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Palaeontology

The first fossil parrot (Aves, Psittaciformes) from Siberia and its implications for the historical biogeography of Psittaciformes

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Modern parrots (crown Psittaciformes) are a species-rich group of mostly tropical and subtropical birds with a very limited fossil record. A partial tarsometatarsus from the late Early Miocene of Siberia (Baikal Lake) is the first pre-Quaternary find of crown Psittaciformes in Asia (and Siberia in particular) and is also the northern-most find of this bird order worldwide. This find documents a broad geographical distribution of parrots during the warmest phase of the Miocene (the so-called 'Miocene Climatic Optimum'), which has implications for the historical biogeography of Psittaciformes. The presence of parrots on both sides of the Pacific Ocean at the end of the Early Miocene implies a (most probably eastwards) trans-Beringian dispersal which likely took place about 16–18 Ma. The broad Eurasian distribution of parrots in the past further supports a hypothesis that ancestors of modern genera *Coracopsis* and *Agapornis* could reach Africa from Eurasia.

1. Introduction

Parrots (order Psittaciformes) are a very speciose and easily recognizable group of birds, inhabiting mostly subtropical and tropical regions of both New and Old Worlds. Parrots of the modern morphological type (crown Psittaciformes) first occur in the palaeontological record at the Oligocene/Early Miocene boundary [1], and the Miocene Epoch (23–5.3 Ma) was obviously an important stage in their evolution, because the diversification of several lineages of Psittaciformes apparently took place during this time interval [2–6]. However, the evolutionary history of crown Psittaciformes remains very poorly known, because the Miocene fossil record of parrots is restricted to several taxa known from Western and Central Europe [1,7–9], Australia and New Zealand [10]. Additionally, one taxon has been described from the Miocene of North America [11].

Here, I report a partial tarsometatarsus of a small parrot from the late Early Miocene (approx. 18–16 Ma) of the Baikal region (Eastern Siberia). This find is the first evidence of crown Psittaciformes in Asia and is the northernmost record of the order Psittaciformes worldwide, which has implications for the evolution of modern diversity and historical biogeography of parrots.

2. Systematic palaeontology

Psittaciformes

Psittacoidea (*sensu* [12]) gen. indet. (?aff. *Mogontiacopsitta*)

Referred material: Borissiak Paleontological Institute of RAS (PIN 2614/218), incomplete left tarsometatarsus.

Figure 1. Map showing current Old World distribution of parrots (black area), Miocene finds of parrots in Europe (white stars) and position of Tagay locality (black star).

