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## PRIMOBUCCO MCGREWI (AVES: CORACII) FROM THE EOCENE GREEN RIVER FORMATION: NEW ANATOMICAL DATA FROM THE EARLIEST CONSTRAINED RECORD OF STEM ROLLERS

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**ABSTRACT**—The Eocene Green River Formation provides one of the richest records of fossil birds worldwide. As part of a reevaluation of this avifauna, we describe 12 new specimens of the stem roller *Primobucco mcgrewi* from the well-dated ( $51.66 \pm 0.09$  Ma) Fossil Butte Member (FBM) of the Green River Formation of Wyoming. FBM specimens represent most of avian diversity in the Green River Formation and include the oldest well-constrained record of the roller lineage (Coracii). These fossils provide new anatomical data, including the first observations on the palate, and broaden our understanding of the distribution, abundance, and taphonomy of *P. mcgrewi*. Using museum records and lithological comparisons, 14 of the 15 known *P. mcgrewi* specimens can now be assigned to specific quarries within Fossil Lake. The species is now known from five distinct localities representing both nearshore and mid-lake environments and accounts for >10% of the 148 FBM avian specimens reviewed in this study. Pectoral elements are disproportionately represented in the FBM *P. mcgrewi* specimens, and more than half of the sample exhibits broken elements. These new fossils and other key specimens from the Eocene of North America and Europe clarify our understanding of the evolution of the clade Coracii. Extant parts of this lineage (i.e., Coraciidae and Brachypteraciidae) have specialized ecologies and restricted Old World distributions, whereas stem representatives appear more generalized and were a major component of some North American avifaunas.

### INTRODUCTION

Rollers (Coracii) are represented by two extant groups: Coraciidae (true rollers) and Brachypteraciidae (ground rollers). Coraciidae are open-area hunters known for their acrobatic display flights, and are presently distributed throughout Asia, Europe, Africa, Madagascar, and Australia (Fry et al., 1992; Fry, 2001). The more terrestrial Brachypteraciidae are primarily leaf-litter foragers and are restricted entirely to Madagascar (Langrand, 2001). All extant rollers are characterized by large heads and colorful plumage. These birds are primarily predaceous, consuming invertebrates and small vertebrates. Stem members of the roller lineage reveal that the elongate wings of Coraciidae and elongate legs of Brachypteraciidae are restricted to those extant clades (Mayr and Mourer-Chauviré, 2000). Hence, the range of ecologies in extinct rollers may have been distinct from that observed in living true rollers and ground rollers.

The roller stem lineage is known from an array of taxa including *Eocoracias brachyptera*, *Geranopterus alatus*, and *Geranopterus milneedwardsi* from the Eocene Messel and Quercy deposits of Europe (Mayr and Mourer-Chauviré, 2000) and *Paracoracias occidentalis* from the Green River Formation (Clarke et al., 2009). *Geranopterus bohemicus*, from the Miocene of the Czech Republic, may represent the youngest pre-Holocene record of Coracii, but is presently known from only a single partial tarsometatarsus (Mayr and Mourer-Chauviré, 2000).

