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FOSSIL PASSERINES FROM THE EARLY PLIOCENE OF KANSAS AND THE EVOLUTION OF SONGBIRDS IN NORTH AMERICA

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Abstract.—Seven living species of passerines are identified or tentatively identified from the early Pliocene Fox Canyon locality (4.3–4.8 mya), Rexroad Formation, Meade Basin, southwestern Kansas. All seven species occur in Kansas today, primarily as winter residents or transients, and their migratory behavior may extend to the early Pliocene as well. A review of all known passerines from the Neogene of North America indicates that many modern taxa began to appear in the early Pliocene, much earlier than previously believed. This fossil evidence agrees with some mitochondrial DNA analyses for the estimated age of divergence for living species of longspurs (*Calcarius lapponicus* and *C. mccownii*), but similar estimates for the divergence of *C. ornatus* using cytochrome-*b* analyses is at least 3 my younger than indicated by the fossil evidence. The fossil songbirds, as well as other vertebrate taxa from the Meade Basin, also indicate a paleoenvironment of short-grass prairie and shrubland with wetlands and ponds nearby, similar to that found in the area today. This prairie–steppe habitat first appeared in the Meade Basin by the early Pliocene and remained relatively stable until the Pleistocene, when it periodically appeared and disappeared with climate change. High seasonal productivity associated with this habitat in the early Pliocene may have promoted migratory behavior and speciation events in songbirds during a period of relative climatic stasis. *Received 2 January 2005, accepted 5 January 2006.*

Key words: *Calcarius*, early Pliocene, fossil Passeriformes, migration, molecular clocks, songbird evolution.

Paserinos Fósiles del Plioceno Temprano de Kansas y la Evolución de las Aves Canoras en Norte América

Resumen.—Siete especies de aves paserinas que existen en la actualidad han sido identificadas o identificadas tentativamente en la Formación Rexroad del Plioceno temprano (4.3–4.8 ma) en la localidad Fox Canyon, Meade Basin, suroeste de Kansas. Las siete especies se encuentran en Kansas en la actualidad, principalmente como residentes de invierno o transeúntes, y su comportamiento migratorio podría extenderse también al Plioceno temprano. Una revisión de todos los paserinos del Neogeno de Norte América indica que muchos taxa modernos empezaron a aparecer en el Plioceno temprano, mucho antes de lo que se creía anteriormente. Esta evidencia fósil concuerda con algunos análisis de ADN mitocondrial en cuanto a la edad estimada de la divergencia entre las especies vivientes *Calcarius lapponicus* y *C. mccownii*, pero estimados similares de la divergencia de *C. ornatus* obtenidos mediante análisis del citocromo *b* son al menos tres millones de años más recientes que lo que indica el registro fósil. Las aves canoras fósiles, además de otros taxa de vertebrados del Meade Basin, también indican la existencia de un paleoambiente de praderas de pastos cortos y matorrales con humedales y estanques, similar al ambiente que se encuentra en el

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área actualmente. Este hábitat de praderas y estepas apareció por primera vez en el Meade Basin en el Plioceno temprano y permaneció relativamente estable hasta el Pleistoceno, cuando apareció y desapareció periódicamente con los cambios climáticos. La alta productividad estacional asociada con este hábitat en el Pleistoceno temprano podría haber promovido el comportamiento migratorio y eventos de especiación en las aves canoras, durante un período con clima relativamente estático.

Fossil passerines are known from numerous localities in North America, ranging in age from the early Miocene to late Pleistocene (Brodkorb 1978). Most often, these fossils are fragmentary postcranial remains that are difficult to identify beyond family or genus. As a result, songbirds are underrepresented in the fossil record, though their remains can be abundant at some localities.

In the summers of 1947, 1950, and 1951, Hibbard (1952) recovered thousands of bones of small mammals, birds, and reptiles from Pliocene deposits at Fox Canyon, Rexroad Formation, Meade County, Kansas. Although Hibbard and others considered the Rexroad Formation to be late Pliocene in age, a recent review of the rodent fauna, along with a reanalysis of the geology and paleontology of fossil sites in the Meade Basin, now places the age of the Fox Canyon local fauna as early Pliocene (early Blancan; 4.3–4.8 mya; Martin et al. 2000).

