全北区古近纪的鸟类动物群

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摘要:中国的较高纬度地区有着丰富且交通无阻的含化石地层,故在全北区生物地理的研究中占有独特的位置。它提供了欧洲和北美新生代早期沉积之间的联系。这些动物群中所含丰富多样的鸟类动物群,直到目前才得到足够的关注。早始新世时,在全球范围内,甚至在高纬度地区,都遍布着热带森林;在怀俄明州的绿河湖区,还发现了棕榈叶的化石。因而,德国Messel的鸟类动物群表现出与非洲热带森林较近的亲缘关系,怀俄明州绿河的鸟类动物群与南美洲热带地区关系密切,也就不足为奇了。实际上,古近纪的标志性特征是温暖潮湿的生态系统在全球广泛分布,削弱了高纬度地区对生物分布所起的屏障作用。晚始新世-渐新世全球温度的下降,致使新近纪加剧了大陆隔离并促成了生态变化,进而导致了现代鸟类在分类上的多样性。

关键词:Messel, 始新世,绿河组,鸟类,新生代气候,生物地理,迁移

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PALEOGENE AVIFAUNA OF THE HOLARCTIC

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Abstract　China occupies a unique position in studies of Holarctic biogeography by having rich and accessible fossil deposits at relatively high latitudes. It provides a connection between the early Cenozoic deposits of Europe and North America. These faunas contain a diverse avifauna that is only now receiving adequate attention. The Early Eocene was a time of world-wide tropical forests, even at high latitudes (Martin, 1994), and the Green River lakes in Wyoming preserve the fossil leaves of palm trees. It is no surprise that the avifauna of Messel, Germany shows affinity with the tropical forests of Africa and that of the Green River in Wyoming with Tropical South America. In fact, the signature feature of the Paleogene was a universal distribution of warm moist ecosystems resulting in a reduction of the effectiveness of high latitude barriers to distribution. The Late Eocene-Oligocene drop in global temperatures resulted in increased continental isolation and precipitated the ecological changes that characterize the Neogene and resulted in the modern taxonomic diversity of birds.

Key words　Messel, Eocene, Green River Formation, Aves, Cenozoic climate, biogeography, migration

1　Introduction

In a volume celebrating the centennial of the American Ornithologists' Union, Martin (1983) reviewed the origin and early evolution of birds, as it was known at that time. In the

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subsequent two decades there was an unprecedented expansion in interest in the study of fossil birds including the formation of an international society to promote paleo-ornithology (Society of Avian Paleontology and Evolution). In 2000 this organization held its international meeting in China reflecting the enhanced status that this country had achieved in paleontology. However, over two thirds of this new interest centered on avian origins and birds from the age of dinosaurs, so that a statement in Martin (1983 : 322) remained valid:

"*Far less is known about the Paleocene avian radiation than about that of the Cretaceous. This situation may improve with a revival of interest in Paleocene fossil mammals. With rare exceptions, the finding of Cenozoic fossil birds has been a by-product of collecting the more common and extensively studied fossil mammals. Like the mammals, the earliest Paleocene birds seem to be mostly a continuance of the latest Cretaceous kinds. These belong to a basic shorebird adaptive type rather than any modern taxonomic entity. Probably many of these birds, if fully known, would be members of extinct groups or would show trends culminating in very different taxonomic groups later in the Tertiary.*"

Most of our knowledge of the early Tertiary avian radiation comes from Europe and North America. The Middle Eocene Messel locality near Darmstadt, Germany and the London Clay in England provide most of the European examples. The Early Eocene Green River Formation in western Wyoming and Colorado accounts for the bulk of the North American record. During the Late Paleocene through the Middle Eocene, boreotropical flora extended across China, Siberia, Alaska and Canada (Wolfe, 1980), and land connections existed beween Siberia and North America (Beringia) as well as between North America and Europe (DeGeer Route of McKenna, 1975). Tropical organisms could have achieved a "holarctic distribution" unhindered by latitudinal filtering effects (Martin, 1994). We see this reflected in bird genera shared by Eurasia and North America at this time (*Messelornis*, *Gastornis*, *Juncitarsus*, *Palaeotis*), some of whom either lacked or had limited flight capability.

