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New Birds from the Lower Eocene Green River Formation, North America

ILKA WEIDIG

Forschungsinstitut Senckenberg, Senckenberganlage 25, 60325 Frankfurt, Germany
ilka.weidig@senckenberg.de

ABSTRACT. The Lower Eocene Green River Formation has yielded a large number of hitherto mostly undescribed birds. In this study, I describe a new species and genus as the first representative of Zygodactylidae from the New World. Furthermore, new specimens are referred to *Gallinuloides wyomingensis* (Galliformes), *Messelornis nearctica* (Gruiformes), and *"Neanis" kistneri* (?Galbulae). Based on the new specimens, I reveal additional information on the osteology and the systematic affinities of these species. The new specimens corroborate the fact that there is a strong similarity between the Green River avifauna and that of the roughly contemporaneous avifauna of Messel (Germany). In both sites, Messelornithidae and small arboreal birds are predominant in the fossil record.

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Situated in Wyoming, Utah and Colorado (USA), the Green River Formation was formed in the early Tertiary when the climate was warm-temperate to subtropical (Grande 1980). The Green River Formation contains the largest number of complete or nearly complete articulated bird skeletons from the North American Tertiary (Grande, 1980). However, only few species are described so far, and most of these species are based on a single specimen each. The first fossil bird described from the Green River Formation was the galliform *Gallinuloides wyomingensis* Eastman, 1900. Among the more abundant taxa from the Green River Formation are the Presbyornithidae with *Presbyornis pervetus* Wetmore, 1926, which were described in detail by Feduccia & McGrew (1975) as well as Olson & Feduccia (1980) and Ericson (1997, 1999, 2000). Additional taxa include gruiform, "caprimulgiform" and coraciiform birds (for details see Table 1).

In this paper, a new species referred to Zygodactylidae Brodkorb, 1971, which so far were only known from the Old World, as well as new specimens of three already known Green River species, *Gallinuloides wyomingensis* Eastman, 1900, *Messelornis nearctica* Hesse, 1992, and *Neanis kistneri* (Feduccia, 1973), are described.

Material and methods

Osteological nomenclature follows Baumel & Witmer (1993). The dimensions are in millimetres and they represent the overall length of the bone along its longitudinal axis. The following abbreviations are used to indicate the collections in which the specimens are deposited: BHI Black Hills Institute, Black Hills, South Dakota, USA; FMNH Field Museum of Natural History, Chicago, Illinois, USA; MCZ Museum of comparative Zoology, Cambridge, Massachusetts, USA, NAMAL North American Museum of Ancient Life, Lehi, Utah, USA; SMF Senckenbergmuseum Frankfurt, Germany; SMNK Staatliches Museum fuer Naturkunde Karlsruhe, Germany; USNM National Museum of Natural History, Washington, DC, USA; UWGM University of Wyoming Geological Museum, Laramie, Wyoming, USA; WDC Wyoming Dinosaur Center, Thermopolis, Wyoming, USA.

Table 1. Hitherto described bird taxa from the Green River Formation.

taxon			references
Lithornithiformes	Lithornithidae	*Pseudocrypturus cercanaxius* Houde, 1988	Houde (1988)
Pelecaniformes	Limnofregatidae	*Limnofregata azygosternon* Olson, 1977	Olson (1977)
Pelecaniformes	Limnofregatidae	*Limnofregata hasegawyi* Olson & Matsuoka, 2005	Olson & Matsuoka (2005)
?Phoenicopteriformes	Juncitarsinae	*Juncitarsus merkeli* Peters, 1987	Peters (1987)
Anseriformes	Presbyornithidae	*Presbyornis pervetus* Wetmore, 1926	Feduccia & McGrew (1975), Olson & Feduccia (1980), Ericson (1997, 1999, 2000)
Galliformes	Gallinuloididae	*Gallinuloides wyomingensis* Eastman, 1900	Eastman (1900), Mayr & Weidig (2004), this study
Gruiformes	Messelornithidae	*Messelornis nearctica* Hesse, 1992	Hesse (1992), this study
ordo inc. sed.	Foratidae	*Foro panarium* Olson, 1992	Olson (1992)
"Caprimulgiformes"	Preficinae	*Prefica nivea* Olson, 1987	Olson (1987)
"Caprimulgiformes"	Fluvioviridavidae	*Fluvioviridavis platyrhamphus* Mayr & Daniels, 2001	Mayr & Daniels (2001)
Coraciiformes s.s.	Primobucconidae	*Primobucco mcgrewi* Brodkorb, 1970	Brodkorb (1970), Mayr *et al.* (2004)
ordo inc. sed.	?Leptosomidae	*Plesiocathartes wyomingensis* Weidig, 2006	Weidig (2006)
ordo inc. sed.	?Leptosomidae	*Plesiocathartes major* Weidig, 2006	Weidig (2006)
?Piciformes	?Gracilitarsidae	*Neanis schucherti* Shufeldt, 1913	Shufeldt (1913)
?Piciformes	?Galbulae	*"Neanis" kistneri* Feduccia, 1973	Feduccia (1973), this study
Psittaciformes	Messelasturidae	*Tynskya eocaena* Mayr, 2000	Mayr (2000b)
Psittaciformes	Halcyornithidae	*"Primobucco" olsoni* Feduccia & Martin, 1976	Feduccia & Martin (1976)
Coliiformes	Sandcoleidae	*Anneavis annae* Houde & Olson, 1992	Houde & Olson (1992)
Passeriformes	Zygodactylidae	2 species	this study

Systematics

Galliformes Temminck, 1820

Gallinuloididae Lucas, 1900

Included genera: *Gallinuloides* Eastman, 1900, *Paraortygoides* Mayr, 2000.

Gallinuloides wyomingensis Eastman, 1900

Holotype. MCZ 342221, complete articulated skeleton on a slab.

Referred specimen. WDC-CGR-012, complete articulated skeleton, from the 18-inch-layer (F1-locality of Grande, 1980), Upper Fossil Butte Member of Fossil Lake, Kemmerer, Wyoming (Fig. 1) (also shown in Mayr & Weidig, 2004).

The locality of the holotype (MCZ 342221) is described as "fish-bearing shales near Fossil, Wyoming" by Eastman (1900: 54), which, according to Grande (1980), belongs to the same locality as the WDC specimen.

Remarks. An emended diagnosis of the Gallinuloididae, a differential diagnosis to separate *Gallinuloides* from *Paraortygoides*, characters pertinent to the systematic position of Gallinuloididae as well as the dimensions of the WDC specimen are already given in Mayr & Weidig (2004). In the following, additional characters of *Gallinuloides wyomingensis* visible on the WDC specimen are described.

Description. The skull of *Gallinuloides* is small in relation to overall body size as in other galliform birds. The beak of this fossil bird is relatively short and its oval nasal openings are large. *Gallinuloides* differs from extant galliforms in having a small processus postorbitalis, lacking an ossified aponeurosis zygomatica, having a well-developed os ectethmoidale (Mayr & Weidig, 2004) and a rather small prefrontal. In accordance with modern galliforms, the foramen magnum is shifted caudad. On the quadratum, the small knob between the processus oticus and the processus mandibularis which occurs in all Cracidae is absent in *Gallinuloides*.

The mandible of *Gallinuloides* has a short symphysis mandibularis and fenestrae mandibulares seem to be absent. Lucas (1900) stated that a processus retroarticularis is not present; in this respect, *Gallinuloides* would differ from all modern galliforms. However, the mandible of the holotype is only very poorly preserved and the presence, or absence, of a processus retroarticularis cannot be determined. Unfortunately, the WDC-CGR-012 specimen cannot clarify this point. Due to a slight slant of the mandible, the caudal end is not clearly visible and it is not possible to discern whether a processus retroarticularis is present.

The coracoid is rather stout; the processus acrocoracoideus is somewhat larger than that of *Paraortygoides* and is slightly hooked. In agreement with *Paraortygoides* and *Paraortyx* (Mayr, 2000a; Mourer-Chauviré, 1992), a very small processus procoracoideus is present. The processus lateralis of the coracoid is only moderately extended, but, in contrast to extant genera, is divided into two tips. The facies articularis sterni is very high as in modern galliforms.