In 1995, I examined fossil birds from the Meade Basin housed at the University of Michigan Museum of Paleontology (UM). At that time, a collection of uncatalogued bird remains from Fox Canyon was found in a small box labeled with the number 28103, the locality name, location, and date of collection as 1951 by Hibbard. This box contained dozens of passerine and other bird bills and mandibles, elements that are more easily and reliably identified to species than postcranial remains. Undoubtedly, recovery of these remains required hundreds of hours of screen washing and sorting during Hibbard's field seasons. Here, more than 50 years since these fossils were recovered, I present the identification of most of these remains and review the fossil record and evolution of songbirds in North America.

Methods

All fossil specimens were identified using the collections of Recent skeletal material at the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. Terminology follows that of Howard (1929). Measurements of bill length (BL) were taken from the distal edge of the nares to the tip of the beak; bill width (BW) was taken at the widest point of the maxilla, usually at mid- to distal nares. All measurements were completed with digital calipers to the nearest 0.01 mm. Morphological features of the premaxillae and mandibles used to identify fossil taxa in comparison with living species include the relative size and shape of the external openings of the nares, shape and angle of the nasal bar, position and alignment of foramina, angle of the dorsal surface of the premaxilla with the tomia and nasal bar, position and depth of ventral grooves on the premaxilla, and angle and shape of the distal symphysis of the mandible in cross-section. Similarity of these features, as well as quantitative comparisons, allowed confident identifications of the fossil material. All fossils are housed at the University of Michigan and catalogued with UM numbers.

Systematic Paleontology

Order Passeriformes

Family Mimidae

Mimus polyglottus (Linnaeus 1758)

Referred material.—Premaxilla, UM 52094.

Description.—This specimen compares well in size and features with the living species (Fig. 1A).

Remarks.—The Northern Mockingbird is a common summer resident throughout Kansas, and perhaps year-round in eastern Kansas (Thompson and Ely 1992). It is found in Meade County from March to October (Flowers 1995).

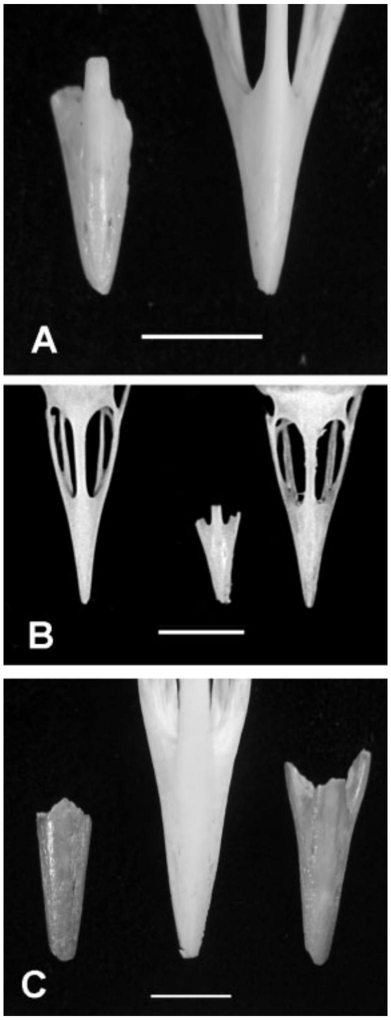

Fig. 1. (A) Dorsal view of the bill of *Mimus polyglottus* (USNM 611204; right) compared with the fossil from Fox Canyon (UM 52094; left) referred to this species. (B) Dorsal view of the bill of male *Anthus spragueii* (USNM 344535; right) and *A. rubescens* (USNM 611029; left) compared with the fossil from Fox Canyon (UM 52145; middle) referred to *Anthus* cf. *A. spragueii*. (C) Dorsal view of the bill of *Sturnella neglecta* (USNM 611525; middle) compared with the fossils from Fox Canyon (UM 52089, left; UM 52088, right) referred to *Sturnella* cf. *S. neglecta*. Scale bar = 5 mm in all photos.

Family Motacillidae

Anthus cf. *A. spragueii* (Audubon 1844)

Referred material.—Fourteen premaxillae, UM 52144–52157; distal mandibular symphysis, UM 52158.

