, 5), and possibly some vertebrae from outcrops CBI-14 and CBI-57.

Diagnosis. Same as for the genus.

Comments. The holotype specimen (PO 4602) of *K. mengi* was first figured (fig. 2, 3a-3), under the number PO 3486, and identified, in the figure caption, as the synsacrum of a large ichthyornithid from outcrop CBI-52. *K. mengi* was a chicken-sized bird which had a stout synsacrum with an enlarged third pair of transverse processes. Originally placed in the Kuszholiidae *incertae sedis*, *Kuszbolia* was later assigned to the Patagopterygiformes (Nesov and Panteleev, 1993), so far known only from the Coniacian–Santonian of Argentina. This hypothesis has yet to be verified, but it should be noted that the synsacra of *Kuszbolia* and *Patagopteryx* are similar in that they both have an enlarged third pair of transverse processes and a convex ventral synsacrum. By contrast, *Patagopteryx* lacks the pleurocoels, a concave caudal articular surface, and a ventrally convex synsacrum, that are present in *Kuszbolia*.

Fossil feathers

Subclass Praeornithes Rautian, 1978

Order Praeornithiformes Rautian, 1978

Family Praeornithidae Rautian, 1978

Praeornis Rautian, 1978

Praeornis scharovi Rautian, 1978

Holotype. PIN 2585/32, flight feather. Aulic (Mikhailovka) locality, Chimkent Province, Kazakhstan. Balabansai Svita, Late Jurassic.

Diagnosis. Relatively large bird, the size of a crow; edges of the barbs absolutely flat since they do not break up into barbules; barbs have pulp caps; outer and inner sides of barbs flattened and broadened, thus showing some similarity to vanes; the vanes located near to the dorsal side of the barb shaft, which is filled by the pulp caps; barbs form a complete vane; the number of the barbs in one centimetre is not more than four; the plane of the vane is twisted; the outer vane is narrower than the inner vane; the distal portion of the shaft of the flight feather is noticeably flexed in the horizontal plane; the pulp caps are large; pulp caps in the shaft are larger than ones in the barbs; ends of the barbs are clearly pointed.

Comments. This feather-like specimen (Figure 27.9) (Rautian, 1978) is possibly the earliest known record of a feather, but is doubted by some. Nesov (1992d) discussed the relationships of *Praeornis scharovi*, rejecting the designation of this specimen as avian, and supporting the conclusions of Bock (1986) who regarded this enigmatic fossil as a plant. New investigation of this specimen, using scanning electron microscopy (Glazunova *et al.*, 1991), supports its avian assignment, but the particular identity of this specimen remains unresolved.

Cretaceous feathers

A detailed record of fossil feathers from the former USSR was published by Nesov (1992b, d) and numerous fossil feathers from the Lower Cretaceous of Mongolia and Siberia were recorded and figured by Kurochkin (1985a, b, 1988).

There are a number of avian feathers from the

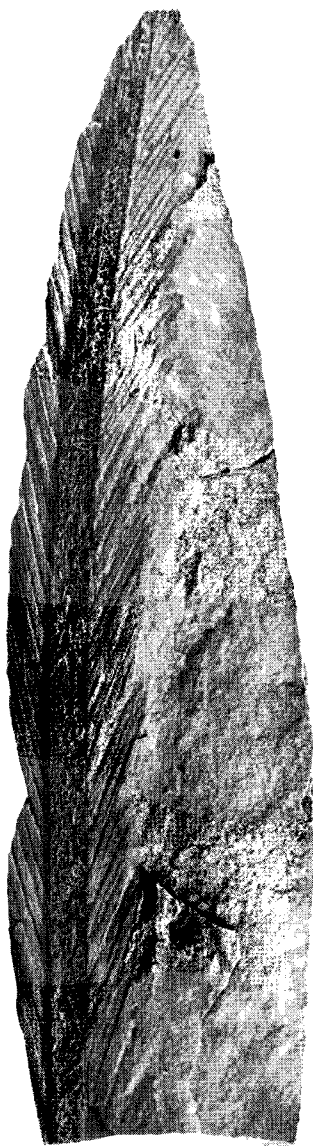


Figure 27.9. *Praeornis scharovi* Rautian, 1978. Holotype PIN 2585/32. Scale bar = 10 mm.