The humerus most closely resembles that of the extant *Leipoa ocellata* (Megapodiidae) and has a rounded and short crista deltopectoralis. Eastman (1900) remarked that *Gallinuloides* has a "broad deltopectoral crest"; however, it is not very broad for a galliform bird, having approximately the same relative size as that of *Leipoa* and is thus somewhat larger than that of *Paraortygoides*. As in extant galliforms, the ventral surface of the crista deltopectoralis is perpendicular to the cranial surface of the humerus shaft. The crista bicipitalis is rather small and the humeral shaft is slightly sigmoidally curved. The fossa m. brachialis is large but only moderately deep as in modern *Leipoa, Alectura* (Megapodiidae) and *Ortalis* (Cracidae). The tuberculum supracondylare ventrale is rather pronounced.

The ulna is considerably curved and shows no papillae remigiales, its overall morphology resembles that of *Paraortygoides*. However, in contrast to *Paraortygoides*, the ulna of *Gallinuloides* is slightly longer than the humerus. The olecranon of *Gallinuloides* is moderately long, it is slightly

Figure 1. *Gallinuloides wyomingensis*, referred specimen WDC-CGR-012, scale bar 20 mm.

longer than that of *Paraortygoides*. An impressio brachialis is present. The dorsal side of proximal end bears a distinct impression, distally of the processus cotylaris dorsalis. This impression is also exhibited by *Paraortygoides* (Mayr, 2000a) and the cracids.

The carpometacarpus resembles that of *Paraortygoides*, the ossa metacarpalia are straight and parallel, the spatium intermetacarpale is narrow (Mayr & Weidig, 2004). The processus extensorius is large, and its tip is pointed proximo-cranially. The distal end of the carpometacarpus resembles that of *Paraortygoides* very closely: the synostosis metacarpalis distalis is long and fairly wide, the os metacarpale majus protrudes cranially, and the proximal phalanx of the digitus major has a long, deep sulcus and a deep, but small, oval fenestration. The distal phalanx of the digitus majoris distalis is longer than the proximal phalanx and the digitus alulae bears a claw.

In accordance with the condition seen in extant galliforms and *Paraortygoides*, the tibiotarsus of *Gallinuloides* is the longest limb element. The proximal end bears medium-sized cristae cnemiales. At the distal end, the condylus medialis is narrower mediolaterally than the condylus lateralis but protrudes considerably farther cranially. The same proportions are found in modern galliforms. However, in contrast thereto, both condyli have about the same size in *Paraortygoides* (Mayr, 2000a). The incisura intercondylaris is narrower than in *Paraortygoides*. A comparatively broad pons supratendineus is present.

The tarsometatarsus measures about two thirds of the length of the tibiotarsus. Not many details are discernible on the proximal end of the tarsometatarsus. At least one foramen vasculare proximale is present. The hypotarsus is not visible in either the holotype or the new specimen, therefore Lucas' (1900) comments on it are only speculation. The tarsometatarsus of *Gallinuloides* has a large foramen vasculare distale, that of *Paraortygoides* is smaller. In distal view, the trochleae metatarsorum are situated along a curved line. The trochlea metatarsi III is the longest trochlea, followed by the trochlea metatarsi IV. The trochlea metatarsi II is considerably shorter than the trochlea metatarsi IV. In *Gallinuloides*, the trochlea metatarsi II extends plantad, to approximately the same degree as in *Paraortygoides*.

Discussion. Since the original description of *Gallinuloides wyomingensis*, various taxa have been included in the Gallinuloididae, and different systematic positions have been proposed (see e.g., Crowe *et al*., 2006; Crowe & Short, 1992; Dyke, 2003; Lucas, 1900; Mayr, 2008a; Mayr & Weidig, 2004). Based on the WDC specimen, Mayr & Weidig (2004) published an amended diagnosis of the Gallinuloididae, including only *Gallinuloides* and *Paraortygoides* in the taxon. According to Mayr & Weidig (2004), the Gallinuloididae belong to the stem-group of the Galliformes and represent a sister-taxon to all modern crown-group galliforms, since they exhibit several plesiomorphic characters such as the presence of a well-developed os ecthemoidale, poorly developed processus postorbitales, a cup-like cotyla scapularis of the coracoid, a long, slender scapula with a pointed caudal end, robust scapi claviculae of the furcula, a sternum with an apex carinae that is not displaced caudally, a narrow, elongated carpometacarpus with a straight os metacarpale minus, splayed trochleae metatarsorum, and the absence

Figure 2. *Messelornis nearctica*, FMNH A 716, scale bar 20 mm.

of ossified tendons. This result was recently supported by a phylogenetic revision using both morphological and molecular data of *Gallinuloides wyomingensis* and modern galliforms undertaken by Ksepka (2009), which also placed *Gallinuloides* clearly outside crown-group galliforms.

Messelornithidae Hesse, 1988

Included genera: *Messelornis* Hesse, 1988, *Itardiornis* Mourer-Chauviré, 1995.

Messelornis nearctica Hesse, 1992

Holotype. SMF Av 406, complete skeleton.

Referred specimens. FMNH A 716, disarticulated partial skeleton lacking the skull and distal ends of the wings (Fig. 2); SMNK-PAL 3810, nearly complete skeleton with feather remains (Fig. 3); USNM 776273, partial skeleton lacking the skull and the left wing (Fig. 4); USNM 336269, right leg with foot, parts of the pelvis and some vertebrae (Fig. 5); USNM 336277, left leg with foot, slab and counterslab (Fig. 6); BHI 1283, left leg, pelvis (Fig. 7); BHI 1292, both legs, pelvis, some vertebrae; BHI 1294, parts of the sternum, wing (Fig. 8); tentatively referred: USNM 776275, tip of bill, crushed skull, both wings, coracoid.

The new specimens exhibit the typical features of Messelornithidae (Hesse, 1992) such as skull with nostrils extending far forward, compact, bowed ulna with short, broad, blunt olecranon, carpometacarpus with broad processus extensorius, tarsometatarsus with short, broad trochlea metatarsi III. Contrary to Hesse's (1992) diagnosis, the trochlea metatarsi IV is longer than trochlea metatarsi II. According to Hesse (1992), *M. nearctica* differs from other members of the family mainly in details of the hypotarsus which are not recognizable in any of the new specimens. Additionally, the toes are longer and more slender compared to *M. cristata* (Hesse, 1992), a character which can also be seen in the new specimens. In addition to the features mentioned by Hesse, the os metacarpale minus is slightly longer than the os metacarpale majus in *M. nearctica* (same length in *M. cristata*).

Dimensions. see Table 2 and 3.

Description. The new specimens differ considerably in size (Table 1). This is in accordance with the type species of Messelornithidae, *Messelornis cristata* from Messel (Hesse, 1988a; Hesse & Habersetzer, 1993). A detailed description of the holotype of *M. nearctica* is given by Hesse (1992). In the following, only new features visible on the referred specimens are mentioned.