Description.—These specimens were compared with *Anthus rubescens*, *A. lutescens*, *A. cervinus*, *A. furcatus*, *A. correndera*, and *A. spragueii*. *Anthus rubescens* has a relatively long, narrow bill that distinguishes it from the other taxa (Table 1 and Fig. 1B), whereas *A. spragueii* is more robust with some overlap in width, but not in length, with *A. rubescens*. *Anthus lutescens* is more robust than *A. spragueii*, but overlaps in length and width with that species (Table 1). These measurements include both the Panamanian ($n = 4$) and Argentine–Brazilian ($n = 4$) subspecies of *A. lutescens*, which differ slightly in size. *Anthus cervinus* has a relatively flatter bill in lateral view, with a bill length similar to *A. spragueii*, but slightly narrower bill width (Table 1). Only one specimen of *A. furcatus* and one of *A. correndera* were available for comparison. The former species, however, has a shorter but broader bill, whereas the latter has a longer and broader bill compared with the fossil material. With the exception of *A. furcatus*, the fossils appear to be shorter than all five living taxa examined here, only one modern specimen of *A. spragueii* (USNM 290117) being close in size. The fossils are also slightly narrower than all three living species, but are tentatively referred to *A. spragueii* on the basis of closer similarities to that species (Fig. 1B).

Remarks.—Sprague's Pipit is an uncommon transient in spring and fall, or a casual resident, in central and eastern Kansas, but has not been reported from the Meade Basin; it prefers short-grass prairie and does not associate with the American Pipit, which occurs primarily in moist areas or along shorelines (Thompson and Ely 1992). The fossils from Fox Canyon indicate a range extension for this species to the southwest portion of the state.

Family Emberizidae

Zonotrichia sp.

Referred material.—Premaxilla, UM 52142.

Description.—This specimen is shorter and more robust than *Zonotrichia leucophrys* and *Z.*

Table 1. Bill length (BL) and bill width (BW) (in mm) of Recent and fossil pipits (*Anthus* spp.). For Recent taxa, mean ± standard deviation (SD) is provided in the first row with range in the second row. Measurements of fossil specimens referred to *Anthus* cf. *A. spragueii* (listed by UM catalogue numbers) are also provided.

Species	BL	BW
A. spragueii (*n* = 7)	6.39 ± 0.42	3.07 ± 0.13
	5.7–6.94	2.81–3.19
UM 52144	5.79	
UM 52146	5.46	2.46
UM 52147		2.21
UM 52150		2.42
UM 52156	5.1	2.35
UM 52157	5.65	
A. lutescens (*n* = 8)	6.24 ± 0.29	2.84 ± 0.13
	5.99–6.67	2.64–3.07
A. rubescens (*n* = 9)	6.53 ± 0.20	2.76 ± 0.14
	6.35–6.97	2.59–3.03
A. cervinus (*n* = 8)	6.38 ± 0.14	2.79 ± 0.15
	6.14–6.55	2.49–2.94
A. furcatus (*n* = 1)	5.55	2.86
A. correndera (*n* = 1)	6.68	3.08

albicollis, and larger and more robust than *Z. capensis*. It is close to *Z. albicollis* and *Z. querula*, but the fossil is slightly shorter and broader than in these two species. *Melospiza melodia*, once considered congeneric with *Zonotrichia* (American Ornithologists' Union [AOU] 1998), has a distinctly longer bill. The fossil may represent an undescribed species of *Zonotrichia* but is too fragmentary for sufficient diagnosis, and additional specimens are needed.

Junco hyemalis (Linnaeus 1758)

Referred material.—Premaxilla, UM 52090.

Description.—This specimen compares well in size and features with the living species.

Remarks.—The Dark-eyed Junco is a common winter resident throughout Kansas and the Meade Basin (Thompson and Ely 1992, Flowers 1995). One fossil of this species has been reported from the middle to late Pleistocene of Colorado (Emslie 2004); it also is known from the late Pliocene (early Irvingtonian) through late Pleistocene (Rancholabrean) of Florida (Emslie 1998).

Calcarius mccownii (Lawrence 1851)

Referred material.—Premaxilla, UM 52143.

Calcarius lapponicus (Linnaeus 1758)

Referred material.—Eight premaxillae, UM 52095–52102.

Calcarius ornatus (Townsend 1837)

Referred material.—Thirty-nine premaxillae, UM 52103–52141.