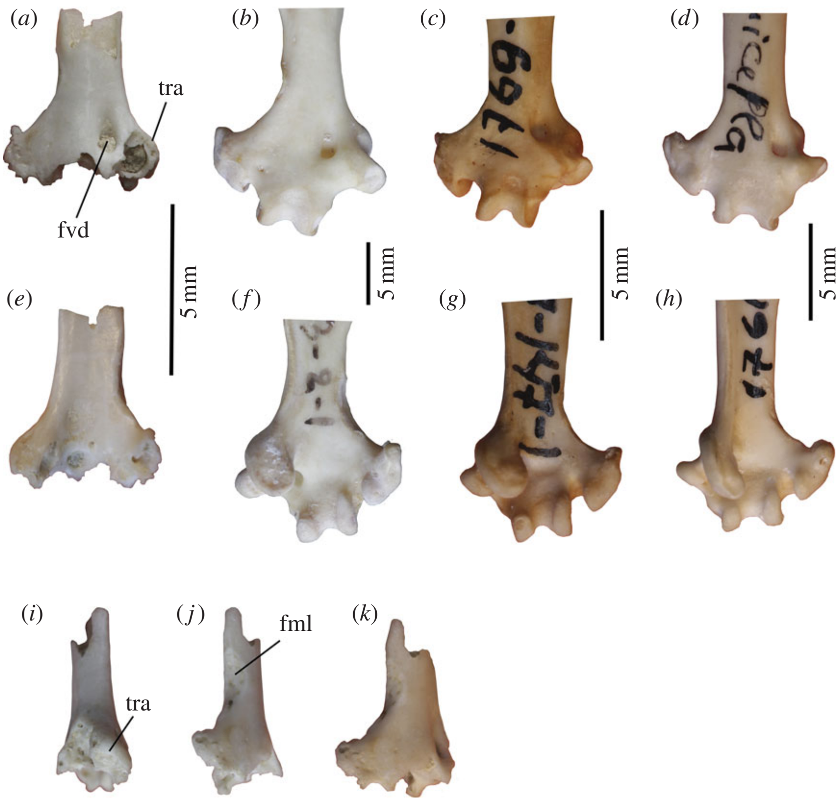

Figure 2. Fossil parrot from Siberia compared with selected extant taxa: (*a,e,i,j,k*) PIN 2614/218, Early Miocene of Tagay (Eastern Siberia); (*b,f*) *Calyptorhynchus funereus* (PIN 93-2-1), modern; (*c,g*) *Aratinga euops* (PIN 97-147-1), modern; (*d,h*) *Lorius lory* (PIN 92-23-1), modern. Upper row, dorsal view; middle row, plantar view; (*i*) lateral view; (*j*) medial view; (*k*) dorsomedial view. fml, fossa of metatarsal I; fvd, distal vascular foramen; tra, accessory trochlea of metatarsal IV. (Online version in colour.)

Locality and age: Tagay Bay, Olkhon island (Baikal Lake); Irkutsk Region; Eastern Siberia, Russia (figure 1); Khalagay formation, late Early Miocene. For associated fauna and age, see [13–17].

Description and comparisons: The specimen PIN 2614/218 is a fragmentary distal tarsometatarsus missing the articular parts of the metatarsals (figure 2). The most distinctive feature of the specimen PIN 2614/218 is that it has extremely splayed metatarsals II and IV. Although a somewhat similarly diverged metatarsal IV occurs in several other bird groups (e.g. Galbulidae), the strongly medially offset trochlea of metatarsal II can be found only in Psittaciformes. The dorsal aperture of the distal vascular foramen in the fossil specimen and in extant Psittaciformes is bounded laterally by a bony bridge, which connects the trochlea of metatarsal IV with the accessory trochlea of metatarsal IV. In birds without zygodactyl feet, this bony bridge is absent. The base of the accessory trochlea of metatarsal IV is also preserved in PIN 2614/218. Its orientation indicates that it was positioned mainly in a transversal plane, as in extant parrots.

The morphology of the Siberian specimen indicates that it is phylogenetically more derived than the basal clades Strigopoidea (New Zealand kakapo and kea) and Cacatuoidea (Australasian cockatoos) [12]. Strigopoidea have a poorly diverged accessory trochlea of metatarsal IV (likely a primitive feature; see figs in [10,18]), whereas in the Siberian fossil it is very strongly laterally displaced, as in some extant Psittacoidea. The specimen markedly differs from the examined Cacatuoidea (*Cacatua*, *Nymphicus*, *Eolophus*) in having a straight lateral margin of the shaft (concave in Cacatuoidea). The specimen is intermediate in size between modern *Agapornis personata* and *Aratinga euops*, being proportionally and structurally very close to the latter species. The shaft is narrow (shaft width at the level of the fossa of metatarsal I, 1.9 mm) and its plantar surface (slightly concave as in *Aratinga*) is emarginated by a moderately prominent lateral plantar ridge. PIN 2614/218 differs from *Aratinga* by a notably more ventrally displaced trochlea of metatarsal II. PIN 2614/218 differs from *Agapornis* (and other structurally similar genera, for example, *Psephotus* and *Melopsittacus*) in having more strongly diverged metatarsal trochleae II and IV. The fossa of metatarsal I is positioned on the medial surface of the tarsometatarsus, unlike some extant taxa (including *Psephotus* and *Platycercus*, where it is shifted plantarly).