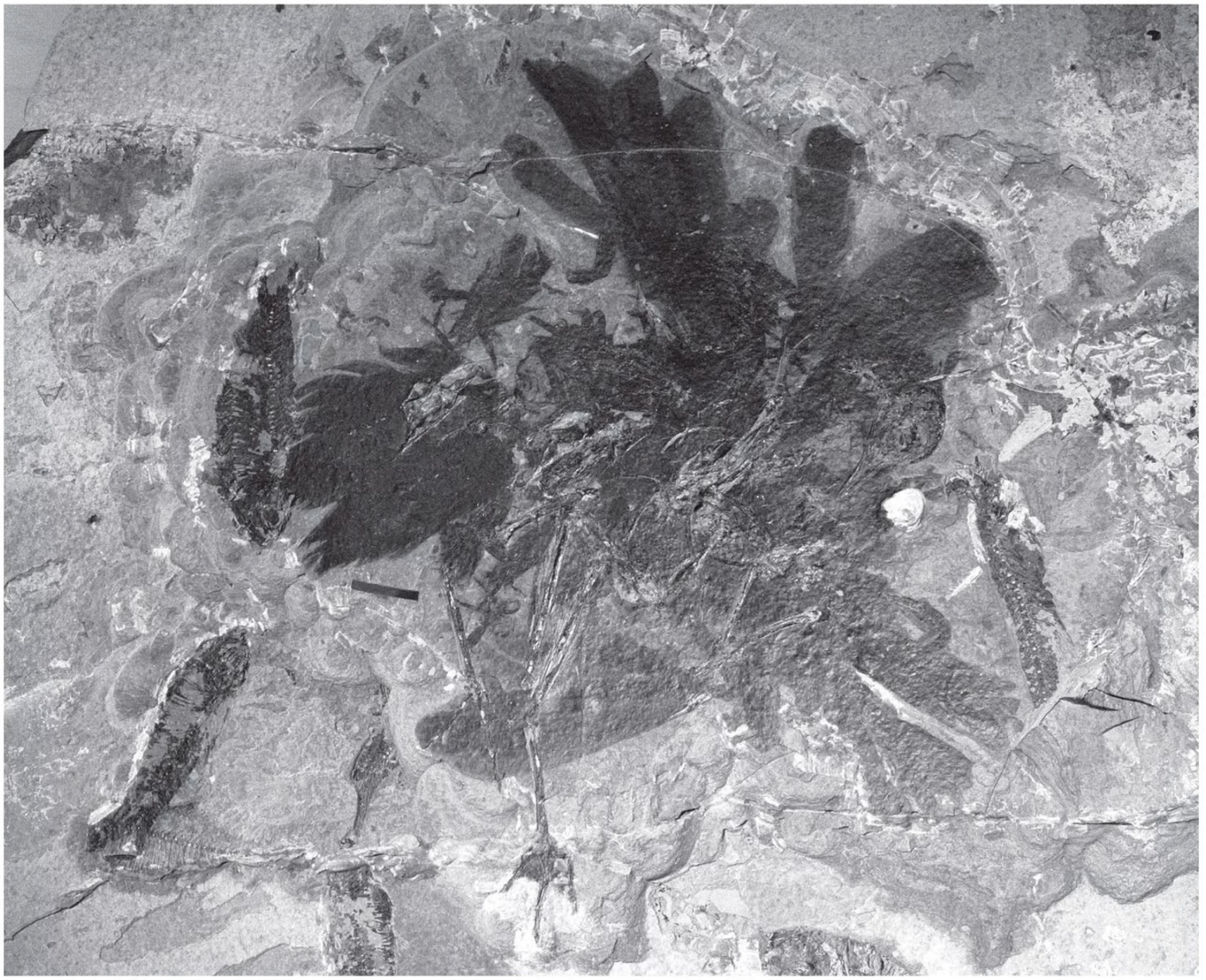

Figure 3. *Messelornis nearctica*, SMNK-PAL 3810, scale bar 20 mm.

The coracoid is short, but not as broad as in *Itardiornis*. The processus acrocoracoideus is hooked. The processus procoracoideus is very large as in *Eurypyga*. On the cranial surface two marked lines are visible. The angulus medialis is blunt and broad. A short but pronounced facies is visible dorsally of the facies articularis sternalis. The U-shaped furcula is small and rather wide; it seems to have a very small apophysis furculae. The scapula is short, but slender. It broadens in the curvature, the caudal end is pointed.

The sternum is moderately long and rather slender. A spina externa is not visible. Four incisurae intercostalis are present. The margo costalis reaches far caudad, it is nearly half as long as the whole sternum. The margo caudalis is not completely preserved in any of the specimens. Hesse (1992) stated that the taxon Eurypygoidea (Eurypygidae + Messelornithidae) is characterized by a "short, broad sternum, with two to three notches on each side" (Hesse 1992:171). The new specimens show at least two incisurae, i.e. one per side. Since the middle portion of the margo caudalis is not preserved in any specimen, it is not possible to determine the exact number of incisurae. In relation to the total sternum length, the incisurae are deeper than in *Eurypyga*.

The humerus resembles that of *Messelornis cristata*. The tuberculum supracondylare ventrale is extremely pronounced and sharp. The humerus shaft is bowed. The condylus ventralis is proximo-distally narrow, and sharp. As in *Itardiornis*, the sulcus transversus is short, but well marked. The ulna is already described in detail in Hesse (1992). Hesse (1992: 173) stated that the "humerus (is) a little shorter than ulna". This is not true for the new specimens, both in the FMNH PA 716 and the SMNK PAL 3810 specimen the ulna is shorter than the humerus (Table 2). The os metacarpale minus of the carpometacarpus is straight; a very small processus intermetacarpalis is present as in *Messelornis cristata* and *Itardiornis*. In contrast to *Messelornis cristata*, the os metacarpale minus seems to be slightly longer than the os metacarpale majus. Hesse (1992) stated that the carpometacarpus is shorter in relation to the wing than in *Messelornis cristata*. However, the difference in length between the holotype of *Messelornis nearctica* and of *Messelornis cristata* is only very small (21% in *Messelornis nearctica* versus 22.4% in *Messelornis cristata*, Hesse, 1988a). The new specimens show that this character is somewhat variable, they differ in their relative length of the carpometacarpus (up to 23.2% in the FMNH PA 716 specimen), which is not shorter than in *Messelornis cristata*.

The pelvis has a long processus terminalis ischii, which reaches the pubis. The foramen obturatum seems to be closed. The femur is strongly bowed. A trochlea fibularis is present with a high lateral edge. The tibiotarsus is the longest

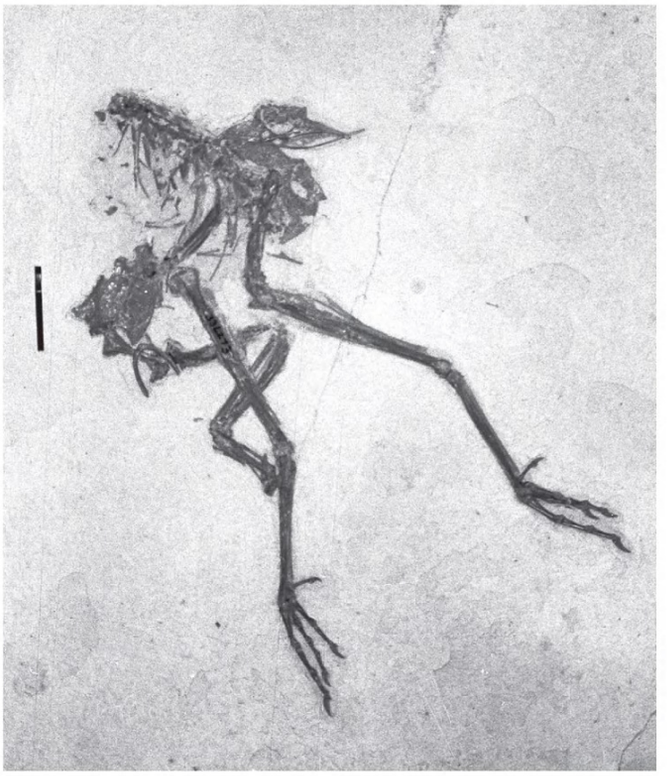

Figure 4. *Messelornis nearctica*, USNM 776273, scale bar 20 mm.

limb element. The proximal end of the tibiotarsus shows large cristae cnemiales; the crista fibularis is pronounced. A sulcus m. fibularis is not visible in any specimen, probably due to poor preservation. The trochlea cartilaginis tibialis is proximo-distally low, but caudo-cranially deep. The tarsometatarsus closely resembles that of *Messelornis cristata*. The hypotarsus is quite small, the number of cristae hypotarsi is not recognizable. The trochlea metatarsi III is the longest, followed by the trochlea metatarsi IV and then the trochlea metatarsi II; the difference in length between trochlea metatarsi IV and trochlea metatarsi II is less distinct than in *Itardiornis*. The trochlea metatarsi II is projected well plantad. The plantar surface of the trochlea metatarsi II is not flattened, but rounded as in *Itardiornis* (Mourer-Chauviré, 1995). A foramen vasculare distale is present. The toes have the usual number of phalanges. Compared to *Messelornis cristata*, the toes are relatively longer.