*Primobucco* is the smallest-bodied and most widespread taxon of stem roller. It includes three species: *Primobucco mcgrewi*, *Primobucco perneri*, and *Primobucco frugilegus* (Brodkorb, 1970; Houde and Olson, 1989; Mayr et al., 2004). The first of these species to be named, *Primobucco mcgrewi*, was reported from Eocene Green River Formation deposits by Brodkorb (1970). Initially, the poorly preserved holotype wing was identified as a puffbird (Bucconidae). Houde and Olson (1989) subsequently considered the holotype of *Primobucco mcgrewi* difficult to place within Aves, but noted that a nearly complete referred specimen (USNM 336284) indicated that the species could have affinities to Brachypteraciidae (Atelornithidae of Houde and Olson, 1989). Mayr et al. (2004) formally described this specimen and recognized *Primobucco mcgrewi* as a stem roller. These authors also described two new European species (*Primobucco perneri* and *Primobucco frugilegus*) from the early middle Eocene Messel deposits and assigned a partial tarsometatarsus from the early Eocene of Condé-en-Brie, France, to *Primobucconidae* indet. Two specimens of *Primobucco frugilegus* preserve seeds as gut contents (Mayr et al., 2004), and one specimen of *Eocoracias brachyptera* preserves a single seed within the stomach area (Mayr and Mourer-Chauviré, 2000). Hence, basal rollers appear to have had a more omnivorous diet than their extant relatives (Mayr et al., 2004). Among the 12 living species of true rollers, only *Coracias garrulus* (European Roller) is known to habitually consume fruits (grapes and figs; Fry, 2001). Additionally, *Coracias cyanogaster* (Blue-bellied Roller) has been documented occasionally taking oil-palm nuts (Fry et al., 1992). Brachypteraciidae are entirely predaceous (Langrand, 2001).

As part of a major ongoing reevaluation of the abundant and exceptionally preserved avian specimens from the Fossil Butte Member (FBM) of the Eocene Green River Formation, we

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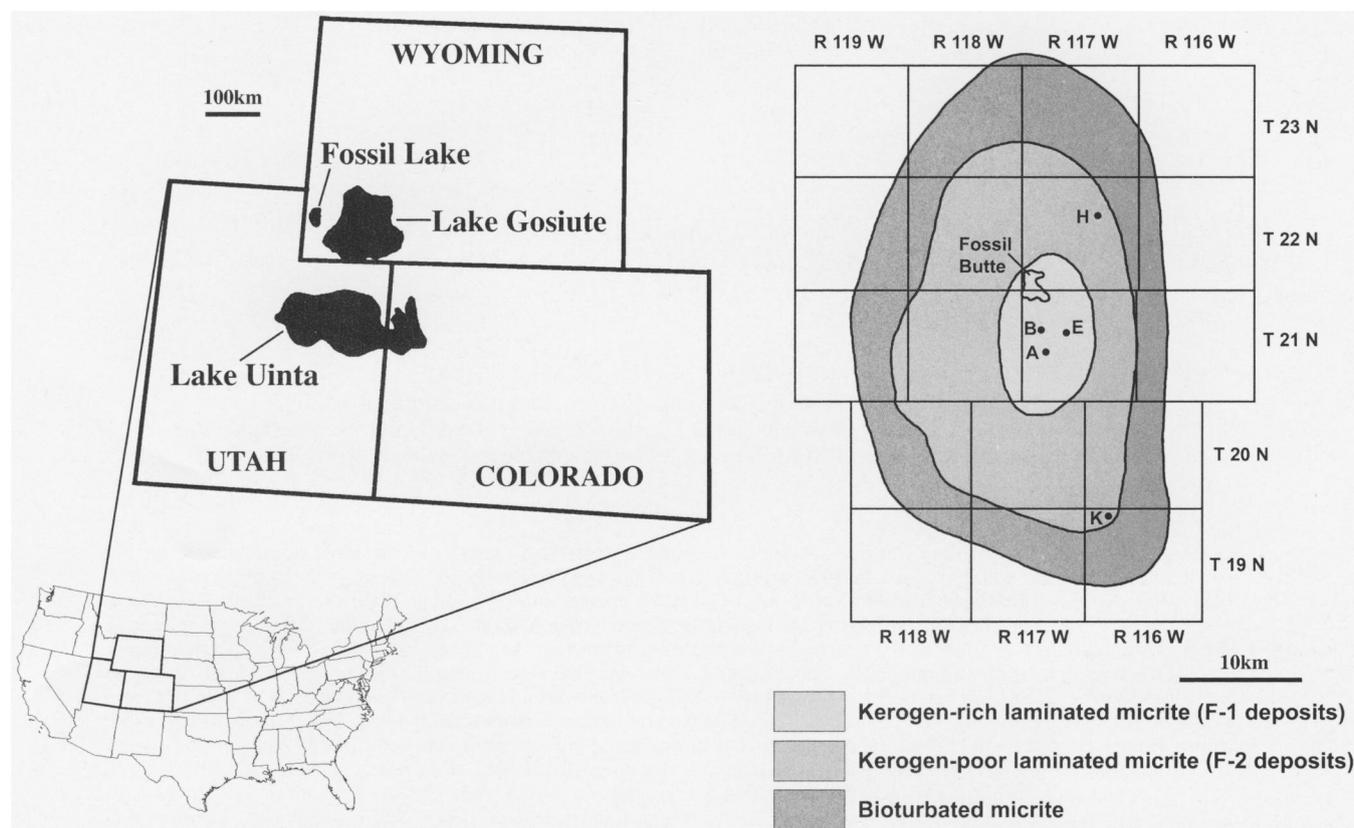