Description.—Specimens of the three longspur species referred to above were compared with modern skeletons of these species and one other, Smith's Longspur (*Calcarius pictus*). All four species can be distinguished by relative size and shape of the premaxilla (Fig. 2A). The largest and most robust bill occurs in McCown's Longspur (*C. mccownii*), which overlaps in length only with Chestnut-collared Longspur (*C. ornatus*; Table 2). The premaxilla of *C. mccownii* is broader and more robust, with a larger nasal bar, than in *C. pictus*, Lapland Longspur (*C. lapponicus*), and *C. ornatus*, and this distinct species was once classified in the monotypic genus *Rhynchophanes* (AOU 1998). Of the other species, *C. ornatus* is the smallest, with a relatively shorter beak with a broad base that does not overlap in size with *C. mccownii* or *C. pictus*, and only slightly overlaps in length with this last species and *C. lapponicus* (Table 2 and Fig. 2B). *Calcarius lapponicus* also has a relatively long bill that overlaps in length with *C. mccownii* but is more slender, with no overlap with *C. mccownii* and *C. pictus* (Table 2 and Fig. 2C).

Remarks.—Of the four longspur species that occur in North America, only the Lapland Longspur is common-to-abundant in winter throughout Kansas, whereas the Chestnut-collared Longspur is an uncommon transient and winter resident in central and western Kansas, including the Meade Basin. Smith's and McCown's longspurs are uncommon transients and rare winter residents, with the former occurring more in eastern Kansas and the latter in the western half of the state (Thompson and Ely 1992, Flowers 1995). Although the Chestnut-collared Longspur once bred in prairies near Hays, Kansas (Flowers [1995] citing

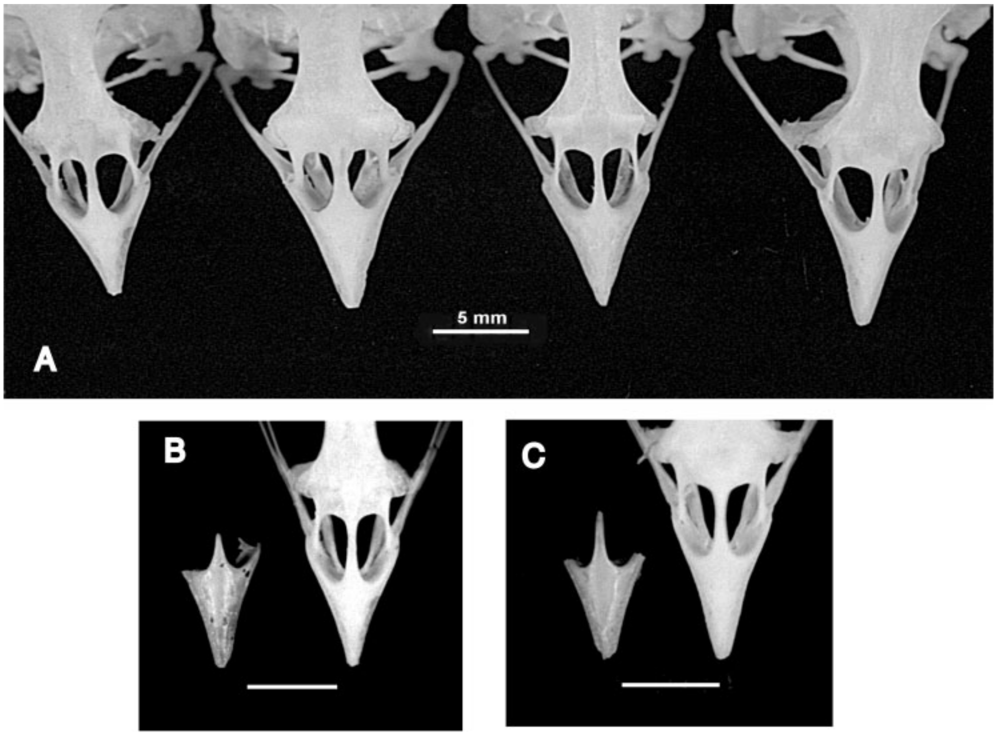

Fig. 2. (A) Dorsal view of the bill of male longspurs; from left to right, *Calcarius ornatus* (USNM 499786), *C. mccownii* (USNM 320800), *C. pictus* (USNM 489748), and *C. lapponicus* (USNM 611498). Note the differences in relative length, width, and shape of nares and nasal bar in each. (B) The fossil from Fox Canyon (UM 52131, left) referred to *C. ornatus* compared with USNM 499786. (C) The fossil from Fox Canyon (UM 52095, left) referred to *C. lapponicus* compared with USNM 611498). Scale bar = 5 mm in all photos.