Lower Cretaceous of Western and Central Mongolia. Feather localities include: Hötöl, Khyra, Gurvan Ereen, Erdene Uul, Khurilt Ulaan Bulag, Kholboot, Shine Khudag, Böön Tsagaan, Altan Teel, Myangat, Andai Khudag and Ulaan Tolgoi. Among them, the

fossiliferous deposits of the first three localities belong to the lowermost svitas of the Neocomian. In addition, the Lower Cretaceous localities of Baisa, Ust' Kara, Pad' Semen, and Turga in Transbaikalia, Russia, have yielded about three dozen feathers. Isolated feathers have been collected from the Late Cretaceous localities of Yantardakh (north of the Krasnoyarskii Krai, Khatanga River), Amka (Khabarovskii Krai, Okhotskii Region), Obetzautzii Creek (Magadan Province, Tenkinskii Region) in Russian Siberia, and Taldysai (Dzhezkazgan Province) which yielded *Cretaviculus sarysuensis* based on feather remains (Bazhanov, 1969; Shilin and Romanova, 1978) and Tulkeli (Kizylordin Province) (Shilin, 1977) in Kazakhstan.

Unfortunately, so far, Cretaceous feathers have provided little information on birds of the period. However, the specimens mentioned above are preserved in very different conditions. Some represent impressions of the feather structure, while others show different kinds of mineralization of the feathers. Most specimens represent small body contour feathers, but they do not show the microstructure of the distal barbules or microscopic barbicels which are of taxonomic significance in modern birds. Some specimens from Gurvan Ereen represent flight and tail feathers, and some are represented by plumules. One specimen from Baisa shows color patterns.

Fossil avian eggs

There are a number of fossil avian eggs and eggshell remains from the Upper Cretaceous of Mongolia, Kirgizstan and Uzbekistan (Chapter 28).

Non-avians

Class Reptilia Linnaeus, 1758

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Family Parvicursoridae Karhu and Rautian, 1996

Mononykus (Perle *et al.*, 1993)

Type species. *Mononykus olecranus* (Perle *et al.*, 1993).

Holotype. MGI 107/6, posterior part of skull, most of the precaudal vertebrae, all four limbs, thoracic girdle and portion of ilium and pubis. Bügiin Tsav Locality,

South Mongolia. Nemegt Formation, Upper Cretaceous (Maastrichtian?).

Referred material. A skull fragment and part of an articulated postcranial skeleton, MGI 100/99; Tögrögiin Shiree, South Mongolia; Djadokhta Formation, Upper Cretaceous (Campanian?).

Diagnosis. Edentulous maxilla; pronounced pectoral crest of humerus; single distal condyle of humerus; ventral tubercle of humerus pronounced; extremely short shafts of ulna and radius; very long olecranon process of ulna; carpometacarpus massive, short, quadrangular with no intermetacarpal space; manus digit 1 much larger than digits 2 and 3; claw of manus digit 1 robust; coracoid not expanded ventrally; sternal carina thick; one posterior dorsal vertebra biconvex and synsacrum procoelous; zygapophyses, costal fossa, and transverse process of anterior dorsal vertebrae on same level; sharply keeled posterior centra on synsacrum vertebrae; elongate haemal arches; ischium extremely slender; robust and horizontally projected antitrochanter; two cnemial crests on tibiotarsus; medial margin of ascending process of astragalus excavated by deep notch; metatarsal III limited to distal third, triangular in cross-section. This diagnosis is assembled from the original diagnoses in Perle *et al.*, (1993, 1994).

