

Cenozoic Phoenicopteriform Birds from Central Asia¹

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Abstract—A new phoenicopteriform bird, *Palaelodus kurochkini* sp. nov., is described from the terminal middle Miocene of Mongolia (the Sharga locality) on the basis of a partial tibiotarsus and tentatively associated fragmentary tarsometatarsus, carpometacarpus and proximal phalanx of the major wing digit. This is the first record of the extinct phoenicopteriform family Palaelodidae in Asia and shows that the genus *Palaelodus* is one of few taxa in the Sharga fauna to have a wide distribution range. Two other fossils of Phoenicopteriform birds from the Cenozoic of Central Asia are also restudied in this work; *Agnopterus turgaiensis* from the early Oligocene of Kazakhstan is provisionally placed within the extant family Phoenicopteridae, and *Cygnopterus lambrechtii*, also from the Lower Oligocene of Kazakhstan, is identified as belonging to an indeterminate phoenicopteriform family.

Keywords: Phoenicopteriformes, Palaelodidae, *Agnopterus*, Mongolia, Kazakhstan, Miocene, Oligocene

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INTRODUCTION

Until the end of the 20th Century, the fossil record of Cenozoic birds in Asia was extremely poorly known, especially when compared with the extensively studied Cenozoic bird record from Europe and North America. Progress in this field began in the 1970s and 1980s when a series of papers describing Paleogene and Neogene birds from Asia were published (Kurochkin, 1968a, 1968b, 1976, 1980, 1981, 1985; Harrison and Walker, 1982; Hou, 1987, 1989, 1990; Cheneval et al., 1991; see also Rich et al., 1986 for review of published works on fossil birds from China, Japan and Southeast Asia). Although more recent works have also substantially increased our knowledge of the Cenozoic fossil record of birds from Asia (Clarke et al., 2005; Hou et al., 2000, 2005; Mayr et al., 2007, 2010; Zelenkov and Kurochkin, 2009a, 2009b, 2010, 2012a, 2012b; Hwang et al., 2010; Kurochkin and Dyke, 2010, 2011; Zhang et al., 2010; Zelenkov, 2011a, 2011b, 2012a, 2012b; Wang et al., 2012a, 2012b) most taxa still remain extremely poorly studied. Phoenicopteriformes are just one of these groups as their fossil record in Asia is limited to just a few finds. As currently understood, the order Phoenicopteriformes includes extant flamingoes (family Phoenicopteridae) and the fossil family Palaelodidae. The fossil flamingo genus *Agnopterus* is also often placed in its own family Agnopteridae, within the order (but see below).

Only a few phoenicopteriform birds have been previously documented from pre-Quaternary Cenozoic

deposits in Asia. *Agnopterus turgaiensis* Tugarinov, 1940 was initially described based on a fragmentary tibiotarsus from the Oligocene Chelkar-Teniz locality in Central Kazakhstan (Tugarinov, 1940) and a fragmentary humerus from the nearby locality Kur Sai was later assigned to *Agnopterus turgaiensis* (see Mlíkovský and Švec, 1986). All other published data on Asian Cenozoic flamingoes are represented by finds of extant genera. The fossil species *Phoeniconaias minor* Cheneval et al., 1991 has been described from the Early Miocene of North Thailand and is known from a series of postcranial bones (Cheneval et al., 1991) and a fragmentary tarsometatarsus and possible tibiotarsus from the late Miocene of Pakistan were referred to *Phoenicopterus* cf. *ruber* Linnaeus, 1758 (Harrison and Walker, 1982). The taxonomic status of these finds remains to be confirmed.

In this paper, I review the known remains of Central Asian phoenicopteriform birds, including those previously assigned to *Agnopterus turgaiensis*, and describe a new species in the genus *Palaelodus* (Palaelodidae) from the latest middle Miocene of Mongolia. The family Palaelodidae includes long-legged aquatic birds that have a skull that superficially resembles cranes (Cheneval and Escuillié, 1992). The oldest finds of Palaelodidae come from the early Oligocene of Egypt and Belgium (Rasmussen et al., 1987; Mayr and Smith, 2002). In the Neogene, these birds enjoyed an almost global distribution (see review in Worthy et al., 2010) but were until now not known from Asia. A fragment of distal tibiotarsus, a tentatively associated fragmentary tarsometatarsus, a fragmentary carpometacarpus and a proximal phalanx of a