Allen [1872]), and the McCown's Longspur also breeds in the Great Plains, the Lapland Longspur migrates to tundra habitat in Alaska and Canada in summer. Fossils of *C. lapponicus* and *C. ornatus* also have been reported from the early Pleistocene (~1.6 mya) of Colorado (Emslie 2004).

Family Icteridae

Sturnella cf. *S. neglecta* Audubon 1844

Referred material.—Premaxilla, UM 52088; distal premaxilla, UM 52089.

Description.—These specimens were compared with premaxillae of *Sturnella neglecta*, *S. magna,* and *S. militaris*. *Sturnella magna* is distinctly larger and more robust, with a broader bill and a relatively more robust nasal bar than *S. neglecta* or *S. militaris*. The fossil specimens compare well in characters to *S. neglecta*, except that UM 52088 is slightly smaller and shorter (Table 3 and Fig. 1C). Specimen UM 52089 is very similar in size and characters to *S. neglecta* but is too fragmentary for measurements. *Sturnella militaris* is smaller than *S. neglecta* but differs in having a shorter and more curved bill in lateral profile and a deeper trough on the ventral surface (bill flat and trough shallow in *S. neglecta, S. magna*, and the fossil material). Indeed, the strong differences in the skull and bill of *S. militaris* compared with *S. magna* and *S. neglecta* suggest that it may belong in a different genus, as has been proposed previously (AOU 1998).

Remarks.—The fossil material is tentatively referred to *S. neglecta* and may represent a small temporal form of this species. Additional fossil material is needed to determine its exact systematic status.

Table 2. Bill length (BL) and bill width (BW) (in mm) of Recent and fossil longspurs (*Calcarius* spp.) (see Table 1 for explanation).

Species	BL	BW
C. pictus (*n* = 6)	5.39 ± 0.31	5.79 ± 0.18
	5.18–5.99	5.53–6.08
C. lapponicus (*n* = 20)	5.57 ± 0.36	5.03 ± 0.18
	4.93–6.19	4.69–5.36
UM 52095	5.44	4.35
UM 52099	5.44	
UM 52100	5.48	
UM 52101	5.04	
C. mccownii (*n* = 6)	6.33 ± 0.37	6.06 ± 0.19
	5.88–7.00	5.83–6.33
UM 52143	5.31	
C. ornatus (*n* = 11)	5.02 ± 0.40	5.04 ± 0.27
	4.21–5.46	4.52–5.44
UM 52103	5.39	
UM 52129	5.28	
UM 52130	4.95	
UM 52131	5.6	
UM 52132	4.79	
UM 52133	5.24	
UM 52134	4.44	
UM 52135	4.46	
UM 52136	4.91	
UM 52137	5.82	
UM 52138	5.38	
UM 52139	5.34	
UM 52140	4.83	
UM 52141	5.18	4.82

Table 3. Bill length (BL) and bill width (BW) (in mm) of Recent and fossil meadowlarks (*Sturnella* spp.) (see Table 1 for explanation).

Species	BL	BW
S. neglecta (*n* = 11)	14.85 ± 1.31	7.32 ± 0.57
	13.46–17.53	6.35–8.13
S. magna (*n* = 8)	15.84 ± 1.32	7.81 ± 0.42
	13.72–17.27	6.86–8.13
UM 52088	10.16	5.59