Comments. In recent years, there has been much discussion about the relationships of *Mononykus*. I do not consider it or its relatives to be avian but, because it has been assigned by some to Aves, it must be discussed here.

Cladistic analysis has suggested that *Mononykus* falls within Metornithes as a sister-group to Ornithothoraces (Norell *et al.*, 1993; Perle *et al.*, 1993, 1994; Chiappe *et al.*, 1996). *Archaeopteryx* is excluded from this evolutionary lineage and assigned to the Avialae *sensu* Gauthier (1986) placing *Archaeopteryx* as a sister-group to taxa including Maniraptora and traditional Aves, though in a recent paper Chiappe *et al.* (1996) changed Avialae to Aves for the taxon Metornithes + *Archaeopteryx*. At the same time, the cladistic approach utilizing the total group concept indicates theropodan relationships for *Mononykus* (Patterson, 1993a, b).

In spite of that, most palaeontologists using a morpho-phylogenetical concept of homology-analogy have found evidence of a non-avian, theropodan nature for *Mononykus* (Ostrom, 1994; Wellnhofer, 1994; Kurochkin, 1995c; Martin, 1995b; Zhou, 1995; Feduccia, 1996). The unambiguous relationships of *Mononykus* to birds was established on five (Perle *et al.*, 1993) or six (Chiappe *et al.*, 1996) characters: prominent ventral processes on cervicodorsal vertebrae, longitudinal and rectangular sternum, ossified sternal keel, ischium more than two-thirds of pubic length, carpometacarpus formed from fused distal carpals and metacarpals, prominent antitrochanter, and short fibula. All these characters can be explained as bipedal and digging adaptations (Zhou, 1995), and most are represented among different velociraptorine or maniraptoran theropods. Such characters as a single-headed quadrate, biconvex posterior dorsal vertebrae and opisthocoelous thoracic and cervical vertebrae, articulation of the cervical ribs at the same level as the cranial zygapophyses and transverse processes, an obtuse apex of the scapula that should be directed dorsad in natural articulation to the coracoid (the position of the scapula should be vertical, not horizontal as it was figured in the original reconstructions (Perle *et al.*, 1994 figs. 9 and 20)), a wide coracoid lacking an acrocoracoid, a single distal condyle of the humerus, femur longer than the metatarsus, and with a fourth trochanter, and unfused metatarsals with a proximally declined third metatarsal all clearly point to the theropodan nature of *Mononykus* (Kurochkin, 1995c). Indeed Ostrom (1994, p. 172), concluded that '*Mononykus* was not a bird, . . . it clearly was a fleet-fossorial theropod.'

Recently, Karhu and Rautian (1996) described a new maniraptoran, *Parvicursor remotus*, from the Late Cretaceous of Mongolia and discussed in detail the arctometatarsalian type of metatarsus. *Parvicursor* is extremely similar to *Mononykus* and both show the arctometatarsalian pes with a proximally declined third metatarsal. On this basis, Karhu and Rautian (1996) argued that arctometatarsalian theropods are not closely related either to Sauriurae, or to Ornithurae.

Discussion

Feather records show a wide distribution of birds from the earliest Cretaceous in the western part of Mongolia and in the southern part of Eastern Siberia. Late Cretaceous feather records confirm the existence of birds in Kazakhstan, Northern Siberia, Mongolia, and the Far East of Russia. Unfortunately, feathers reveal nothing regarding the taxonomic identity of these birds, but because of the wide distribution of downy and fine contour feathers they indicate the extensive distribution of birds with a warm-blooded physiology in the Early Cretaceous. These types of feathers may be associated with the origin of neognathous birds.

By contrast, the contour plumage for enantiornithine birds is problematic. Chinsamy *et al.* (1994, 1995) reported growth rings in the femora of Argentinian enantiornithines indicating cyclical growth of bones during life and slower growth rates than in extant birds. This also provides indirect evidence of their physiology, thus Chiappe (1995) and Chinsamy *et al.* (1995) have suggested that enantiornithines did not have endothermy or ectothermy, but some kind of intermediate level of metabolism. In any case, as this level of physiology is more similar to a reptilian mode of physiology, than an avian one, this may be sufficient to reject the idea of a good covering of contour feathers in the enantiornithines.