FIGURE 1. Map showing the extent of the Green River Lake Complex during the late early Eocene, modified from Grande and Buchheim (1994). Fossil Lake is enlarged at right, with localities of the Fossil Butte Member that have yielded *Primobucco mcgrewi* specimens labeled. Locality letters and the distribution of the three major lithotypes (i.e., KRLM, KPLM, and BM) correspond to the system of Grande and Buchheim (1994): **A**, locality A, Lewis Ranch site 1 (F-1); **B**, locality B, Lewis Ranch site 2 (F-1); **E**, locality E, Wyoming State Commercial site 1 (F-1); **H**, locality H, Thompson Ranch (F-2); **K**, locality K, Warfield Springs (F-2 equivalent deposits).

identified 12 undescribed fossils assignable to *Primobucco mcgrewi*. The FBM deposits have yielded the majority of avian species described thus far from the Green River Formation, and many additional species remain undescribed. They represent an essentially contemporaneous sample of nearshore and mid-lake deposits from Fossil Lake, the smallest of the major Green River lakes (Fig. 1; McGrew and Casilliano, 1975; Grande, 1984, 1994, 2001; Buchheim, 1994a, 1998; Grande and Buchheim, 1998). Arguably, this is the best sample and closest approximation of a single avifauna from the Eocene of North America. The vast majority of avian fossils from the Green River Formation are derived from the middle unit of the FBM. The upper bound of the middle unit is a K-spar tuff for which Buchheim and Eugster (1998) reported an  $^{40}\text{Ar}/^{39}\text{Ar}$  age of  $50.2 \pm 1.9$  Ma. More recently, Smith et al. (2008) refined the age of this tuff to  $51.66 \pm 0.09$  Ma from multicrystal analyses (sanidine) yielding Gaussian-distributed apparent ages with few outliers. The fossil-bearing deposits under study have been identified to the lower and middle units within the FBM (Buchheim, 1994a, 1998).

Here, previously unreported aspects of the morphology of *Primobucco mcgrewi* are described, and the known distribution of this species within Fossil Lake is expanded. Hitherto known from only three specimens, *P. mcgrewi* is now represented by at least 15 individuals from multiple localities. This species is now recognized as one of the most common components of the Fossil Lake avifauna. Because the holotype (UWGM 3299) consists only of a right wing (Brodkorb, 1970) and the first referred specimen consists of a right wing associated with parts of the pectoral girdle (UWGM 14563; Mayr et al., 2004), most of our understanding of

this species has previously come from a third, nearly complete referred skeleton (USNM 336284; Houde and Olson, 1989; Mayr et al., 2004). Though most elements are intact in USNM 336284, preservation is poor in several key regions of the skeleton (e.g., pectoral girdle) and the skull only allows assessment in lateral view. Thus, the new specimens fill in important gaps in our knowledge of the morphology of *Primobucco mcgrewi*.

#### TAXONOMIC REMARKS

The taxonomic history of “Primobucconidae” is complex. This reflects an evolving understanding of the relationships of extinct Eocene taxa, motivated by advances in avian phylogenetics and the discovery of more complete fossils. Until recently, the taxon Primobucconidae has consistently included a group of species now understood to represent a polyphyletic assemblage with little bearing on the evolutionary history of rollers (Mayr et al., 2004).