Figure 5. *Messelornis nearctica*, USNM 336269, scale bar 20 mm.

Table 2. *Messelornis nearctica*, length of the limb bones compared to other messelornithids, in mm, measurements of *M. cristata* after Hesse (1988a), measurements of *M. russelli* and *Itardiornis hessae* after Mourer-Chauviré (1995).

	CO	HU	UL	CM	FE	TT	TM
Messelornis nearctica							
SMF Av 406	19.0	35.5	36.0	19.0	35.0	63.0	46.0
FMNH PA 716	20.7	35.9	33.7	20.8	ca. 38.2	63.2	47.4
SMNK PAL 3810	18.2	33.0	32.0	18.5	34.0	52.8	39.2
USNM 336269	—	—	—	—	—	65.0	46.6
USNM 336273	ca. 17.5	ca. 30.0	29.4	16.9	ca. 29.5	50.2	35.1
USNM 336275	18.5	ca. 26.0	33.8	ca. 16.0	—	—	—
USNM 336277	—	—	—	—	ca. 38.7	67.2	48.0
BHI 1283	—	—	—	—	33.7	54.9	—
BHI 1292	—	—	—	—	36.2	64.5	47.3
BHI 1294	—	—	ca. 34.0	17.9	—	—	—
Messelornis cristata							
SMF ME 807a,b,c	21.0	36.0	34.5	20.5	35.0	ca. 62.0	52.5
Messelornis russelli							
BR 14033	—	ca. 52.0	—	—	—	—	—
Itardiornis hessae	31.7	ca. 46.0	—	—	—	—	—

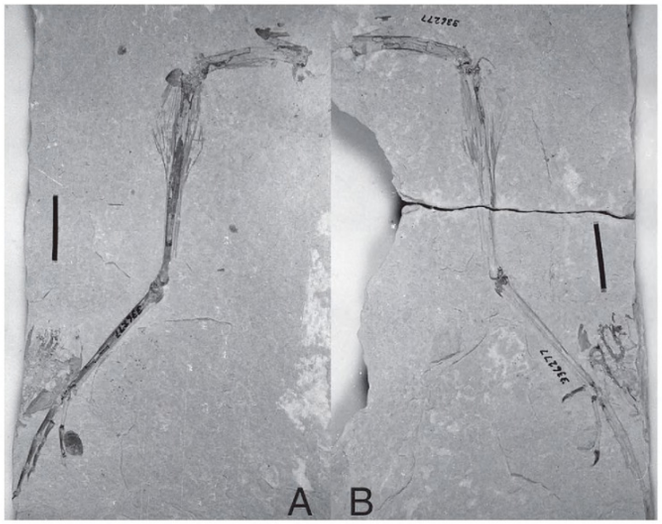

Figure 6. *Messelornis nearctica*, USNM 336277, A = slab, B = counterslab, scale bar 20 mm.

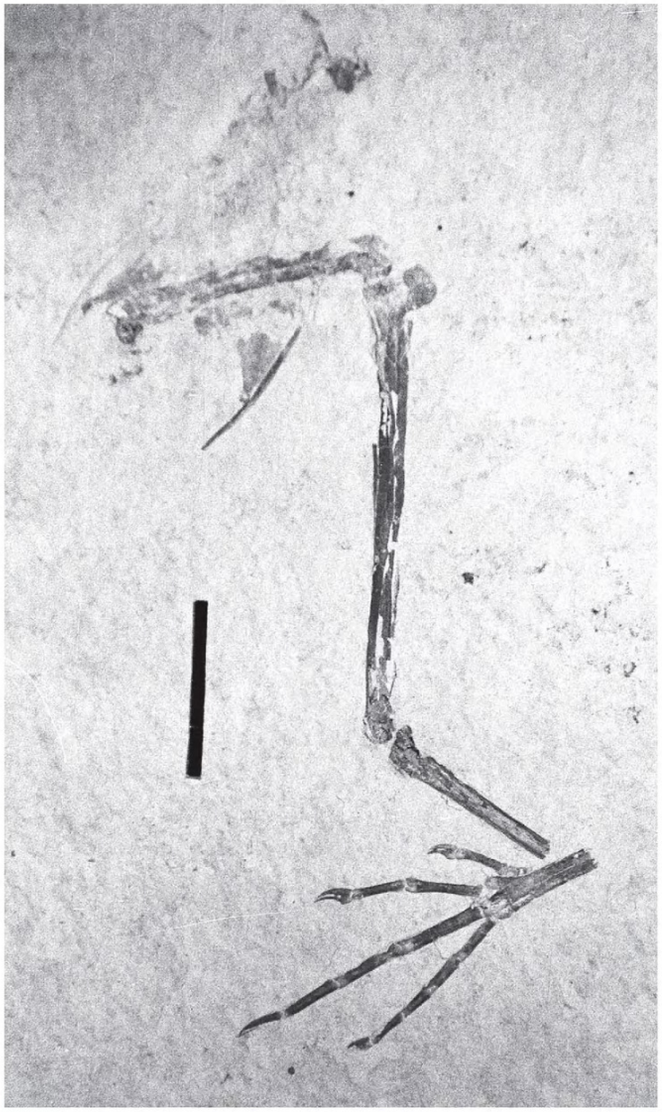

Figure 7. *Messelornis nearctica*, BHI 1283, scale bar 20 mm.

Only in the SMNK PAL 3810 specimen are several scattered feathers preserved. In all specimens, several ossified tendons are preserved. Most occur at tarsometatarsus, tibiotarsus, humerus, radius and ulna. Some tendons are scattered on the slabs, their origin is not discernible. The tendons at the tibiotarsus are split proximally.

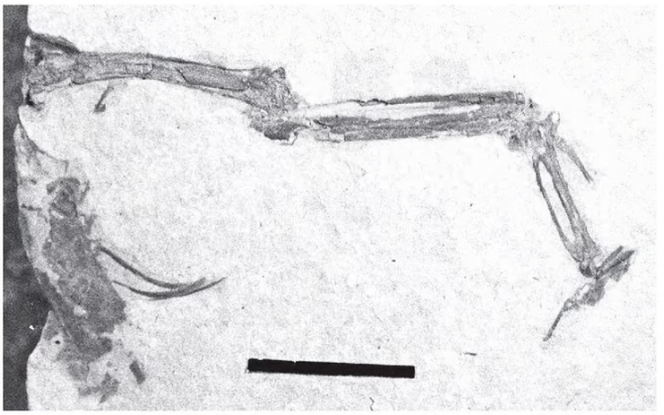

Figure 8. *Messelornis nearctica*, BHI 1294, scale bar 20 mm.

Discussion. The fossil Messelornithidae were originally described by Hesse (1988a). Besides the type species *Messelornis cristata* from Messel, the Messelornithidae comprise *Messelornis russelli* and *Itardiornis hessae* from the Quercy in France (Mourer-Chauviré, 1995), as well as *Messelornis nearctica* from the Green River Formation (Hesse, 1992). Hesse (1988b) regarded the Eurypygidae to be the closest modern relative of the fossil Messelornithidae. This view was widely accepted (e.g., Cracraft, 2001; Peters, 1991) and supported by Livezey (1998) although Mourer-Chauviré (1995) noted some parallelism with Rallidae. Mayr (2004a) regarded the Messelornithidae as the sister-taxon to rails and finfoots and supported his classification with derived characters shared by the taxon (Messelornithidae + (Rallidae + Heliornithidae)).

The type species of the Messelornithidae, *Messelornis cristata*, was thoroughly described (Hesse, 1988a,b, 1990); an extensive study of the osteology of this species was based on a total of 346 specimens. The description of the Green River species *Messelornis nearctica*, however, was based on a single, nearly complete, but crushed specimen (Hesse, 1992). The new specimens described above reveal additional osteological features which have been unknown so far. In addition, they show that some details of the original description (Hesse, 1992) are not wholly correct, because they were only based on one specimen; this mainly concerns size-related features.