Discussion

All specimens reported here represent the earliest fossil record for each taxon. In addition, the seven identified species (excluding *Zonotrichia* sp., but including the tentative identifications of *A. spragueii* and *S. neglecta*) currently occur in Kansas, either as summer or winter residents or as transients during migration and, with other vertebrate taxa from Fox Canyon (Becker 1987), reflect a paleoenvironment of short-grass prairie–shrubland with wetlands and ponds nearby. Thus, a prairie–steppe community appears to have persisted in this region of the Great Plains since the early Pliocene. A near-continuous, 4.2-my record of rodent and other vertebrate remains from Fox Canyon and 11 other localities in the Meade Basin, however, indicate that episodes of faunal turnover have occurred, with at least two immigration events in the early Pliocene (Martin and Fairbanks 1999). In addition, pollen evidence indicates that spruce and pine forests invaded the region of southwestern Kansas, northeastern Oklahoma, and southeastern Colorado during glacial intervals in the Pleistocene (Martin and Fairbanks 1999). Drier grasslands and steppe habitat seem to periodically dominate during interglacials since the early Pliocene. What is striking about this record, though, is that living species of longspurs and other passerines had already evolved by the early Pliocene and, moreover, during a long period of climatic stasis. At least 12 other taxa of birds have been reported or described from Fox Canyon, most of which are extinct species, including one other passerine, the extinct swallow *Hirundo aprica* (Feduccia 1967). However, tentative identifications of one modern owl (*Otus* cf. *O. asio*; Ford 1966) and a flicker (*Colaptes* sp.) described as probably representing the living *C. auratus* (Feduccia 1987) are also known from this locality.

For many years, avian paleontologists and ornithologists believed that most living species of birds did not arise until the late Pleistocene, by the close of the Ice Ages (see review in Klicka and Zink 1997). Brodkorb (1966) was one of the first to suggest that this evolution took place much earlier, or by the early Pleistocene, though he rejected a Pliocene origin. Since the early 1980s, however, fossil evidence has been building to support a much earlier origin for many songbirds, as well as for species in other avian orders. Conversely, Klicka and Zink (1997) refer to the late Pleistocene origin of living birds as an "entrenched paradigm" within ornithology and falsify this paradigm using mitochondrial DNA and sequence divergence for many avian lineages. However, it is unclear why they believed that this was necessary; I doubt that any avian paleontologist today believes that living songbird species did not originate until the late Pleistocene. As the basis for this "entrenched paradigm," Klicka and Zink (1997) primarily cite literature on fossil birds published no later than 1971, or they refer to textbooks that also cite only older papers.

Although a late Pliocene origin for modern birds, especially songbirds, has been more readily accepted in recent decades, data presented here indicate that the age is even older, extending to the early Pliocene, at least for pipits, longspurs, and meadowlarks. Limited molecular analyses of various species and groups of songbirds also tend to indicate an early divergence of living species. For example, Lovette and Bermingham (1999) provide molecular evidence for a late Miocene–early Pliocene origin for 24 species of North American *Dendroica* warblers. They hypothesize that these species underwent an explosive radiation, first at 4.5–7.0 mya and again at 2.3–3.5 mya. In addition, Klicka and Zink (1997) used mitochondrial DNA divergence and the molecular clock to show that longspurs (*C. lapponicus*, *C. ornatus*, and *C. mccownii*) diverged between 4.35 and 4.60 mya, a conclusion that agrees well with the fossil evidence presented here. Further, Klicka et al. (2003) used cytochrome-*b* analysis to date the origin of the *Calcarius* lineage to 4.4–6.2 mya, but placed the divergence of *C. ornatus* and *C. pictus* at only 1.5 to 2.0 mya, with *C. lapponicus* as the older lineage. This estimate is >3 my too young for *C. ornatus* unless only *C. pictus* diverged by 1.5 mya, but Klicka et al. (2003:172) concluded that both these sister species are "of relatively recent origin…near the onset of the Pleistocene" on the basis of sequence divergence data.

Avise and Walker (1998) reviewed molecular evidence for 63 avian species to argue that most exhibit sequence divergence dates within the Pleistocene, contrary to the findings of Klicka and Zink (1997; see also Klicka and Zink [1999] for a rebuttal). However, at least two species reviewed by Avise and Walker (1998), *Ammodramus maritimus* and *Branta canadensis*, have a fossil record that indicates that their divergence estimates are >1 my too young (Emslie 1998). Recently, Johnson and Cicero (2004) provided new molecular-clock estimates for 39 pairs of sister species, including 12 pairs previously analyzed by Klicka and Zink (1997) and seven non-passerine pairs, to again argue that most speciation events occurred during the Pleistocene. While still referring to a Pleistocene divergence for *C. ornatus–C. pictus* at 1.45 mya, they also estimate divergences for *Anas discors–A. cyanoptera*, *Rallus longirostris–R. elegans*, *Centrocercus urophasianus–C. minimus*, *Zenaida macrouri–Z. graysoni*, and *Zonotrichia leucophrys–Z. atricapilla* that range from 0.5 to 2.2 mya too young for one or both of the sister species in each of these pairs, on the basis of fossil evidence (see Emslie 1992, 1998, 2004).