Brodkorb (1970) named *Primobucco mcgrewi* from a single fragmentary specimen, considering it to be a member of the Bucconidae (puffbirds). Shortly thereafter, Feduccia (1973) named the species “*Primobucco*” *kistneri* from a more complete skeleton. Feduccia and Martin (1976) transferred “*Primobucco*” *kistneri* to “*Neanis*” *kistneri* and coined the family name Primobucconidae, which they considered to belong within Galbulae (puffbirds and jacamars). These authors included eight species in the family: *Primobucco mcgrewi*, “*Primobucco*” *olsoni*, *Neanis schucherti*, “*Neanis*” *kistneri*, *Uintornis lucaris*, *Uintornis marionae*, *Botauroides parvus*, and

*Eobucco brodkorbi*. However, subsequent work has revealed “Primobucconidae” sensu Feduccia and Martin (1976) to be polyphyletic.

Houde and Olson (1989) recognized that “Primobucconidae” (sensu Feduccia and Martin, 1976) incorporated taxa from at least three unrelated avian groups. These authors removed four species (*Uintornis lucaris*, *Uintornis marionae*, *Botauroides parvus*, and *Eobucco brodkorbi*) from Primobucconidae and referred them to Sandcoleiformes (Houde and Olsen, 1992), a clade now understood to be part of the Coliiformes stem group (mousebirds; Mayr and Peters, 1998). Mayr (2002) subsequently recognized “*Primobucco*” *olsoni* as a stem member of Psittaciformes (parrots) and referred the species to *Pulchrapollia* (Psittaciformes: Pseudasturidae). Mayr (2005a) also recognized *Neanis schucherti* as part of Gracilitarsidae, an extinct clade of Pici-formes (woodpeckers, toucans, puffbirds and allies).

The relationships of “*Neanis*” *kistneri* remain uncertain. Feduccia (1973) provided essentially no description or diagnosis. However, the presence of a zygodactyl foot clearly precludes affinities with Coracii. As noted by Houde and Olson (1989), the holotype specimen differs markedly from *Neanis schucherti* and further lacks important diagnostic features of the family Gracilitarsidae (proximally expanded humerus and slender, elongate tarsometatarsus exceeding the humerus in length). Thus, “*Neanis*” *kistneri* should be removed from *Neanis*, preferably in the context of a proper diagnosis and complete description.

Two incomplete bones from the early Eocene London Clay were previously considered to represent European occurrences of Primobucconidae. Olson and Feduccia (1979) referred the holotype of *Parvicuculus minor* (a partial tarsometatarsus) to Primobucconidae, although Harrison (1982) disputed this assignment and instead argued for affinities with Cuculiformes (cuckoos and allies). Mayr and Mourer-Chauviré (2004) described a second specimen of *Parvicuculus*, and concluded there is no evidence for placing this taxon within either Coracii or Cuculiformes. Harrison (1982), in the same article arguing for the exclusion of *Parvicuculus minor* from Primobucconidae, assigned a less complete proximal tarsometatarsus to the group. Though the affinities of this second London Clay specimen remain uncertain, the lack of the sharp, proximodistally elongate medial hypotarsal crest (see Harrison, 1982:fig. 4a and text), a feature present in stem and crown rollers, indicates this specimen is not closely related to Coracii. Mayr (2005b) noted that *Primobucco* may nonetheless be represented in the early Eocene of England (pers. comm. from M. Daniels in Mayr, 2005b), though the material forming the basis for this observation has yet to be published.