Messelornis nearctica has as large a size-range as *Messelornis cristata*. Sexual dimorphism might be an explanation for the large size-range; it is possible to divide the ten specimens described above into two groups: four small specimens (SMNK PAL 3810, USNM 336273, USNM 336275 and BHI 1294) and the remaining six large specimens (Table 2). Hesse (1990) reported that, within the Gruiformes, males tend to have slightly longer limb bones than females, but the length of the limb bones of both sexes overlap considerably. Thus, the Green River specimens might represent four female individuals and six male individuals. However, in *Messelornis cristata*, which is known from a far larger sample, it is not possible to clearly distinguish two groups that represent the sexes (Hesse, 1990).

All Green River specimens seem to be adults, which is in accordance with the findings from Messel (Hesse, 1990). As it was already proposed for *Messelornis cristata* (Hesse, 1990), this might indicate that the nests of *Messelornis nearctica* were not situated directly at the shore of the lake. The adult birds, however, probably spent a considerable

Table 3. *Messelornis nearctica*, proportions of limb bones, compared to the holotype of *Messelornis cristata* (measurements of *Messelornis cristata* after Hesse, 1988a, measurements of *Messelornis russelli* and *Itardiornis hessae* after Mourer-Chauviré, 1995).

	HU:UL	HU:CM	HU:TM	UL:TT	UL:TM	CM:TM	TT:TM
Messelornis nearctica							
SMF Av 406	0.99	1.87	0.77	0.57	0.78	0.41	1.37
FMNH PA 716	1.07	1.73	0.76	0.53	0.71	0.44	1.33
SMNK PAL 3810	1.03	1.78	0.84	0.63	0.82	0.47	1.35
USNM 336273	1.02	1.78	0.85	0.59	0.84	0.48	1.43
Messelornis cristata							
SMF ME 807a,b,c	1.04	1.76	0.69	0.56	0.66	0.39	1.18

amount of time close to the shore, considering the number of adult specimens.

Zygodactylidae Brodkorb, 1971

Included genera: *Zygodactylus* Ballmann, 1969, *Primoscens* Harrison & Walker, 1977, *Primozygodactylus* Mayr, 1998, *Eozygodactylus* n.gen.

Taxonomic remarks. The Primoscenidae Harrison & Walker, 1977 were described based on a single carpometacarpus. Mayr (1998) included additional species which were represented by complete skeletons and emended the diagnosis, mentioning the resemblance of Primoscenidae to the Zygodactylidae Brodkorb, 1971. Due to a new species of Zygodactylidae, Mayr (2008b) synonymized the Primoscenidae Harrison & Walker, 1977 with the Zygodactylidae Brodkorb, 1971.

The two species from the Green River Formation fit well with Mayr's (1998) emended diagnosis of Primoscenidae, being small zygodactyl birds with a long, slender tarsometatarsus and a large processus intermetacarpalis of the carpometacarpus. Furthermore, the new species exhibit the apomorphies of the clade (*Primozygodactylus* + *Zygodactylus*) listed by Mayr (2008b): (1) trochlea metatarsi II of tarsometatarsus much shorter than trochlea metatarsi III and (2) with well-developed, plantarly projecting process, and (3) trochlea metatarsi IV with large trochlea accessoria, which is separated by a furrow from the trochlea metatarsi IV. According to Mayr (1998), the very long and slender tarsometatarsus that distinctly exceeds the humerus in length is another possible apomorphy of this clade, a character that is also found in the species described below.

Eozygodactylus n.gen.

Type species. *Eozygodactylus americanus* n.gen. and n.sp.

Etymology. *Eozygodactylus*—*Eos* Greek for dawn, *Zygodactylus*—for the zygodactyl foot.

Diagnosis. Within the Zygodactylidae, *Eozygodactylus* n.gen. is diagnosed as follows: (1) humerus with large processus supracondylaris dorsalis; (2) digitus minoris widens distally; and (3) pelvis with foramen obturatum open.

Character (1) is shared with *Zygodactylus* and a not yet named specimen from the London Clay held in a private collection (see also below); *Eozygodactylus* might be congeneric with the latter. Character (2) is autapomorphic for *Eozygodactylus*. Character (3) is plesiomorphic and also occurs in many other bird taxa such as e.g., Numididae, Charadriidae, Burhinidae, Rallidae, Phoenicopteridae, Threskiornithidae and Coraciidae, but not in *Primozygodactylus* (the pelvis is unknown for *Primoscens* and *Zygodactylus*).

Differential diagnosis. *Eozygodactylus* n.gen. differs from: (*a*) the Eocene *Primozygodactylus* Mayr, 1998 in: Scapula more strongly curved, humerus with smaller crista bicipitalis, carpometacarpus with larger difference in length between the ossa metacarpalia, sternum relatively longer craniocaudally; (*b*) the Eocene *Primoscens* Harrison & Walker, 1977 (the differential diagnosis is not only based on the holotype of *Primoscens minutus*, which only consists of a carpometacarpus, but also on specimen WN 87558A from the private collection of Michael Daniels that Mayr (1998) referred to the genus *Primoscens* [for figures, see Mayr, 1998: 78]) in: Humerus with processus supracondylaris (absent in cf. *Primoscens*), longer carpometacarpus (8.8 mm in *Eozygodactylus* versus 6.9 mm in *Primoscens*); and (*c*) the lower Oligocene–Miocene *Zygodactylus* Ballmann, 1971 in: Coracoid with medium-sized processus procoracoideus (absent in *Zygodactylus*), carpometacarpus with less difference in length between the ossa metacarpalia, legs relatively shorter.

Eozygodactylus americanus n.gen. and n.sp.

Holotype. USNM 299821, partial articulated skeleton lacking the pelvis and the legs (Fig. 9).

Type locality. Tynsky Quarry (F2), Kemmerer, Lincoln County, Wyoming, USA.

Type horizon. Tertiary, Eocene, Wasatchian, Green River Formation, Fossil Butte Member.

Paratype. WDC-CGR-014, articulated skeleton lacking the skull—the "skull" is painted by the preparator; from 18-inch-layer (Fig. 10).

Referred specimen. Tentatively referred: UWGM 40705, left wing, scapula, coracoid, parts of the sternum; from split-fish-layer.

Etymology. *americanus*—after *America*, the continent in which the Green River Formation is situated.

Diagnosis. As for genus.

Dimensions. See Table 4, 5 and 6.

Description. *Eozygodactylus americanus* resembles *Primozygodactylus danielsi* in its size and is thus one of the smaller species of the Zygodactylidae, but still larger than *Primoscens minutus*. Unless otherwise indicated, the description is mainly based on the USNM 299821 and WDC-CGR-014 specimens, since they are more complete and better preserved.

Figure 9. *Eozygodactylus wyomingensis* n.gen. and n.sp., holotype, USNM 299821, scale bar 20 mm.

The skull in USNM 299821 is slightly crushed, but some features may still be recognized. The prefrontal is not visible, it is either absent or hidden by the ripped and dislocated sclerotic ring. The preserved parts of the sclerotic ring do not allow detailed comparison with the sclerotic ring of *Primozygodactylus* (Mayr, 1998: fig. 21). With a length of approximately 13 mm, the maxilla is slightly shorter than that of *Primozygodactylus danielsi* (the two species have the same overall size). The narial opening is long, it measures about three quarters of the length of the maxilla. An ossified nasal septum does not seem to be present which is in accordance with *Primozygodactylus*, the Passeriformes and most Pici. The processus orbitalis of the quadratum is short in contrast to the elongated process of the Pici and Passeriformes.

As in *Primozygodactylus*, the symphysis mandibularis measures one fifth of the whole mandible. A groove is situated at the location where a fenestra mandibulae would otherwise be present.

The coracoid is long and slender, but neither the distal nor the proximal end are well enough preserved to show any details. A medium-sized processus procoracoideus is present (UWGM 40705). *Primozygodactylus* has a rather small processus procoracoideus, whereas cf. *Primoscens* has a very large processus procoracoideus (Mayr, 1998: fig. 22).

The scapula is bent more sharply than that of *Primozygodactylus*. The acromion is only moderately long and thus is similar to *Primozygodactylus danielsi*, whereas *Primozygodactylus major* has a very long acromion (Mayr, 1998: fig. 22).