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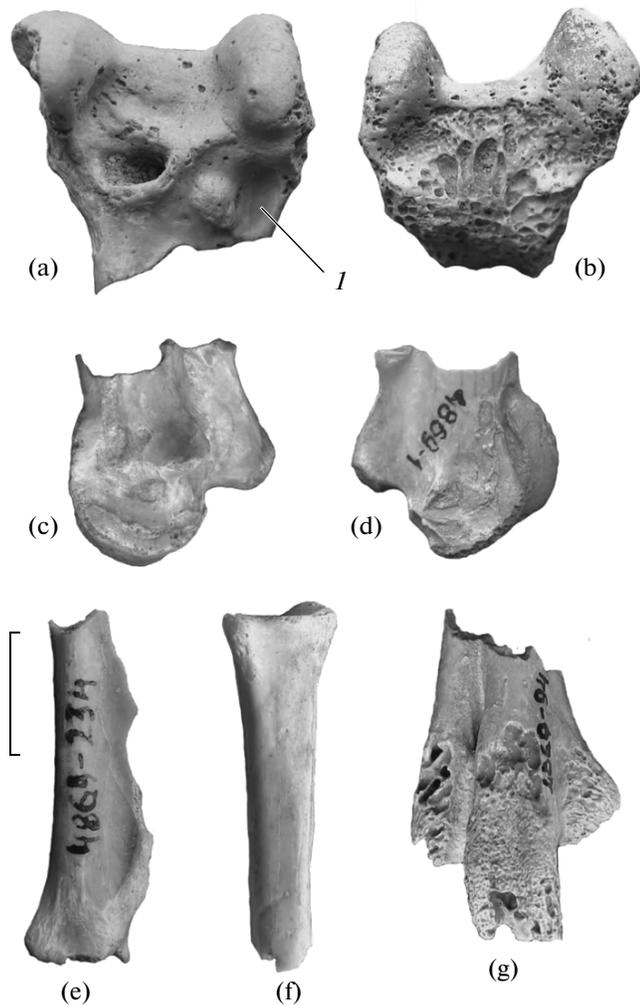


Fig. 1. *Palaelodus kurochkini* sp. nov. from the middle Miocene Sharga locality: (a, b) holotype PIN, no. 4869/233, distal fragment of right tibiotarsus in cranial (a) and distal (b) views, (c, d) proximal fragment of right carpometacarpus, specimen PIN 4869/1 in ventral (c) and dorsal (d) views, (e, f) basal phalanx of major wing digit, specimen PIN 4869/234 in dorsal (e) and cranial (f) views, (g) distal tarsometatarsus, specimen PIN 4869/94 in dorsal view. Designations: (1)—a distinct pit just lateral to the tuberculum for the lateral attachment of retinaculum extensorium tibiotarsi. Scale bar, 1 cm.

wing major digit all from the Sharga locality and presented here constitute the first finds of the family Palaelodidae from Asia.

The Sharga locality is situated in the Shargyn-Govi area, southeast of the Great Lakes Depression in Western Mongolia (Kurochkin, 1985, Fig. 1). Miocene lacustrine sediments are exposed near Shargyn Tsagaan lake which is situated in the center of Shargyn Govi. The first few avian bones from Sharga (also known as “point 1080” and “Ikh-Berhe-Tologoi”) were collected by the Joint Soviet-Mongolian Geological expedition in the late 1960s. These materials were later described by Kurochkin (1980, 1985) as *Anas*

soporata, *Palaeoaramides tugarinovi*, *Porzana risilla*, *Tringa* sp., *Anthus* sp., and *Oenanthe deserti*. Rich additional fossil bird materials from Sharga were then collected by teams of the Joint Soviet-Mongolian and Russian-Mongolian Paleontological Expeditions from the 1970s to the 2000s. At the time of description, the beds in Shargyn-Govi were considered to be the same age as Neogene sediments within the Great Lakes depression (late Miocene-Pliocene), mostly because they were not so thoroughly studied as mammalian remains are rare in this area. The study of fossil fish, however, has shown that the Neogene beds in the Shargyn-Govi are middle-late Miocene in age (Sytchevskaya, 1989), and later studies on small mammals have confirmed this age determination (MN 7-8; NMU 7) (Zazhigin and Lopatin, 2000, 2001). Preliminary studies on the fossil birds from Sharga agree with this age correlation.