The above-mentioned taxonomic revisions indicate there are currently three valid species assignable to *Primobucco*, the sole genus retained in Primobucconidae (Mayr et al., 2004). *Primobucco mcgrewi* is the only North American species. Cracraft (1971, 1981) proposed a classification of rollers reflecting the phylogenetic relationships of extant taxa that includes the higher taxa Coracii and Coracioidea. Clarke et al. (2009), applying these names in the context of extinct diversity, suggest that the name Coracii be used for the clade uniting all stem and crown members of the roller total group (including *Primobucco*), and that the name Coracioidea be used for the crown clade of rollers (Coraciidae + Brachypteraciidae). We employ this taxonomy throughout this paper. The Coracii affinities of *Primobucco* are well supported (Mayr et al., 2004; Clarke et al., 2009). Although the three recognized species are strikingly similar in morphology, it should be noted that support for monophyly of *Primobucco* (or Primobucconidae) was not recovered in a recent analysis (Clarke et al., 2009). *Primobucco* species were recovered in an unresolved polytomy at the base of Coracii. These three species differ primarily in size and proportions (Mayr et al., 2004).

**Institutional Abbreviations**—**FMNH**: Department of Geology, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **SMF**: Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; **USNM**: National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.; **UWGM**: University of Wyoming Geological Museum, Laramie, Wyoming, U.S.A.; **WSGS**: Wyoming State Geological Survey, Laramie, Wyoming, U.S.A.

#### SYSTEMATIC PALEONTOLOGY

CORACIIFORMES Forbes, 1884  
CORACII Wetmore and Miller, 1926  
*PRIMOBUCCO MCGREWI* Brodkorb, 1970

**Holotype**—UWGM 3299 (partial wing)

**Referred Specimens**—(newly referred specimens indicated with asterisks; see Tables 1–2 and Figs. 2–5): FMNH PA 345\*, FMNH PA 346\*, FMNH PA 611\*, FMNH PA 724\*, FMNH PA 733\*, FMNH PA 735\*, FMNH PA 737\*, FMNH PA 738\*, FMNH PA 758\*, FMNH PA 759\*, UWGM 14563, USNM 336284, WSGS U-93-1A\*.

**Locality and Horizon**—Fossil Butte Member of the Eocene Green River Formation, Wyoming. Approximately  $51.66 \pm 0.09$  Ma in age (Smith et al., 2008). See Table 1 for quarry data for individual specimens.

**Emended Diagnosis**—The 12 newly referred specimens are identical in morphology and proportions to the previously identified specimens of *Primobucco mcgrewi* for all anatomical elements preserved in common. All specimens are within 10% of the size of the holotype and previously referred specimens. The differential diagnosis from the two European *Primobucco* species offered by Mayr et al. (2004) is confirmed with this larger sample. *Primobucco mcgrewi* is significantly smaller than *Primobucco frugilegus* (Table 2; compare table 1 of Mayr et al., 2004) and differs in proportions of the rostrum and hind limb from *Primobucco perneri* (Mayr et al., 2004). The new sample cannot speak to hind limb proportions, though it confirms a shorter rostrum (relative to total skull length) as a diagnostic feature of *Primobucco mcgrewi* relative to *Primobucco perneri*. We also identify a more shallow medial insure of the caudal margin of the sternum as diagnostic for *Primobucco mcgrewi* relative to *Primobucco perneri* (condition unknown in *Primobucco frugilegus*).

**Description and Comparison**—The description focuses on elements and morphologies of the new specimens that were unknown or undescribed from previously reported material. Unless otherwise indicated, features noted are present in all specimens preserving the element. For morphologies that are observable in only a few exemplars, the relevant specimen numbers are cited.

Complete skulls are preserved in FMNH PA 724+758, and a partial skull is preserved in FMNH PA 733. As in other Coracii, the skull of *Primobucco mcgrewi* is large relative to body size. The beak is triangular and relatively narrow. In ventral view (FMNH PA 758), the beak shape is similar to extant *Coracias* and unlike the wide-beaked *Eurystomus*. The frontals narrow notably between the orbits, and a fully ossified interorbital septum is present (FMNH PA 733). A nasal septum was reported as absent in one specimen of *Primobucco mcgrewi* by Mayr et al. (2004), and FMNH PA 724 appears to confirm this feature. In Coracioidea, a complete nasal septum is present (Cracraft, 1971). As in other Coracii, the head of the lacrimal is expanded (FMNH PA 724), though the descending process is not well preserved in any specimen. The postorbital process is elongate, slender, and subcylindrical, but is damaged or obscured in all specimens. As preserved in both FMNH PA 724 and FMNH PA 733, the postorbital process contacts the jugal bar. However, this appears to be the result of crushing given the relatively short length of the process and compression of the skulls. In FMNH PA 758, only the ventral tips of the processes are visible. It seems most likely that