The sternum resembles that of *Primozygodactylus* (Mayr, 1998: fig. 24), it is stocky, relatively short and mediolaterally broad. It is nearly as long as the humerus and, in relation to the wing, thus considerably longer than that of *Primozygodactylus danielsi*. The margo caudalis shows four incisurae, the incisurae laterales are deeper than the incisurae mediales. In *Eozygodactylus*, the trabeculae laterales and intermediales widen toward their caudal ends and reach further caudad than the trabecula mediana of the sternum. The trabeculae laterales reach even farther distad than the trabeculae intermediales. The spina externa is not visible in any specimen. The exact number of ribs is not determinable, at least four of them possess a processus uncinatus.

The humerus closely resembles that of Passeriformes. In accordance with WN 88583A and WN 92747 (collection Daniels from the London Clay, shown in Mayr, 1998: 79, pl. 7), the crista bicipitalis is only of moderate size, whereas *Primozygodactylus* has a pronounced crista bicipitalis. The tuberculum ventrale is prominent. The crista deltopectoralis of *Eozygodactylus* is low and short as in the other members

Figure 10. *Eozygodactylus wyomingensis* n.gen. and n.sp., paratype, WDC-CGR-014, scale bar 20 mm. The skull is fabricated.

Table 4. Green River Zygodactylidae, length of the limb bones, compared to *Primozygodactylus danielsi*, left/right, in mm (measurements of *Primozygodactylus danielsi* after Mayr, 1998).

	CO	HU	UL	CM	FE	TT	TM
Eozygodactylus americanus n.gen. and n.sp.							
USNM 299821	—	16.8/16.8	ca. 19/19.1	—/8.8	—	—	—
WDC-CGR-014	13.8/ca. 13.1	—/ca. 17.2	ca. 18.2/—	8.8/—	19.7/—	—/30.6	21.7/21.8
UWGM 40705	—	—	19.6	9.2	—	—	—
Zygodactylidae indet.							
NAMAL 2000-0217-004	10.5/—	13.5/ca. 13	18/18	7/ca. 7	—	19/20	14/14
BHI 1285	—	12.0/12.2	—	7.4/—	12.2/12.5	21.5/21.6	14.5/14.4
UWGM 21421	—	—	—	—	—/ca. 12	—/22	—/14.5
Primozygodactylus danielsi	13.5	16.7	19.0	8.4	16.9	27.9	20.0

of Zygodactylidae, it only measures about a fourth of the length of the humerus. The crista deltopectoralis approaches the shaft, whereas in *Primozygodactylus*, the crista is nearly parallel to the humerus shaft. As in *Primozygodactylus*, the shaft is only slightly curved. The apparently stronger curvature of the left humerus shaft in the USNM specimen is due to a fracture in the middle of the bone. The distal end of the humerus shows a pronounced processus supracondylaris dorsalis, which is similar in its size and location to that of the *Zygodactylus* and Passeriformes. *Primozygodactylus* and WN 87558A (cf. *Primoscens*) have a considerably smaller processus supracondylaris dorsalis (Mayr, 1998: fig. 25), which is oriented less proximad, but is perpendicular to the shaft. The fossa m. brachialis is moderately deep. As in *Primozygodactylus* and modern Piciformes, the ulna is longer than the humerus. The ratio humerus:ulna is concordant with that of *Primozygodactylus danielsi* and of *Primozygodactylus ballmanni*. However, the ulna is shorter than the tarsometatarsus in *Eozygodactylus*, whereas the two bones have nearly the same length in *Primozygodactylus*. In contrast to most Pici and many Passeriformes, the ulna lacks papillae remigiales. In *Primozygodactylus*, papillae remigiales are also absent. Neither the olecranon nor the distal end are discernible in any specimen. The carpometacarpus of *Eozygodactylus americanus* resembles closely that of *Primoscens* and of *Primozygodactylus*. The most conspicuous character is the large processus intermetacarpalis which reaches as far as to the os metacarpale minus, but is not fused to it. The os metacarpale minus is longer than the os metacarpale majus. The difference in length is larger than in *Primozygodactylus*. The proximal end of the carpometacarpus is only poorly preserved and thus allows few observations. The proximal end of the os metacarpale minus bears a slight tubercle, which probably corresponds to the "transverse ridge extending to the pisiform process" as described by Harrison (1982: 78). In how far this tubercle reaches the processus pisiformis is not visible in *Eozygodactylus*. A comparable tubercle is not visible in *Primozygodactylus*, but this might be due to preservation (Mayr, 1998). In *Eozygodactylus*, the processus extensorius is turned proximad to a greater extend than in *Primozygodactylus* (Mayr, 1998: fig. 26). As in *Primozygodactylus*, the synostosis metacarpalis distalis is broad. In contrast to *Primozygodactylus* (Mayr, 1998: fig. 26), the cranial margin of the os metacarpale majus is nearly straight and shows only a slight concave curvature. The phalanges match those of *Primozygodactylus*. The digitus alulae has only one phalanx. The distal phalanx of the digitus majoris is long and slender.

In contrast to *Primozygodactylus* and extant Passeriformes and Pici, the foramen obturatum is open caudally. In accordance with *Primozygodactylus*, the processus terminalis ischii is narrow and the distal end seems to be widened. The description of the legs is only based on the WDC specimen, since the other two specimens lack the hind limbs. As in *Primozygodactylus*, the tibiotarsus is by far the longest limb element. The distal condyles are craniocaudally deep and low, even lower than in *Primozygodactylus*. The tarsometatarsus is long and slender and in that respect resembles that of Passeriformes. Very few details are discernible at the proximal end, the hypotarsus seems to be small. The foramen vasculare distale is large and oval. In distal view, the trochleae are aligned as a curve, not planar like in passerines. The trochlea metatarsi III reaches considerably farther distad than the trochleae metatarsorum II and IV, which are approximately of the same length. The trochlea metatarsi II is only poorly preserved and a plantarly directing process is not visible. The fourth toe is opposed to the second and the third toe. All toes have the usual number of phalanges. The toes are longer than those of *Primozygodactylus* and have different proportions (tab. 5). The claws are short with a pronounced sulcus neurovascularis.

Table 5. *Eozygodactylus americanus* n.gen. and n.sp., specimen WDC-CGR-014, length of pedal phalanges, compared to *Primozygodactylus danielsi*, specimen SMF 2522, in mm (measurements of *Primozygodactylus danielsi* after Mayr, 1998).

	I1	I2	II1	II2	II3	III1	III2	III3	III4	IV1	IV2	IV3	IV4	IV5
Eozygodactylus americanus n.gen. and n.sp.														
WDC (left)	5.4	2.5	—	5.1	2.9	ca. 6.0	5.7	4.7	ca. 2.7	—	2.8	2.6	2.6	—
WDC (right)	ca. 5.6	ca. 2.0	5.9	5.2	ca. 2.2	ca. 4.6	5.7	4.8	3.3	2.7	2.9	2.6	2.6	—
Primozygodactylus danielsi														
SMF	4.0	2.4	4.8	4.3	2.4	5.7	4.9	4.3	2.6	2.9	2.9	2.5	2.5	2.0

Table 6. Green River zygodactylids, limb proportions compared to the Messel species of Zygodactylidae (measurements of *Primozygodactylus* after Mayr, 1998).