The fossil specimens of Phoenicopteriformes from Central Asian localities are deposited in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia (PIN). Fossil remains of Palaelodidae were studied in the Museum für Naturkunde, Berlin, Germany (NMB) and the National Museum of Natural History, Washington DC, USA (NMHN). For comparison, the following extant and fossil species of Phoenicopteriformes were used: *Juncitarsus gracillimus*, *Palaelodas ambiguus*, *P. gracilipes*, *P. crassipes*, *Megapalaelodus goliath*; *Leakeyornis aethiopicus* (cast), *Phoenicopterus ruber*, *Ph. chilensis*, *Ph. croizeti*, *Phoeniconaias minor* (cast), and *Phoenicoparrus andinus* (cast).

Osteological terminology in this work follows Baumel and Witmer (1993).

SYSTEMATIC PALEONTOLOGY

Order Phoenicopteriformes Sharpe, 1891

Family Palaelodidae Stejneger, 1885

Genus *Palaelodus* Milne-Edwards, 1863

Palaelodus kurochkini Zelenkov, sp. nov.

E t y m o l o g y. In memory of the late Prof. Evgeny Kurochkin.

H o l o t y p e. PIN, no 4869/233, distal fragment of right tibiotarsus; Sharga locality (“Ikh-Berkhe-Tologoi”), Western Mongolia, Gobi-Altai aimag, Shargyn-Govi, about 12 km to the south of the lake Shargyn Tsagaan nuur; Ooshin formation, terminal Middle Miocene (MNU 7).

Description (Fig. 1). Diagnosis of the new species: large palaelodid (the size of *Palaelodus ambiguus*), distal tibiotarsus with a shallow but distinct pit on the cranial surface of tibiotarsus just lateral to the tuberculum for the lateral attachment of retinaculum extensorium tibiotarsi, and with the medial edge of the pons supratendineus not excavated as a furrow.

Other characters: on the tibiotarsus, the lateral tuberosity for the attachment of the retinaculum

extensorium tibiotarsi is prominent, located laterally to the pons supratendineus and separated from the lateral margin of the bone; the medial edge of the pons supratendineus is not excavated as a furrow; the incisura intercondylaris is deep and wide (in distal view, the width of the incisura considerably exceeds the width of any of the condyles); the condyli lateralis et medialis have deep tendinal pits just caudad of their cranial projections; in cranial view, the cranial part of the condylus medialis is displaced medially such that it is entirely mesad of the supratendinal bridge; the condylus lateralis is narrow in cranial view; the condylus medialis is far offset medially, resulting in a wide incisura intercondylaris; the distal margins of the condyles are distinctly notched; the incisura intercondylaris lacks a prominent distally directed articular facet for the eminentia intercotylaris of the tarsometatarsus.

M e a s u r e m e n t s in mm. Holotype: distal width, 18.4 (actual), 19.7 (restored); distal height across the sulcus intercondylaris, 14.0 (restored); carpometacarpus (specimen PIN, no. 4869/1): cranio-caudal width, 19.9; dorsoventral width, 11.1; length of os metacarpale alulare—15.0; proximal phalanx of the major digit (specimen PIN, no. 4869/234): dorsoventral width at proximal end, 9.5; distal tarsometatarsus (specimen PIN, no. 4869/94): width at the base of foramen vasculare distale, 10.4.

C o m p a r i s o n s. The new species differs from all other palaelodids because the medial edge of the pons supratendineus is not excavated as a furrow and by the presence of a shallow but distinct pit on the cranial surface of tibiotarsus just lateral to the tuberculum for the lateral attachment of retinaculum extensorium tibiotarsi (Fig. 1). It further differs from *P. gracilipes*, *P. crassipes*, *P. pledgei*, *P. wilsoni*, and *P. aotearoa* by larger size.

R e m a r k s. The tibiotarsus is one of the most easily identified elements in the skeleton of Palaelodidae. Specimen PIN 4869/233 is the size of extant *Ph. ruber* and is referred to this family because of the following characters (see also Lydekker, 1891; L. Miller, 1950; Švec, 1981; Baird and Vickers-Rich, 1998; Worthy et al., 2010): (1) lateral tuberosity for the attachment of the retinaculum extensorium tibiotarsi is prominent, located laterally to the pons supratendineus and separated from the lateral margin of the bone; (2) incisura intercondylaris deep and wide (in distal view, the width of the incisura considerably exceeds the width of either of the condyles); (3) condyli lateralis et medialis have deep tendinal pits just caudad of their cranial projections; (4) distal margins of the condyles are distinctly notched; (5) incisura intercondylaris lacks a prominent distally directed articular facet for the eminentia intercotylaris of the tarsometatarsus; (6) in cranial view, the cranial part of the condylus medialis is displaced medially such that it is entirely mesad of the supratendinal bridge. An additional character defining

the family, which is also present in the new species, is the narrow condylus lateralis in cranial view.