The interplay between climate and evolution is the most interesting aspect of these early avifaunas. Even with the discovery of nearly complete skeletons, the phylogenetic position of most of the early forms remains controversial, and some must be regarded as ecomorphs of modern taxa rather than their ancestors. This situation parallels closely that of early mammals with many early Tertiary forms belonging to extinct orders and the modern families mostly appearing in the Late Eocene–Oligocene (Martin and Miao, 1995).

China will play a seminal role in our understanding of the origin and dispersal of the modern avifauna, lying as it does, along one of the main dispersal routes between North America and Eurasia. Some pioneering work has been done in this area by Lianhai Hou. In fact, Hou is the father of palaeornithological studies in China and published briefly on the early Cenozoic Chinese avifauna including a new genus of giant ground bird within the Gastornithiformes, and several water-marginal species (Hou, 2003). The relationships of these forms to the species found in Europe and North America requires further investigation (Mayr, 2009). One Paleocene taxon, *Qinornis* (Xu, 1995), seems to be especially distant from modern forms (Mayr, 2009). Most of China's and Central Asia's rich fauna of Paleogene birds remains to be described and we must extrapolate from the better known European and America avifaunas.

Towards the end of the Cretaceous and into the early Paleogene, global temperatures were falling and vegetation communities were developing a more "open" structure. The end Cretaceous avifauna experienced the same sort of reorganization as did the other components of the vertebrate fauna suggesting similar ecological factors. The upland avifauna of enantiornithines, oviraptorsaurs and dromaeosaurs became totally extinct as did the archaic ichthyornithiform and hesperornithiform birds in the marine realm. The freshwater shorebird ecotypes passed through the extinction event with relatively little disturbance as did many of the amphibians, reptiles and mammals that occurred with them in this ecology. So much so that it is often difficult to distinguish the Lower Paleocene faunas from those of the latest Cretaceous on the basis of these organisms.

The Late Paleocene through Early Eocene was a time of increasing global temperatures culminating in the Paleocene/Eocene thermal maximum, a time of world wide tropical forest, even at high latitudes (Martin, 1994). The Green River lakes in Wyoming preserve the fossil leaves of palm trees, and north of Greenland, Elsemere Island supported a paratropical flora and fauna.

2 Avifauna of the Green River and Messel

The area surrounding both the Green River lakes and Messel in Germany included many tropical trees that formed a canopy with a thick layer of leaf litter on the forest floor. This provided a rich environment for Eocene invertebrates. Many modern forest vertebrates have long tactile snouts designed to probe among the fallen leaves. This way of life is reflected in the long flexible snouts found in early Cenozoic mammals and in the preserved bills of the Lower Eocene lithornithid bird, *Paracathartes* whose postcranial skeleton resembles a modern forest bird, the kiwi (Houde, 1988). *Paracathartes* is related to tinamou-like birds *Pseudocrypterus*, and *Lithornis*, thought by Houde (1986, 1988) to be close to the base of the modern ratite radiation. The latter two genera probably inhabited the more open areas at the forest margin. The lithornithids combine a palaeognathous palate with a carinate sternum (Houde, 1986, 1988) supporting the notion that ratites are derived from flighted birds who lost that capability independently (Houde and Olson, 1981). A large flightless genus, *Remiornis*, from the French Late Paleocene was postulated by Martin (1992) as the oldest ratite. Martin (1983) pointed out that after the extinction at the end of the Cretaceous, mammals were small and often arboreal, and the risks correlated with ground nesting would have been less compared to later continental faunas. Many of the birds at this time resembled the large bodied island birds that develop where there are few terrestrial predators. As a result, the early Tertiary avifauna contained an unusual diversity of forms with no or limited flight capabilities and large size.