The Siberian specimen differs from *Archaeopsittacus verreauxi* from the Early Miocene of France by a notably smaller size (it is more than 1.5 times smaller), smaller dorsal aperture of the distal vascular foramen, and a strongly laterally protruding accessory trochlea of metatarsi IV. The only described tarsometatarsus of *Pararallus dispar* from the Middle Miocene of France [9] is fragmentary and cannot be informatively compared with the Siberian specimen. The specimen PIN 2614/218 is however some 25% smaller than *Pararallus dispar*, but is of a similar size to the Middle Miocene *Bavaripsitta* from Germany [8]. PIN 2614/218 cannot be referred to *Bavaripsitta* because of more splayed metatarsals and thus a visibly narrower shaft. *Xenopsitta* from the Early Miocene of the Czech Republic [7] is larger and has a concave medial margin of the shaft, contrasting with a nearly straight shaft in PIN 2614/218. PIN 2614/218 cannot be referred to *Nelepsittacus* from the Early Miocene of New Zealand [10], because it lacks a groove running proximally from the distal vascular foramen on the dorsal surface (an apomorphy of *Nelepsittacus*). The Siberian specimen is close in morphology and also in size to *Mogontiacopsitta miocaena* from the latest Oligocene/Early Miocene of Bavaria [1]. No clear differences between the two taxa can be noted, but the preservation of the specimen PIN 2614/218 does not allow robust classification as *Mogontiacopsitta*.

3. Discussion

Tagay is the only known Early Miocene Asian locality with a representative avian fauna [19]. The discovery of a parrot in this locality thus substantially increases our understanding of the ecological composition of the Early Miocene Asian avian faunas [19] and for the first time indicates their affinities with contemporary European avian communities, where parrots are relatively well represented [7–9]. In line with this, a recently described grebe from Tagay is also quite similar to Early Miocene European grebes [16], and other birds from Tagay [12] also support affinities between the Siberian and Western European avifaunas during the Early Miocene. Importantly, the fauna of ectothermic snakes from Tagay is also similar to the contemporary faunas from France [20], which indicates relatively close environmental conditions in the Baikal region and Western Europe at that time. It should be noted, however, that the presence of parrots alone cannot serve as an indication of especially warm climate. Although modern parrots are indeed most diverse in subtropical and tropical areas, they are also present in temperate zones (e.g. New Zealand and South America) and furthermore sometimes inhabit low-productivity environments (e.g. *Melopsittacus undulatus*; *Cyanoliseus patagonus*). Nevertheless, the climate at the Tagay locality was apparently warm (probably even sub-tropical) as inferred from the presence of snakehead fishes (family Channidae) [13].

The presence of parrots as far north as Siberia supports their broad geographical distribution in Asia during the Miocene (and likely Oligocene) and may have implications for the historical biogeography of Psittacoidea. According to the evolutionary model presented by Schweitzer *et al.* [3], ancestors of the modern genera *Coracopsis* and *Agapornis* independently colonized Africa/Madagascar through a long-distance dispersal across the Indian Ocean. Although plausible, this hypothesis, which is based exclusively on molecular phylogeny and the modern distribution of Psittaciformes, invokes a long-distance dispersal in birds that are mostly non-migratory. An alternative hypothesis to be considered is that Australasian taxa might have colonized Africa via Eurasia in the Oligocene or Early Miocene. This hypothesis does not require a trans-oceanic dispersal of parrots and accounts for the known presence of Psittacoidea in the Miocene of Europe and Northern Asia. Importantly, the only known Early Miocene avian fauna from Namibia [21] shares several taxa in common with contemporary European avian communities, including the terrestrial and likely non-migratory galliform *Palaeortyx*. This implies at least some degree of biogeographical affinity between Early Miocene African and Eurasian avian faunas.

The presence of parrots in Eastern Siberia in the late Early Miocene raises a question of their possible dispersal to North America via Beringia. The only known pre-Quaternary parrot from North America was described as *Conuropsis fratercula*, a fossil relative of the historically extinct Carolina parakeet *C. carolinensis* [11]. *Conuropsis fratercula* comes from beds that are currently considered latest Early–early Middle Miocene in age (16–17 Ma; [22]). This is very close to the estimated age of Tagay locality (16–18 Ma; [12–14]) and both localities refer to the onset of the Middle Miocene Climatic Optimum, the warmest phase of the Miocene, which had its peak around 17–15 Ma [23]. For this temporal period, no faunal connection between North and South America has been established based on palaeontological data [24], so Old World affinities of *Conuropsis fratercula* seem very probable. It should be noted that the generic assignment of *C. fratercula* has never been confirmed. A dispersal of parrots via Beringia during the late Early Miocene is not completely unexpected. Today hummingbirds (Trochilidae), which are also mostly tropical in their distribution, reach as far north as Alaska, and during the warmest phase of the Miocene a more northern distribution of parrots in Asia was likely possible.

Data accessibility. Data can be found in the article.

Competing interests. I have no competing interests.

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