	HU:UL	HU:CM	HU:TM	UL:TT	UL:TM	CM:TM	TT:TM
Eozygodactylus americanus n.gen. and n.sp.							
USNM 299821	0.88	1.91	—	—	—	—	—
WDC-CGR-014	0.94	1.95	0.79	0.59	0.83	0.40	1.40
Zygodactylidae indet.	0.75	1.92	0.96	0.95	1.28	0.50	1.28
Primozygodactylus danielsi	0.88	2.13	0.89	0.72	1.02	0.42	1.43
Primozygodactylus major	0.92	2.24	1.03	0.79	1.11	0.46	1.41
Primozygodactylus ballmanni	0.88	2.23	0.84	0.72	0.95	0.38	1.33

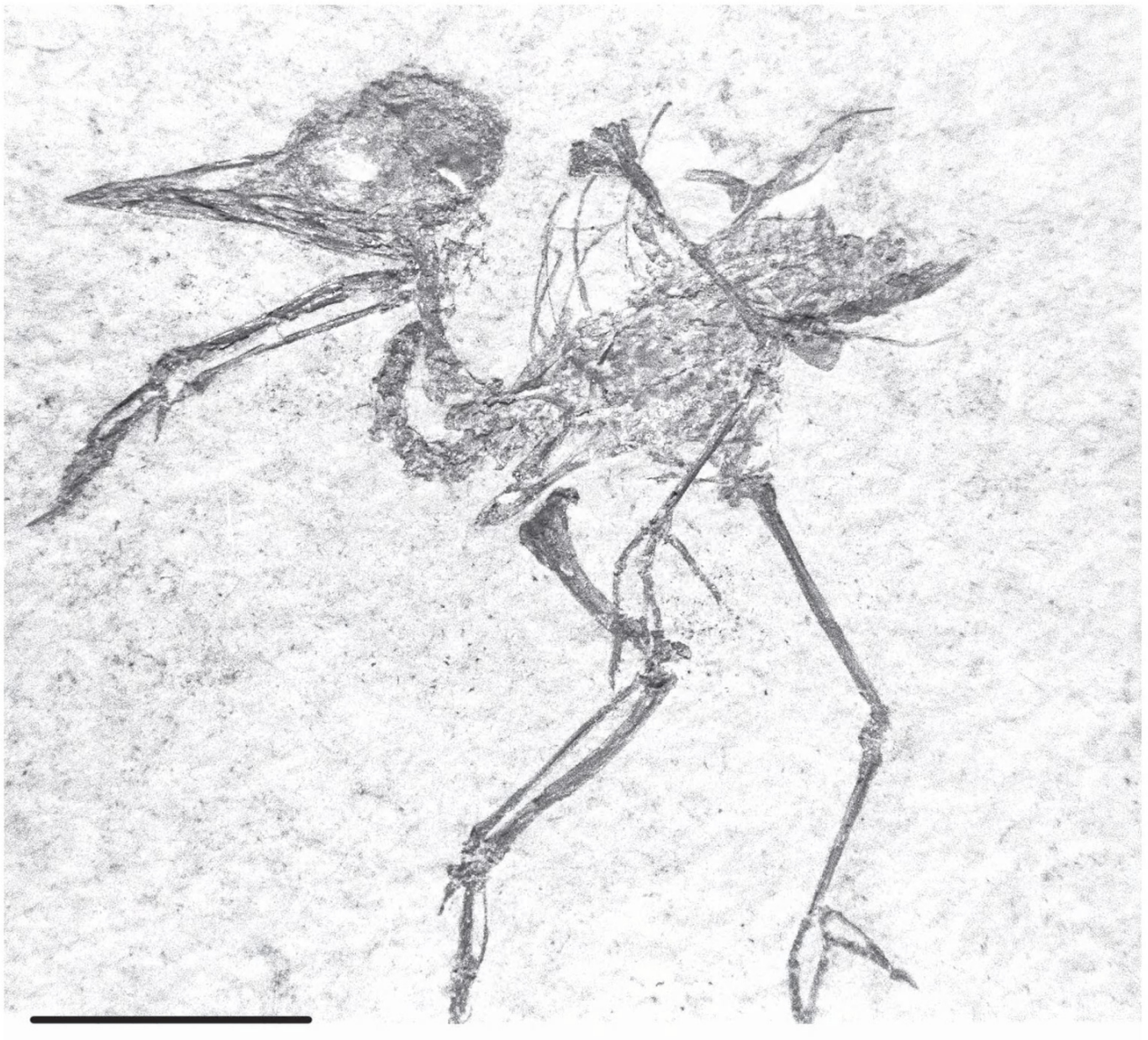

Figure 11. Zygodactylidae indet., NAMAL 2000-0217-004, scale bar 20 mm.

Zygodactylidae indet.

Besides *Eozygodactylus americanus*, a second species of Zygodactylidae occurs in the Green River Formation. It is represented by three specimens: BHI 1285, a complete articulated skeleton; NAMAL 2000-0217-004, also a complete articulated skeleton (Fig. 11) (the counterslab is in private hands and not available for study); and UWGM 21421, consisting of a right leg. These three specimens represent a new species, which differs from *Eozygodactylus americanus* in the following characters: (1) smaller overall size (length of tarsometatarsus 14.5 mm (BHI 1285) versus 21.7 mm in *Eozygodactylus americanus*) (Table 4, 6); (2) humerus with small processus supracondylaris dorsalis; (3) relatively longer ulna, which exceeds the tarsometatarsus in length.

In character (3), the undescribed species also differs from *Primozygodactylus*.

Because neither the BHI 1285 nor the NAMAL 2000-

0217-004 specimen were available for detailed studies, the new species is not named or described in detail. However, a few observations are made. The processus acrocoracoideus of the coracoid is large and hooked distally and resembles cf. *Primoscens* (WN 87558 collection Daniels). The processus procoracoideus is rather large, it seems to be somewhat relatively larger than that of *Eozygodactylus americanus* and clearly larger than that of *Primozygodactylus danielsi*. The extremitas omalis of the furcula is broad like that of *Primozygodactylus*, but contrary to the very narrow extremitas omalis of cf. *Primoscens* (Mayr, 1998: fig. 23). The humerus differs from that of *Eozygodactylus americanus*, but resembles that of *Primozygodactylus* in having a large crista bicipitalis. The processus supracondylaris seems to be considerably smaller than in *Eozygodactylus americanus* and thus is similar to *Primozygodactylus* and cf. *Primoscens* (Mayr, 1998: fig. 25).

Discussion. The fossil Zygodactylidae Brodkorb, 1971 are known from both complete articulated skeletons and three-dimensional preserved bones. Three genera have been described so far: *Zygodactylus* Ballmann, 1969 from the lower Oligocene to Miocene of Europe, originally known from distal tibiotarsi and tarsometatarsi (Ballmann, 1969a,b), until Mayr (2008b) described a new species based on a complete skeleton; *Primoscens* Harrison & Walker, 1977 and the taxon Primoscenidae from the Lower Eocene London Clay of England, was based on and only known from a single incomplete carpometacarpus (Harrison & Walker, 1977) until Mayr (1998) referred additional skeletal elements from the London Clay kept in a private collection; and *Primozygodactylus* Mayr, 1998 from the German Messel site was based on complete articulated skeletons (Mayr, 1998). The Primoscenidae were regarded as Passeriformes in the original description (Harrison & Walker, 1977), but their passeriform affinities were later doubted (Olson & Feduccia, 1979). The Messel specimens led Mayr (1998) to tentatively consider the Primoscenidae to be the sister group of a clade including the Miocene *Zygodactylus* and the Pici, mainly due to the presence of a zygodactyl foot with a trochlea accessoria (a sehnenhalter as described by Steinbacher, 1935). A first cladistic analysis including both the Primoscenidae and *Zygodactylus* resulted in a sister group relationship between the clade (Primoscenidae + Zygodactylidae) and Passeriformes (Mayr, 2004b). A new species of *Zygodactylus* showed the great similarities between *Zygodactylus* and Primoscenidae; in consequence, Mayr (2008b) synonymized Primoscenidae with Zygodactylidae. The new species of *Zygodactylus* also showed that zygodactylids are the sister taxon of Passeriformes (Mayr, 2008b).