Palaelodidae are most similar to Phoenicopteridae in the structure of their tibiotarsus; the new species differs however from Phoenicopteridae as follows: absence of an elongated tuberculum for the lateral attachment of the retinaculum extensorium tibiotarsi, linked to the articular facet for the eminentia intercotylaris; condylus medialis far offset medially, resulting in a wide incisura intercondylaris; an oblique groove on the lateral surface of the distal end absent. The new specimen differs from another phoenicopteriform taxon, *Agnopterus turgaiensis*, from the Oligocene of Kazakhstan (Tugarinov, 1940) because of the presence of a deep incisura intercondylaris in distal view, a rather short tuberculum for the lateral attachment of the retinaculum extensorium tibiotarsi and because of a narrow condylus lateralis. Worthy et al. (2010) considered this rounded and laterally displaced lateral tuberosity for the attachment of the retinaculum extensorium tibiotarsi an autapomorphy of the Palaelodidae. In the new species described here, however, this tuberosity is oval-shaped but is distinctly shorter than in Phoenicopteridae and *Agnopterus*. Another character found in Palaelodidae and distinguishing this family from Phoenicopteridae is a somewhat shortened pons supratendineus (Worthy et al., 2010). However, the pons supratendineus is not shortened in the new species (Fig. 1) although it does not appear to be more elongated than in *Palaelodus ambiguus* and *P. gracilipes*.

Within the family Palaelodidae three genera have been described and the tibiotarsus is not known for the oldest genus *Adelalopus*. The two remaining genera, *Palaelodus* and *Megapaloelodus*, have quite similar morphologies of their distal tibiotarsus (Miller, 1950; Baird and Vickers-Rich, 1998). Baird and Vickers-Rich (1998) reviewed the characters of distal tibiotarsus that had been previously used to distinguish these genera and found that only one of those characters (depth of sulcus extensorius) was valid. Unfortunately, the sulcus extensorius is not preserved in the holotype and the only known tibiotarsus of *P. kurochkini*. The tibiotarsi of *Palaelodus ambiguus* and *Megapaloelodus goliath* overlap in size, and *P. kurochkini* falls within the range of both species. Of note, *P. kurochkini* differs from both *Palaelodus* and *Megapaloelodus* in two characters: the medial edge of the pons supratendineus is not excavated in a furrow (such furrow is evident in all species of *Palaelodus* and in *Megapaloelodus*); a shallow but distinct pit is present on the cranial surface of tibiotarsus just lateral to the tuberculum for the lateral attachment of retinaculum extensorium tibiotarsi (such a pit is totally absent from *Palaelodus* and *Megapaloelodus*). These differences prove that the paleodid from Sharga represents a separate taxon within the family and suggests that it might represent a distinct genus within Palaelodidae. Better preserved material

(at least complete distal tibiotarsus) would be very useful to justify the presence of a new genus; assignment of this species to the genus *Palaelodus* is provisional although it is supported by the morphology of tentatively associated carpometacarpus (see below).

Specimen PIN 4869/1 is a proximal carpometacarpus about 12 percent larger than the corresponding bone of *P. ruber*, but is tentatively assigned to this species; this element is similar to that of Palaelodidae (Švec, 1981, Agnolin, 2009; personal observations) in the general proportions of the os metacarpale alulare and processus extensorius but differs in having a less roundish ventral portion of the trochlea carpalis (Fig. 1). It differs from Phoenicopteridae in the less elevated proximal part of the processus extensorius and short dorsal rim of the trochlea carpalis in dorsal view. A tubercle present on the distal part of the dorsal rim of the trochlea carpalis in *Megapaloelodus* (Agnolin, 2009; personal observations) is absent in *Palaelodus* and in specimen PIN 4869/1. The shape of the processus pisiformis shows notable individual variation in *Palaelodus* (personal observation) and is thus considered here as inconsistent character for comparisons.