Osteological remains are more restricted than feathers, both in terms of their geological and geographical distribution, but they can be attributed to particular avian taxa. A small enantiornithine was present in the Early Cretaceous of Mongolia and during the late Late Cretaceous (Coniacian–Maastrichtian) small and middle-sized enantiornithines inhabited Mongolia and Uzbekistan. Their small size and long, curved pedal claws suggests that they may have been primarily arboreal birds.

Large, flightless hesperornithiforms are known from the Campanian of Russia and Kazakhstan, while small and possibly volant hesperornithiforms have been collected from the Santonian–Campanian beds of Kazakhstan and from the Maastrichtian beds of

Mongolia. This is supported by data from North America concerning the existence of previously unknown small representatives of hesperornithiforms in the interior basin of North America at the end of the Cretaceous.

The Palaeognathae is a separate lineage of neornithine birds that was represented in the Early Cretaceous of Mongolia by *Ambiortus*. In an adjoining region of China, *Otogornis*, a close relative of *Ambiortus*, has been reported from the earliest Cretaceous.

The Neognaths form a fourth group of Cretaceous birds. They were present in the Early Cretaceous as fossil records from Asia and Europe show. New data on birds from Liaoning in China also confirm the existence of neognathous birds in the Early Cretaceous (Hou *et al.*, 1996). In the Late Cretaceous Nemegt Formation undescribed remains from Mongolia indicate the existence of charadriiforms (Graculavidae), anseriforms (Presbyornithidae), pelecianiforms (a cormorant), and procellariiforms (an albatross) in this region. This is concordant with discoveries in North America and Antarctica. The fifth and last group of Asian Cretaceous birds, the Kuszholiidae, of uncertain relationships, is known only from the Late Cretaceous of Uzbekistan.

Most of these avian fossils are represented by fragmentary remains which mainly provide information on the distribution of Mesozoic birds. However, some of the Russian and Mongolian Cretaceous birds, such as *Ambiortus* and *Nanantius*, provide very important evidence of the mode of evolutionary processes in early birds. As I hypothesized (Kurochkin, 1985a, 1991), the known record of Mesozoic birds is more restricted than the true diversity of Mesozoic birds, and *Archaeopteryx* was not the direct ancestor for all later birds. New fossil data on Mesozoic birds (Chiappe, 1995; Feduccia, 1995; Hou *et al.*, 1995, 1996; Kurochkin, 1995c) confirm this assumption and these authors demonstrate a formerly unknown Mesozoic diversity of birds.

Data on Mesozoic birds has only appeared from Russia and Mongolia during the last few decades: this is in contrast to North America where Cretaceous birds have been collected and studied for more than a

century. However, they provide good evidence for a greater avian diversity at higher taxonomic levels in the Mesozoic than in the Cenozoic. So, in the Cenozoic, only two evolutionary lineages: Palaeognathae and Neognathae of the infraclass Neornithes survived. During the Cretaceous, at least, there were five major phylogenetic lineages: the Enantiornithes, Hesperornithes, Ichthyornithes, Palaeognathae, and Neognathae.

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1. The species of *Zhyraornis* listed on pp. 533-534 were assigned by Nesov (1984) to the Ichthyornithiformes, and subsequently to the Enantiornithes by Kurochkin (1996, this paper). However, Zhyraornithidae do not belong to the Enantiornithes, or to any other known fossil or living group of birds, as investigation of these remains in the TsNIGRI and in the PO, and discussion with A. Pantelev showed in February, 1998.
2. New genera and species of Enantiornithes based on coracoids mentioned on pp. 534-545 have been described by Pantelev (1998).

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