TABLE 1. Locality data and completeness of known *Primobucco mcgrewi* specimens.

Specimen	Elements preserved	Broken elements	Locality	Facies
FMNH PA 345	Partially articulated pectoral girdle, wings and ribs	Yes	A	F-1
FMNH PA 346	Disarticulated pectoral girdle wings, and ribs	No	K	F-2 southeastern equivalent (Warfield Springs)
FMNH PA 611	Partially articulated pectoral girdle, wings and ribs	Yes	B	F-1
FMNH PA 724	Articulated skull, vertebrae, pectoral girdle and wings	No	H	F-2
FMNH PA 733	Partial skull and associated mandible	Yes	H	F-2
FMNH PA 735	Articulated partial pectoral girdle and left wing	Yes	H	F-2
FMNH PA 737	Partially articulated pectoral girdle and wings	No	H	F-2
FMNH PA 738	Articulated vertebrae, pectoral girdle and wings	Yes	H	F-2
FMNH PA 758	Articulated skull, vertebrae, pectoral girdle and wings	Yes	H	F-2
FMNH PA 759	Partially articulated pectoral girdle and wings, ribs	No	H	F-2
USNM 336484	Near-complete articulated skeleton lacking left hindlimb	Yes	H	F-2
UWGM 3299 (holotype)	Articulated wing	No	?	F-1
UWGM 12545	Partially articulated pectoral girdle, wings, vertebrae and ribs	No	H	F-2
UWGM 14563	Partially articulated pectoral girdle and wing, vertebrae and ribs (separate from girdle)	No	E	F-1
WSGS U-93-1A	Partially articulated pectoral girdle and largely articulated wings, thoracic vertebrae, scattered ribs	Yes	E	F-1

Locality and facies definitions follow Grande and Bucheim (1994). See Figure 1 for distribution of localities. F-1 deposits are from the mid-lake and F-2 are from the northeastern near-shore.

in life, the postorbital process was elongate but did not contact the jugal bar. The left temporal fossa is exposed in FMNH PA 733 and appears to have been shallow, but preservation is poor and better specimens are desirable to confirm this observation.

Palatal elements are exposed in dorsal view in FMNH PA 733 and ventral view in FMNH PA 758. Splitting of the anterior portion of the skull in FMNH PA 733 reveals the right palatine in dorsomedial view. The palatine has a convex posterior margin. An elongate, narrow strip of bone is identified as the maxillary process of the right palatine. The substantial length of this process is similar to the condition in Brachypteraciidae, as well as *Momotus momota* (Momotidae) and *Merops ornatus* (Meropidae). In Coraciidae, however, the maxillary process extends only a short distance before fusing with the maxilla. The pterygoids are largely exposed in FMNH PA 758 and have a more expanded anterior end than extant Coracioidea. The occipital condyle is very small. A moderately deep subcondylar fossa is present anterior to the condyle. The basal tubera are projected, but less so than in extant Coracioidea. Both quadrates are exposed in caudal view in FMNH PA 758. The otic process is broad and lacks the small pneumatic foramina present in some clades closely related to Coracii (Alcedinidae, Meropidae, Todidae, Momotidae, Upupiformes; Mayr et al., 2003). A small portion of one ceratobranchial is visible, but the urohyal, basihyal, and paraglossale are missing.