From the Green River Formation, six specimens, which represent two species, were available for this study and are described above. In their overall appearance, the specimens from the Green River Formation closely resemble the Messel specimens. However, the Green River specimens can be distinguished from the Messel genus *Primozygodactylus*, mainly by characters of the humerus. Mayr (1998) mentioned several specimens from the London Clay (England) which are in the private collection of Michael Daniels. According to Mayr (1998), the specimens from the Daniels collection represent three different types of Zygodactylidae: One type probably belongs to the genus *Primozygodactylus*, one type represents the genus *Primoscens* and the third type "represents a not yet described genus" (Mayr, 1998: 51). This third type (Mayr, 1998: pl. 7) has a humerus that is very similar to that of *Eozygodactylus americanus* and may belong to the same genus. Both humeri exhibit a pronounced processus supracondylaris dorsalis at the distal end of the humerus, which is also found in some Passeriformes. The smaller species of Zygodactylidae from the Green River Formation differs in several aspects especially of the humerus from *Eozygodactylus americanus*. The humerus of the small Green River species resembles more closely that of cf. *Primoscens*, to which it also corresponds in size. However, it differs from cf. *Primoscens* in the shape of the extremitas omalis of the furcula. A closer study might reveal whether this small species is congeneric with one of the already described genera or if it represents a new genus of Zygodactylidae. Unfortunately, the characters listed by Mayr (2008b) as apomorphies for the clade (Zygodactylidae and Passeriformes) are not visible in any of the Green River specimens, with the exception of a well-developed processus acromialis, which is visible in the NAMAL specimen.

?Galbulae

"Neanis" kistneri (Feduccia, 1973)

Holotype. UWGM 3196, nearly complete articulated skeleton.

Referred specimen. USNM 336268, nearly complete articulated skeleton lacking the left foot (Fig. 12).

In its overall appearance and sitze, the referred specimen corresponds well with the holotype. The specimens share a large bicipital crest of the humerus, a carpometacarpus with straight ossa metacarpalia of identical length and a short synostosis metacarpalis distalis, and a zygodactyl foot with a strong third toe.

Dimensions. See Tables 7 and 8.

Description. The original description is based on the holotype only, given here are additional characters discernible on the referred specimen.

The exact shape of the skull is difficult to determine, because it is somewhat crushed. In accordance with *Galbula*, the os frontale is flat and a fossa temporalis is present. A small, slender piece of bone might represent the broken processus postorbitalis. If this identification is correct, the processus postorbitalis would have a length comparable to *Galbula*. The beak is nearly straight and slender, and shorter than that of Galbulidae. In the mandible, a fenestra caudalis mandibulae is visible.

Table 7. *"Neanis" kistneri*, length of limb bones, left/right, in mm.

	CO	HU	UL	CM	FE	TT	TM
UWGM 3196	11.6/ca. 10.7	17.3/ca. 16.7	20.1/—	9.1/—	—	20.8/20.5	11.5/11.5
USNM 336268	12.7/12.8	17.8/18.5	ca. 22.2/22.1	10.5/10.2	12.7/13.3	—/20.2	—/10.6

Table 8. *"Neanis" kistneri*, proportions of limb bones.

	HU:UL	HU:CM	HU:TM	UL:TT	UL:TM	CM:TM	TT:TM
UWGM 3196	0.86	1.90	1.50	0.97	1.75	0.79	1.81
USNM 336268	0.84	1.81	1.75	1.09	2.08	0.96	1.90

Figure 12. *"Neanis" kistneri*, USNM 336268, scale bar 20 mm.

The coracoid closely resembles that of *Primobucco mcgrewi*. The processus acrocoracoideus is large and slightly hooked, the processus procoracoideus is also large. In its shape, the processus lateralis resembles closely *Atelornis*. The facies articularis sterni is large like that of Galbulae and of Coraciiformes s.s. On the cranial side of the sternal end of the coracoid, a fossa is visible. A comparable fossa is present in Brachypteraciidae and some Bucconidae (*Bucco, Chelidoptera, Monasa*, and rather flat in *Malacoptila striata*). The furcula is rounded V-shaped,

an apophysis furculae is not present.

The humerus resembles closely that of *Primobucco mcgrewi*. The head of the humerus is situated dorsally of the shaft due to the large crista bicipitalis. The crista deltopectoralis is short. The humerus shaft is slightly sigmoidal. The distal end is only poorly preserved and thus does not allow any detailed observations. The ulna is the longest limb element. In contrast to Galbulae, papillae remigiales are not present. The carpometacarpus is moderately long and slender. The ossa metacarpalia are parallel and have the same length. In contrast hereto, the os metacarpale minus is considerably longer than the os metacarpale majus within modern Galbulae. The processus extensorius is slightly turned proximad. The synostosis metacarpalis distalis is short.

Discussion. *"Neanis" kistneri* (Feduccia, 1973) was first described as *Primobucco kistneri*, a member of the Bucconidae (Feduccia, 1973). Together with three more genera, Feduccia & Martin (1976) then referred the species to the Primobucconidae, and transferred *Primobucco kistneri* to the genus *Neanis*. Houde & Olson (1989) regarded the Primobucconidae as a paraphyletic taxon and later referred several genera, which were originally placed into the Primobucconidae by Feduccia & Martin (1976), to the Sandcoleidae. Houde & Olson (1989) regard *"Neanis" kistneri* as "true member(s) of the Galbulae, as evidenced by the structure of the sehnenhalter of the tarsometatarsus" (Houde & Olson, 1989: 2031).

The holotype of *"Neanis" kistneri* clearly exhibits a truly zygodactyl foot with the fourth toe turned backwards and thus differs from the type species of the Primobucconidae, *Primobucco mcgrewi*, which is clearly anisodactyl and belongs to the Coraciiformes s.s. (Mayr *et al*., 2004).

The new specimen is better preserved than the holotype, however, only the dorsal side of the right tarsometatarsus is preserved. Thus, additional information on the sehnenhalter cannot be obtained. Nevertheless, *"Neanis" kistneri* exhibits further characters which it shares with the Galbulae as the shape of the skull, especially of the os frontale, the presence of a fossa temporalis, a large facies articularis of the coracoid and the head of the humerus turned medially. Due to these similarities and the presence of a zygodactyl foot with sehnenhalter, I concur with Houde & Olson (1989) that *"Neanis" kistneri* is indeed related to the Galbulae.

Conclusions

An extensive study of the Green River bird specimens revealed both new species such as the Zygodactylidae, as well as new specimens of already described species. The description of the majority of the bird species from the Green River Formation is based on single specimens. Most of these specimens are fairly complete, but severely crushed and thus reveal only limited information on their taxonomic affinities. Further specimens show important new features that allow new insight into the osteology of these species. For *Messelornis nearctica*, the new specimens show an amount of variation similar to the Messel species *Messelornis cristata*, and the description of *Messelornis nearctica* is revised in several characters. In the case of *Gallinuloides wyomingensis*, the additional data gained from the new specimen allows the recognition of its systematic position as a stem-group representative of the Galliformes (Mayr & Weidig, 2004). The systematic affinities of *"Neanis" kistneri* proposed by Houde & Olson (1989) are supported based on the new specimen.

The Green River Formation consists of deposits of three lakes which all yielded numerous fossils. The lakes range in age from the Upper Paleocene to the Middle Eocene (Grande, 1980). Most of the fossil birds were found in the Lower Eocene deposits of Fossil Lake. They are thus slightly older than the well-known avifauna from Messel (Germany). Many of the bird taxa known from Messel are now also reported from Green River and vice versa (e.g., Mayr, 2000; Mayr *et al*., 2004; Weidig, 2006). With over 340 described specimens, *Messelornis cristata* is by far the most abundant bird from Messel (Hesse, 1990). Until this study, *Messelornis nearctica* from Green River was only known from single specimen. The new specimens reported herein show that the Messelornithidae are among the most abundant species in Green River besides the Presbyornithidae (Feduccia & McGrew, 1975). In contrast hereto, with one respectively two known specimens, early galliforms seem to be rare in both sites. This might be due to different life habits, the early galliforms probably spent considerably less time close to the lakes than *Messelornis*. Messel is especially well known for its abundance of small arboreal birds such as Zygodactylidae, Messelirrisoridae or Gracilitarsidae (Mayr, 1998). With *Eozygodactylus americanus* and the un-named species, the first representatives of Zygodactylidae are now known from the New World. With a total of six specimens in two species, the Zygodactylidae are one of the more abundant avian taxa from the Green River Formation. They are also rather abundant in Messel with twelve specimens in four species (Mayr, 1998; Mayr & Zelenkov 2009). So far, early Galbulae are unknown from Messel or any other contemporaneous site in Europe and might be restricted to the New World.

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