In the tropics the forest edge is often determined by proximity to water, and there may be a region of scrubby vegetation between the canopy forests and the lakes. One probable occupant of this region in the Late Eocene was an archaic gruiiform, *Neocathartes* originally described as the oldest vulture (Wetmore, 1944). More recently it was shown to be a member of an extinct group, Bathornithidae and is considered by some (Olson, 1985) as being congeneric with *Bathornis*. The Bathornithidae are possibly related to giant raptorial flightless birds (Phorusrachidae) in the Tertiary of South America and the modern Cariamidae. Their presence along with the presbyornithids contributes a possible Southern Hemisphere component. *Neocathartes*, with its hooked beak, was probably a predator on small vertebrates that it pursued through understory vegetation using its long legs like the modern secretary bird that hunts in South American grasslands. Grasslands began to develop in the Late Eocene at about the same time as the appearance of *Bathornis* and the spread of grasses had a profound effect on community structure.

The Green River lakes included vast areas of shallow water that abounded with wading birds including many that resemble modern cranes and their relatives (Gruiformes). However, it is not clear that many are actually members of that order. One genus shared between North America and Europe, *Messelornis*, was flightless and thought to be distantly related to the sunbitterns. It belongs to an extinct family, the Messelornithidae. True cranes (Gruidae) are not clearly present.

The Green River deposits have produced the oldest well-preserved remains of waterfowl (Anseriiformes). These all belong to an extinct family of long-legged waders, the Presbyornithidae (Feduccia, 1977, 1978). In the same deposits we find an extremely long-legged protoflamingo, *Juncitarsus* (Olson and Feduccia, 1980a, b) and that genus is also known from Messel in Germany. Presbyornithids are claimed to extend back into the Late Cretaceous but their isolated postcranial remains have previously been confused with shorebirds (Charadriiformes) and flamingos. The fragmentary Cretaceous material may not be certain for either age or taxonomic relationship.

One of the most distinctive features of the Late Paleocene–Early Eocene avifauna is a radiation of giant ground birds, Gastornithiformes. These were first recognized in Europe and are known from England, Germany and France (Martin, 1992) as well as China (Hou, 1980). North American material has usually been assigned to a separate genus, *Diatryma* (Cope, 1876). The European genus, *Gastornis*, was described largely from a composite skeleton (Lemoine, 1881) that seemed to differ greatly from the Matthew and Granger (1917) reconstruction of the skeleton of *Diatryma*. In fact these two genera were commonly placed in separate orders (Gastornithiformes and Diatrymaformes) until Martin (1992) showed that Lemoine's reconstruction was a chimera combining elements from fish, turtles and crocodilians as well as actual *Gastornis* remains. When the nonavian parts were removed, the remainder was remarkably like *Diatryma*; however, the tarsometatarsi differed enough that Martin (1992) maintained both genera. Buffetaut (1997) later included both in *Gastornis*. Andors (1991, 1992) in his revision of *Diatryma* placed Gastornithiformes close to Anseriformes (waterfowl) and suggested that they were gigantic avian herbivores. This contrasted with earlier accounts describing them as predators. Part of Andors' argument was the absence of a raptorial tearing beak in *Diatryma*, however, the anterior margin of the bill is often damaged in fossil birds and some bill specimens of gastornithids seem to show an anterior tearing process. The bill of a juvenile *Diatryma* described under the name *Omoramphus* seems to show such a hook. Even if no hook were present, *Diatryma* is so large compared to the contemporary mammals that it could easily have swallowed them whole. Witmer and Rose (1991) also concluded that *Diatryma* was predaceous based on the remarkable bite force indicated by its jaw morphology.

The presence of *Gastornis* in Europe, Elsemere Island and North America is strong support for some sort of terrestrial continuity of Late Paleocene–Early Eocene communities across the northeast. This is especially significant because such a large groundbird was unlikely to have overwintered in the darkness of the high Arctic and must have been able to make seasonal migrations to more southern latitudes.