Other songbird fossils that have been reported from North America (Table 4) include a collection of unidentified postcranial bones from the early Miocene (early Hemingfordian) of Thomas Farm, Florida (Olson 1985). Becker (1987) lists one bone identified as a warbler (Parulidae) from this largely unstudied collection. The Thomas Farm fossils, however, represent the oldest known record of songbirds in North America (Olson 1985, Hulbert 2001). If songbirds originated in the Southern Hemisphere, as proposed by Feduccia and Olson (1982), Feduccia (1996), and Barker et al. (2004), they did not reach North America until at least the early Miocene, or near the beginning of an "explosive radiation" of the Passeriformes (Feduccia 1995).

Howard (1957) described one species, *Palaeoscinis turdirostris*, from the late Miocene, for which she erected a new family, Palaeoscinidae. Olson (1985:140) believed this family to represent a "generalized oscine" similar to Bombycillidae, Pycnonotidae, and Corvidae, and mentions several other similar fossils from the Calvert Formation, middle Miocene, Maryland. Brodkorb (1972) described an extinct genus and species of jay, *Miocitta galbreathi*, from the late Miocene of Colorado and another, *Protocitta ajax*, from the late Pliocene of Texas and the Meade Basin at Rexroad Ranch. This latter species was the second to be described in this genus; Brodkorb (1957) named *P. dixi* from the late Pleistocene of Florida and Texas. However, Emslie (1998) restudied *P. dixi* and considered it synonymous with *Pica pica*, and *Protocitta ajax* should be re-examined.

Becker (1987) lists several other Neogene localities from which passerines may be represented in the collections, but until now only three have been studied; three others have been added by Emslie (1998) and Olson and Rasmussen (2001). Shufeldt (1913) named an extinct species of emberizid, "*Palaeostruthus*" *hatcheri*, from the late Miocene of Kansas.

Table 4. Fossil passerines identified from the Miocene and Pliocene of North America. Previously described taxa that are no longer considered valid passerines are not included.

Age	Location	Taxon	References
Early Miocene	Thomas Farm, Florida	1 Parulidae; unidentified specimens	Olson 1985, Becker 1987
Late Miocene	California	*Palaeoscinis turdirostris*	Howard 1957, Olson 1985
Late Miocene	Colorado	*Miocitta galbreathi*	Brodkorb 1972
Late Miocene	Kansas	*Ammodramus hatcheri*	Shufeldt 1913, Steadman 1981
Early Pliocene	Florida	Passeriformes, indet.	Brodkorb 1963, Steadman 1981
Early Pliocene	Lee Creek, North Carolina	*Corvus* aff. *ossifragus*	Olson and Rasmussen 2001
Early Pliocene	Yepómera, Mexico	cf. *Passerina* sp.	Steadman and McKitrick 1982
Late Pliocene	Texas; Meade Basin, Kansas	*Protocitta ajax*	Brodkorb 1972
Late Pliocene	Inglis 1A, 1C, Florida	*Aphelocoma coerulescens, Cyanocitta cristata, Corvus ossifragus, Catharus* sp., cf. *Hylocichla mustelina, Turdus* sp. A, *Turdus* sp. B, *Dumetella carolinesis, Toxostoma rufum, Vermivora* cf. *V. celata, Cardinalis cardinalis, Spizella* cf. *S. pusilla*, cf. *Chondestes grammacus, Passerculus sandwichensis, Ammodramus maritimus, Melospiza melodia, Zonotrichia* cf. *Z. albicollis, Zonotrichia* cf. *Z. leucophrys, Agelaius phoeniceus, Sturnella magna, Euphagus cyanocephalus, Molothrus ater*	Emslie 1996, 1998

This specimen was re-examined by Steadman (1981), who considered it indistinguishable from *Ammodramus* and, in fact, very similar to the living *A. savannarum*. However, he maintained the extinct species as *A. hatcheri*. In addition, Steadman (1981) referred another extinct species, *Palaeostruthus eurius*, described by Brodkorb (1963) from the early Pliocene of Florida, to indeterminate Passeriformes.