The partial phalanx of the major digit of the wing in specimen PIN 4869/234 differs from the corresponding bone of Phoenicopteridae in the considerably less curved dorsal portion of the facies articularis metacarpalis.

The partial distal tarsometatarsus PIN 4869/94 is too badly preserved to allow any morphological comparisons but as far as it may be observed this fragment is similar to the tarsometatarsi of Phoenicopteridae and Palaelodidae.

Material. Holotype; the following remains are tentatively referred to this taxon: PIN 4869/1, proximal fragment of right carpometacarpus; PIN 4869/234, fragment of proximal phalanx of major wing digit; PIN 4869/94, distal fragment of right tarsometatarsus.

Family Phoenicopteridae Bonaparte, 1831

Genus *Agnopterus* Milne-Edwards, 1867

Type species. *Agnopterus laurillardi* Milne-Edwards, 1867; Late Eocene of France.

Emended diagnosis. Distal aperture of canalis extensorius roundish; lateral tuberosity for attachment of the retinaculum extensorium tibiotarsi prominent and elongate; articular surface for the eminentia intercotylaris of tarsometatarsus vestigial and not continuous with the lateral tuberosity for the attachment of the retinaculum extensorium tibiotarsi; pons supratendineus proximodistally short; cranial surface positioned between condyles moderately concave; condyles in cranial and distal views not narrowed; lateral surface of the bone in distal view strongly bended in its middle part; sulcus cartilaginis tibiotarsi shallow; distal margins of condyles are not

markedly notched in lateral and medial views; oblique sulcus on the lateral surface of the distal end absent.

Generic composition. *Agnopterus laurillardi* Milne-Edwards, 1867; Late Eocene of France; *A. hantoniensis* Lydekker, 1891, Late Eocene and lower Oligocene of England; *A. turgaiensis* Tugarinov, 1940, early Oligocene of Kazakhstan; *A. sicki* Alvarenga, 1990, late Oligocene-lower Miocene of Brazil.

Comparisons. *Agnopterus* differs from other Phoenicopteridae because of the roundish distal aperture of the canalis extensorius (oval in Phoenicopteridae); vestigial articular surface for the eminentia intercotylaris of tarsometatarsus not continuous with the lateral tuberosity for the attachment of the retinaculum extensorium tibiotarsi; pons supratendineus extremely short proximodistally; lateral surface of the bone in the distal view stronger bended in its middle part; the absence of the oblique sulcus on the lateral surface of the distal end. This specimen differs from Palaelodidae by the condylus lateralis not being narrowed mediolaterally in cranial and distal views; concave cranial surface positioned between the condyles; elongate tuberosity for the attachment of the retinaculum extensorium tibiotarsi; narrow pons supratendineus; not markedly notched distal margins of condyles in lateral and medial views.

Remarks. The genus *Agnopterus*, originally established for *Agnopterus laurillardi* Milne-Edwards, 1867 from the Late Eocene of France, was placed in its own family—Agnopteridae—by Lambrecht (1933). Recently Mlíkovský (2002) referred *A. laurillardi* to the extant family Cariamidae even though earlier Olson and Feduccia (1980) had noted that the holotype of *Agnopterus laurillardi* does not possess any diagnostic characters and thus could not be assigned to Pheonicopteriformes. In fact, Mlíkovský and Švec (1986) incorrectly interpreted Olson and Feduccia (1980) by alleging that Olson and Feduccia showed that *Agnopterus laurillardi* is not a phoenicopteriform. The tibiotarsus of *Agnopterus laurillardi* (figured in Milne-Edwards, 1867) indeed resembles Cariamidae in cranial view, but it has a narrow sulcus cartilaginis tibiotarsi and medially positioned condylus medialis. Both characters are found in Phoenicopteriformes and are absent from Cariamae, so *Agnopterus laurillardi* should be retained in Phoenicopteriformes.