During the Mesozoic, the small birds that flitted from tree to tree were archaic enantiornithine birds with no real affiliation to specific modern taxa. In the modern fauna most small birds belong to the largest avian order, Passeriformes. Passeriformes are not presently known before the Oligocene and very different birds occupied this niche in the Paleogene. The relationships of these birds sparked a remarkable chain of taxonomic confusion that is still not completely resolved, but it largely began when Brodkorb (1970a) described a right wing skeleton from the Lower Eocene of Wyoming as a kind of primitive woodpecker (puffbird, Bucconidae), *Primobucco mcgrewi*. Feduccia (1976) described a partial skeleton from the Green River Formation of Wyoming as *Primobucco kestneri*. He also redescribed *Neanis schucherti* (also from the Green River) and suggested that it was close to *Primobucco*. Schufeldt (1913) had described *Neanis* as a rhinocryptid passeriform and it was considered the oldest fossil of that order. Brodkorb (1970a) also referred *Uintornis lucaris* (Marsh, 1872) to the Bucconidae. Schufeldt (1915) rejected Marsh's assignment, as did Cracraft and Morony (1969), who thought that it was a cuculiform. Brodkorb (1970b) changed to their interpretation. Feduccia and Martin (1976) described a new bird skeleton from the Green River Formation as *Primobucco olsoni*. They thought that this bird was very similar to bucconids and *Uintornis*. In this sense they were going very nearly back to Brodkorb (1970a). They also included *Botauroides parvus* as a relative, although Schufeldt (1915) had described it as a tiny heron. In the same paper Feduccia and Martin (1976) described a new genus *Eobucco brodkorbi* and a new species of *Uintornis*, *U.*

marionae. Feduccia and Martin (1976) thought that these small "perching" birds probably had more affinity to each other than any did with a modern family and created an extinct family, Primobucconidae, thought by them to be primitive Piciformes. They did not have permission to do further preparation on the holotype of *Primobucco olsoni*, and this was done later by Houde and Olson (1989) who concurred that *Primobucco olsoni* was probably affiliated with bucconids, but not congeneric with *Primobucco* which they considered a "roller" (Coraciiformes). This would not be too far from Feduccia and Martin (1976) as some authors treated the primitive piciiforms (Galbulidae and Bucconidae) as a coraciiform suborder, the Galbulae. Feduccia and Martin (1976) also thought that the fossil material was significantly different from the modern Bucconidae (hence the extinct family Primobucconidae). More recently, Ksepka and Clarke (2010) have agreed with the Houde and Olson (1989) conclusion that *Primobucco* was probably a "stem roller".

Houde and Olson (1992) assigned *Eobucco* to a new order Sandcoleiformes based on abundant remains of Early Eocene genera that they named *Sandcoleus* and *Anneavis*. They also included *Uintornis* and *Botauroides*, two genera from the original Primobucconidae. So their new order was composed mostly of the Primobucconidae minus the genotypic species *Primobucco* and "*Primobucco*" *olsoni* (considered by them to be a bucconid). They regarded the Sandcoleiformes as the sister group of the Coliiformes, an extent monotypic order presently confined to Africa. Mayr (2009) presently places the Sandcoleiformes within the Coliiformes as a family, the Sandcoleidae. He included in that family the European genus, *Eoglaucidium* from the Lower Eocene of Geiseltal in Germany that Fischer (1987) had described as an owl. Mayr (2009) also compared "*Primobucco olsoni*" with the European genus *Pseudasturides* whose ordinal affiliations were considered uncertain, although Mayr (2002, 2009) relates it to parrots. The holotype of *Primobucco mcgrewi* has not been re-described, nor has the new preparation of *Primobucco olsoni*. I am uncertain where this leaves us. It does seem clear that "*Primobucco*" *olsoni* should not be included in that genus and I propose the name *Cyrilavis* for that species.

Cyrilavis gen. nov.

Genotypic species *Cyrilavis olsoni*.

Diagnosis As for the species (Feduccia and Martin, 1976).

Etymology Named for Cyril Walker in honor of his many contributions to the study of early Cenozoic birds.