Another early Pliocene (3.7–4.8 mya) passerine is *Corvus* aff. *ossifragus*, identified from the Lee Creek Mine, Yorktown Formation, North Carolina (Olson and Rasmussen 2001). The only other early Pliocene record of a songbird is two fragmentary humeri identified as bunting (cf. *Passerina* sp.) from the late Miocene–early Pliocene (late Hemphillian) Yepómera local fauna, Mexico (Steadman and McKitrick 1982). This local fauna is now considered to be 4.8–4.9 my old (Martin and Fairbanks 1999).

Fossil passerines have also been identified from two late Pliocene (early Irvingtonian, 1.6–2.0 mya) localities in Florida at Inglis 1A and 1C (Emslie 1998). These sites provide evidence for divergence of many living taxa of songbirds by the late Pliocene, including the endemic Florida Scrub-jay (*Aphelocoma coerulescens*) (Emslie 1996; Table 4). For some of these species, Klicka and Zink (1997) estimated divergence times of 3.15 mya (*Toxostoma rufum*), 3.25 mya (*Agelaius phoeniceus*), and 4.35 mya (*Cardinalis cardinalis*), again agreeing with the fossil evidence.

Another subject to consider with regard to the evolution of living songbirds by the early

Pliocene is the origin and evolution of their migratory behavior. Of the species identified here, most do not breed in Kansas and also may not winter there. Species that breed much farther north include *Anthus spragueii*, *Calcarius lapponicus*, and *Junco hyemalis*. *Mimus polyglottus* and *Sturnella neglecta* breed in Kansas but migrate farther south for the winter. If it is assumed that similar behaviors existed in the past, the fossil record from Fox Canyon represents the oldest evidence for migratory behavior in songbirds in North America. Migratory behavior can evolve independently in bird populations, and can appear and disappear in one population with changing environmental conditions (Berthold 1993, Able 1999). Climate change during the Ice Ages is an obvious mechanism for developing migratory behavior, but for the early Pliocene another explanation is needed. The Miocene was a period of explosive diversification in terrestrial mammals—especially ungulates, but also rodents and other groups—as woodland savanna dominated the interior of the North American continent (Webb 1977, MacFadden 1992). Perhaps the development of extensive prairie and steppe habitat in the Great Plains by the late Miocene, which correlates with the disappearance of many mammalian taxa (e.g., browsing horses and other ungulates; Webb 1977), established seasonal conditions of high primary productivity in this region—which promoted migratory behavior, and perhaps speciation events as well, among songbirds.

In summary, fossil evidence from the Pliocene of Kansas and Florida, as well as isolated remains from other regions, indicate that many living species of songbirds arose in the early-to-late Pliocene. In most cases, these results are supported by the molecular data. Although the accuracy of molecular clocks is often at odds with the fossil evidence and, thus, has been questioned (e.g., Graur and Martin 2004), the relative congruity between these methods for determining phylogenetic events in the Pliocene supports the statement by Moore and DeFillippis (1997) that molecular clocks based on cytochrome *b* are reliable for speciation events within the past 9 my but are much less so for older divergences (see also Ericson and Johansson 2003). However, this conclusion may be undermined if additional discrepancies arise for divergence times of living species as new fossils are discovered.

Although climate change during the Ice Ages has been inferred as a major mechanism causing speciation events in Florida (Emslie 1998) and regions surrounding the Central Plains (Mengel 1970, Hubbard 1973), these glacial–interglacial cycles did not commence until the late Pliocene at ~2.5 mya. Prior to this, the early Pliocene is believed to represent a long period of climatic stasis, but this is when the pipits, longspurs, buntings, and meadowlarks first appear in the fossil record. The relatively rapid and numerous glacial–interglacial cycles of the Ice Ages undoubtedly resulted in additional speciation events (see Hubbard 1973), but other speciation events prior to these glacial cycles now need to be considered in regard to the evolution and diversity of songbirds in North America.

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