Agnopterus laurillardi, *A. sicki* and *A. turgaiensis* cannot be assigned to Palaelodidae and may represent closely related forms. The assignment of *A. hantoniensis* to this genus is also provisional. Mayr (2009) considered *A. hantoniensis* a stem group representative of Phoenicopteriformes (see also Mayr, 2009 for review of taxonomy of *A. hantoniensis*). I place the genus *Agnopterus* within the extant family Phoenicopteridae (see also Alvarenga, 1990) mainly because it has a tuberculum bearing the articular surface for the eminentia intercotylaris of the tarsometatarsus (although not as well-developed as in extant Phoenicopteridae),

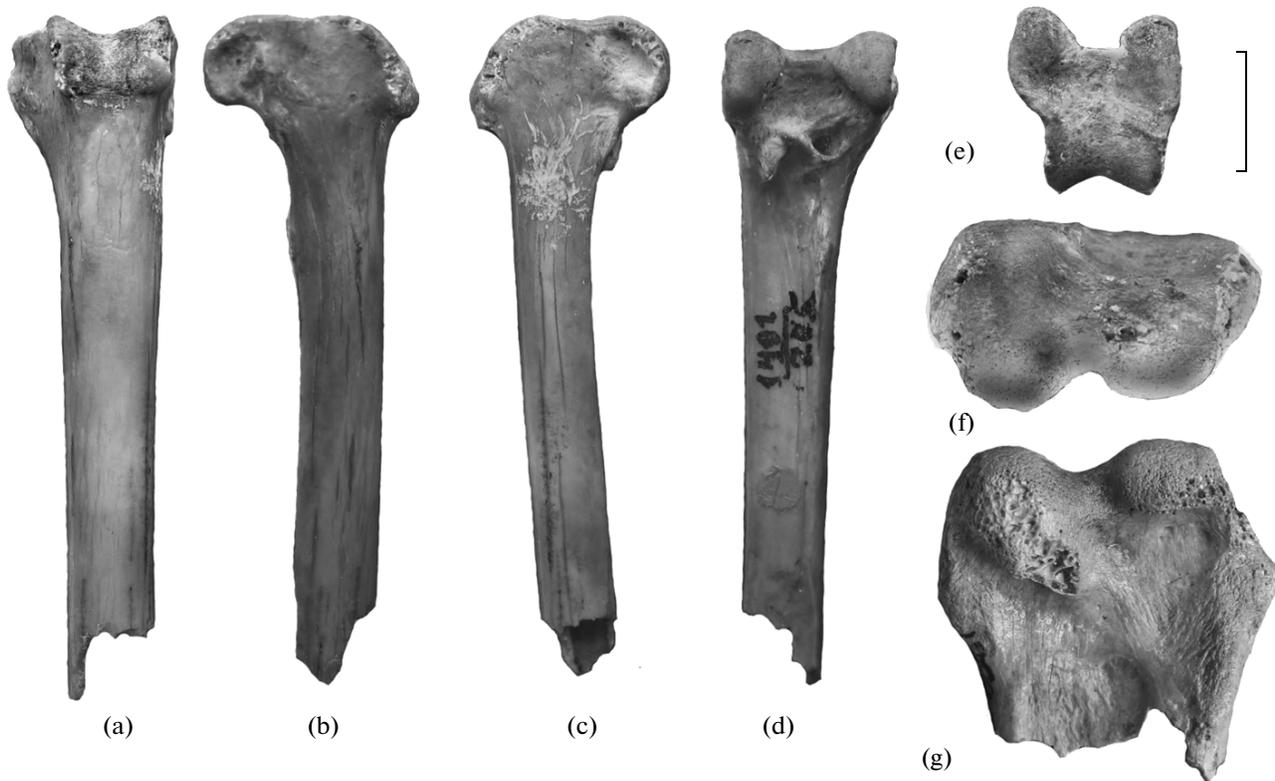


Fig. 2. Representatives of Phoenicopteriformes from the Early Oligocene of Kazakhstan: (a–e) *Agnopterus turgaiensis* Tugarinov, 1940, holotype PIN, no. 1401/205, locality Chelkar-Teniz, distal fragment of left tibiotarsus in caudal (a), medial (b), lateral (c), cranial (d) and distal (e) views, (f, g) “*Cygnopterus*” *lambrechtii*, specimen PIN no. 1399/123, locality Kur-Sai, left distal humerus in distal (f) and cranial (g) views. Scale bar, 1 cm.

but further finds may confirm the validity of the family Agnopteridae.

***Agnopterus turgaiensis* Tugarinov, 1940**

Agnopterus turgaiensis: Tugarinov, 1940, p. 315, Fig. 2; Brodkorb, 1963, p. 271; Dementiev, 1964, p. 688, Fig. 696; Mlíkovský and Švec, 1986, p. 266.