Primoscens minutus (Harrison and Walker, 1977) was assigned by Fedducia and Olson to the Primobucconidae, but Mayr (2009) claims a closer relationship to Passeriformes. As more discoveries are made, it becomes clear that a variety of Eocene birds similar to coracciiforms and occupying the Eocene small perching bird niche in Europe and North America have continued to emerge. This ecospace is presently inhabited by the most abundant and speciose modern birds, the Passeriformes. Passeriforms have no Northern Hemisphere record before the Oligocene and most think that their roots are in the Southern Hemisphere. It is uncertain how phylogenetically close any of these birds are to modern coracciforms. The presence of a metacarpal process in the Sandcoleiiformes is shared by ground-rollers and many of these birds may have their origins entangled in a radiation of roller-like birds. I can agree with Houde and Olson (1992) that the Sandcoleiformes are a unique group of primitive birds without close affiliation with any modern order and doubt that their relationship to the colliformes is as close as Mayr (2009) suggested. They are probably part of an early radiation of land birds most of whom belong to lineages that are now extinct but some produced the Coracciidae and Piciformes, and many other groups of arboreal birds. This would parallel the Condylartha in mammalian paleontology as a paraphyletic grouping containing progenitors of modern orders as well as groups that are totally extinct. It is not accidental that condylarths were contemporary with the "primobucconids" and have suffered a similar taxonomic fate as our knowledge of the Eocene faunas has improved.

3 Migration and dispersal

The todies (Todidae) are presently wholly North American but the extinct genus *Palaeotodus* is known from the Late Eocene of North America and Europe, so we have another example besides the Colliiformes of small arboreal birds that were much more widely distributed across the Holarctic in the Paleogene than are their surviving relatives. The question remains of when and how did these birds disperse? The modern migrational pattern with birds flying to higher latitudes during the summer is due in part to the advantages of a predator poor ecology with nearly twenty four hours of daylight and terrific seasonal productivity. A warm Arctic that was extensively forested must have attracted a diverse assemblage of migrants, few of which could have overwintered during the polar night. *Gastornis* on Elsemere Island poses a special problem as its presence seems to demand a land connection that permitted seasonal migration southwards far enough to overwinter. Migratory patterns meant to exploit the high productivity of warm polar latitudes including a warm phytoplankton rich polar sea present an unusual opportunity for future investigations into the Paleogene avifauna.

Even with a warm Arctic the polar night must have acted as a filter preventing the range extensive of forms that had no way of dealing with it. This may have set a limit on the dispersal routes utilized by some organisms that could only pass when a relatively more southern route was available. Migratory birds might have had an advantage in dispersal if a north-south migratory pattern happened to shift part of its southern destination from one continent to another.

Another consideration is the global climatic trend. While dispersal may result from the overall effects of chance and changing land connections, the trend of global temperatures may be an over-riding factor. Much of what we see as dispersal is actually the expansion of certain habitats into new regions due to climatic change, and may result in the appearance of a new community structure rather than just a few new taxa. This more radical change was often accompanied or preceded by the extinction or expatriation of formally important members of the local community (Martin and Meehan, 2005). If the climatic trend was towards cooling as in the Early Paleocene and most of the rest of the Cenozoic, the new communities will have come from the North in the Northern Hemisphere and northern land connections will seem to be favored. During periods of warming like the Late Paleocene–Early Eocene, they should come from the south. The avifauna of the Green River Eocene does show affiliations with South America (Olson, 1977, 1987) and that of Messel with Africa (Peters, 1991; Storch, 1993).

4 Conclusions

While the record of Cenozoic birds remains inferior to that of mammals it is clearly improving and is already important enough to be considered when we try to understand the origin and spread of Cenozoic communities. As with the mammals, climatic change appears to have been an important controlling factor in both evolutionary radiation and species dispersal. Rather than just a continental version of the "waif dispersal" that governs much of the colonization of islands, I suggest that climatic change towards either warmth or cold governs the extension or contraction of "biomes" either northwards or southwards and individual endemics to these environmental regimes thereby make "first appearances" in regions where they were previously absent. Unlike the accidental dispersal of individual species in island biogeography, community structure and composition accompanies these "first appearances". In this model, the origins of new lineages are expected to occur either north or south of the earliest points of discovery. Unlike its astounding contributions to Mesozoic birds, China has yet to reach its potential contribution to our understanding of the Paleogene world avifauna. This is especially unfortunate because of its position on the route between Asia to North America. I am confident that this record does exist and in the future China will be a major source of new information in this rapidly changing area of research.

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