H o l o t y p e. PIN, no. 1401/205, distal fragment of left tibiotarsus; Chelkar-Teniz locality (Kordikova, 1994, Fig. 1), Central Kazakhstan; “Indricotherium beds”, early Oligocene (MP 22–24).

M e a s u r e m e n t s in mm. Distal width, 13.6; distal height, 15.4; distal height across sulcus intercondylaris, 10.5; maximal cranial width of condylus lateralis, 4.6; maximal cranial width of condylus medialis, 5.1; minimal shaft width, 6.7; width of trochlea cartilaginis tibiotarsi, 9.4.

D e s c r i p t i o n (Fig. 2). The shaft is narrow; condylus medialis is shifted notably medially relative to the shaft; sulcus cartilaginis tibiotarsi is narrow in distal view.

C o m p a r i s o n. Differs from *A. sicki* because of the presence of an indistinct sulcus extensorius (better defined in Phoenicopteridae), narrower pons supratendineus; more distinct bends in the lateral and medial margins of the bone in distal view; narrower

sulcus cartilaginis tibiotarsi. Differs from *A. laurillardi* because of anarrower trochlea cartilaginis tibiotarsi that has a medial crest that is shorter and less prominent, and because of a condylus medialis that is strongly shifted medially in relation to both the shaft and the medial crest of the trochlea cartilaginis tibialis (well visible in distal view). The shaft seems to be more gracile in the *A. turgaiensis*.

M a t e r i a l. Holotype is the only known specimen.

Phoenicopteriformes fam. indet.

“*Cygnopterus*” *lambrechtii* Kurochkin, 1968

Cygnopterus lambrechtii: Kurochkin, 1968b, p. 92; Brodkorb, 1971, p. 175.

Agnopterus turgaiensis: Mlíkovský and Švec, 1986, p. 266.

H o l o t y p e. PIN, no. 1399/123, fragmentary distal left humerus; Kur Sai locality to the north of Lake Chelkar-Teniz, Central Kazakhstan; early Oligocene.

D e s c r i p t i o n. See Kurochkin (1968).

R e m a r k s. The fragmentary distal left humerus (Fig. 2) from the early Oligocene of Central Kazakhstan was initially described as the holotype of the fossil anseriform *Cygnopterus lambrechtii* Kurochkin, 1968 (Kurochkin, 1968b; see also Brodkorb, 1971, p. 175). Later, Mlíkovský and Švec (1986) referred this speci-

men and so synonymized this taxon with the fossil flamingo *Agnopterus turgaiensis*, known on the basis of a distal tibiotarsus from the nearby Chelkar-Teniz locality. They noted that these two specimens come from similarly-aged deposits and considered them to be from a bird of the same size. However, the humerus (specimen PIN, no. 1399/123) derives from a flamingo about 1.5 times larger than *Agnopterus turgaiensis* and thus obviously comes from a different species.

I agree with Mlíkovský and Švec (1986) that humerus PIN 1399/123 belongs to Phoenicopteriformes, but that the exact systematic position of this specimen cannot be established because of its poor preservation. In details, this humerus differs from those of Anatidae because of a concave cranial surface on the distal end. In the general appearance, distal humeri of Gruidae and Phoenicopteridae are quite similar, but PIN 1399/123 is here referred to Phoenicopteriformes because of a well-developed fossa olecrani (absent in Gruidae), a dorsally shifted fossa brachialis (extending ventrally in Gruidae), and a well-marked incisura intercondylaris (poorly developed in Gruidae). PIN 1399/123 also clearly differs from Palaelodidae and the alleged phoenicopteriform *Juncitarsus* because of the lack of development of its tuberculum supracondylare ventrale and sulcus m. humerotricipitalis. When compared to *Juncitarsus* this specimen further differs in its much larger size and because of the wide distal end of the bone. The tuberculum supracondylare ventrale, which is poorly developed in PIN 1399/123, is also not very pronounced in recent Phoenicopteridae. PIN 1399/123 differs from Phoenicopteridae because of the prominent distal surface of the condylus dorsalis and the fact that the fossa brachialis is positioned further from the tuberculum supracondylare ventrale. In Phoenicopteridae, the distal surface of the condylus dorsalis is almost flat (in extant genera) or slightly convex (*Leakeyornis*) and the fossa m. brachialis is wider with its dorsal margin positioned close to the tuberculum supracondylare dorsale. Furthermore, as far as can be judged from the specimen, PIN 1399/123 has a poorly developed sulcus scapulotricipitalis on its caudal surface. The fossa m. brachialis is positioned away from the tuberculum supracondylare ventrale also in Palaelodidae. PIN 1399/123 is also similar in size and proportions to the distal humerus BNMH A 5105 of *Agnopterus* (“*Headonornis*”) *hantoniensis* Lydekker, 1891 from the Late Eocene of England (Harrison and Walker, 1979; see Mayr, 2009, Fig. 10.1). It, however, differs from *Agnopterus hantoniensis* because the condylus dorsalis protrudes far more distally and because the tuberculum supracondylare ventrale is poorly developed.

DISCUSSION

The evolutionary history of phoenicopteriform birds is one of the most intriguing in avian evolution. The only living representatives of this group, flamin-

gos, are large long-legged and long-necked birds traditionally classified within, or close to, the extant order Ciconiiformes (del Hoyo, 1992). Only recently has it been suggested that extant flamingos are the likely sister taxon of grebes, Podicipediformes. This flamingo + grebe clade is recognized by both nuclear and mitochondrial DNA data and is supported by morphological characters (reviewed in Mayr, 2011; but see Livezey, 2011). Swimming adaptations are thought to be plesiomorphic for phoenicopteriforms (Mayr, 2004) since Palaelodidae also exhibit swimming and possibly even diving adaptations (e.g. Cheneval, 1983; Cheneval and Escuillié, 1992). Interestingly, the shaft of the tarsometatarsus in extant flamingos is mediolaterally compressed as in most of the swimming forms and foot-propelling diving (personal observation) and in contrast to, for example, storks (the broad and weakly mediolaterally compressed tarsometatarsus of extant diving oxyurines (Anatidae) may be related to the overall shortness of their foot; the tarsometatarsus is also short and broad in penguins and plotopterids, but these birds are wing-propelled divers). The study of fossil flamingos and related taxa is thus important for unveiling the evolutionary history of these birds even though Central Asian representatives are known to date from scarce material. It is noteworthy, however, that in the Oligocene and Miocene of Central Asia, both Palaelodidae and Phoenicopteridae-like birds were present, although they are not known yet from neighboring fossil sites of similar geological age.

Palaelodidae and Phoenicopteridae are also known from synchronous and closely spaced localities in Australia (Baird and Vicker-Rich, 1998) and from a number of European Neogene sites (e.g., Švec, 1981; Heizmann and Hesse, 1995). Baird and Vicker-Rich (1998) speculated that “similar environmental conditions were required by the members of both families”. The mammal fauna from the Chelkar-Teniz locality is comprised of savanna-like, open and forest landscape dwellers (Kordikova, 1994) although the presence of a number of marine taxa (Kordikova, 1994) clearly indicates that there were periodical marine transgressions in this region. It is thus possible that these Central Asian phoenicopteriform birds inhabited seashores.

The discovery of *Palaelodus* at Sharga adds to our knowledge of the late Middle Miocene birds from Western Mongolia. Recent study of new materials has revealed the presence of the small quail-like phasianid *Tologuica*, an unnamed large phasianid (Zelenkov and Kurochkin, 2009a, 2010), the primitive diving ducks *Sharganetta* and *Nogusunna*, the more advanced *Protomelanitta* (Zelenkov, 2011a), the heron *Ardea sytchevskayae*, two more unnamed herons (Zelenkov, 2011b), a few ducks of the modern genera *Anas* and *Aix*, and the fossil genera *Mioquerquedula* and *Chenoanas* (Zelenkov, 2012a; Zelenkov and Kurochkin, 2012a) all at the Sharga site. A preliminary study also shows that *Oenanthe infima* Kurochkin, 1985, described from Sharga earlier, should be restudied and

its familiar assignment to Turdidae is incorrect (personal observation). Although the Sharga avian fauna displays a high degree of endemism, some genera were widespread or at least are known from outside Mongolia in the Neogene. The Miocene European duck “*Anas*” *velox*, for example, was included in the genus *Mioquerquedula* (Zelenkov and Kurochkin, 2012a), and it has also been supposed that the larger Miocene European duck “*Anas*” *sansaniensis* may be related to *Chenoanas* from Sharga (Zelenkov, 2012a). The late Miocene Chinese duck *Aythya shihuibas* was transferred to the genus *Protomelanitta*, also known from Sharga (Zelenkov, 2012a) and the find of Palaelodidae described here extends the list of widespread Miocene taxa.

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