The mandibular symphysis is short (~1/5 the length of the mandible). A caudal mandibular fenestra is absent in all specimens. The articular region is exposed in lateral and ventral views. As far as can be observed, the projection of the medial process and absence of a retroarticular process resembles the condition seen in extant Coraciidae.

Because few of the new specimens preserve thoracic vertebrae, the vertebral formula remains uncertain. FMNH PA 758 has at least 19 presacral vertebrae and is the only specimen to preserve a small fragment of the sacrum. Because parts of the pectoral girdle overlay the semi-disarticulated vertebrae, it is possible that an additional thoracic vertebra may be hidden. Vertebrae 12–15 bear strong ventral hypapophyses. The ventral face of the 16th vertebra is not visible, but more posterior elements lack hypapophyses. Large depressions mark the lateral faces of the thoracic vertebrae in FMNH PA 738 and FMNH PA 758, and the centra are strongly constricted. The anterior-most sacral vertebra is pre-

served in FMNH PA 758 and also bears a deep lateral depression or fossa. In extant Coracioidea, the thoracic vertebral centra are less constricted and lateral depressions are absent. However, a large pneumatic foramen is present on the lateral face of the centrum of the 13th transitional cervicothoracic vertebra in all representatives of extant Coracii we examined. This foramen is also variably developed in the 14th vertebra in these extant taxa.

The carina extends the entire length of the sternum (FMNH PA 346, FMNH PA 724). An external spine is present and well developed, whereas an internal spine is absent. A large foramen perforates the base of the external spine (FMNH PA 735), a feature shared with extant Coracii. As in Brachypteraciidae, the dorsal surface of the sternum in *Primobucco mcgrewi* lacks pneumatic foramina. A single large foramen is present in Coraciidae. Five ribs articulate with the sternum in FMNH PA 724, as in Coraciidae and the fossil *Eocoracias brachyptera* (Mayr and Mourer-Chauviré, 2000). Only four ribs contact the sternum in Brachypteraciidae. Small pneumatic foramina perforate the sternum at the costal articulations in Coraciidae, but these appear to be absent in *Primobucco mcgrewi*. In all specimens preserving the sternum, the caudal margin is squared, differing from the more angled reconstruction presented for *Primobucco perneri* by Mayr et al. (2004:fig. 1A) and resembling the condition in extant Coraciidae (e.g., Cracraft, 1971:fig. 10). Four caudal incisurae are present. Mayr et al. (2004) described the medial incisure as reaching nearly half the length of the sternum in *Primobucco mcgrewi* and *Primobucco perneri*. However, in all specimens of *Primobucco mcgrewi* preserving the complete sternum (FMNH PA 346, FMNH PA 724, FMNH PA 738, FMNH PA 758), the medial incisure is shallow (the sternum is damaged in USNM 336284). Posteriorly, the slender medial trabeculae show a slight expansion. The broader lateral trabeculae terminate in a wide, inverted triangle-shaped tip. The furcula is U-shaped. The rami are mediolaterally flattened at the omal ends and become more cylindrical near the symphysis. At the symphysis there is a slight thickening, but a hypocleidium is absent. The coracoid has a proximodistally short procoracoid process and lacks a supracoracoid nerve foramen as noted by Mayr et al. (2004). The medial margin is smooth, with a minute notch located at approximately the same level as the tip of the lateral process. The lateral process is well projected and oriented anterolaterally. In dorsal view, the articular facet for the sternum is bounded distally by a strong

TABLE 2. Measurements (in millimeters) of major elements of *Primobucco mcgrewi*.

	FMNH PA 345	FMNH PA 346	FMNH PA 611	FMNH PA 724	FMNH PA 735	FMNH PA PA737	FMNH PA 738	FMNH PA 758	UWGM 3299	UWGM 12545	USNM 336484	UWGM 14563	WGS U-93-1A
Skull				39.7				41.0			40.5		
Mandible								~32.5		15.0/—			16.9/16.3
Mandibular symphysis								6.4	—/27.2	25.3/—	~28/~27	26.8/—	28.4/28.7
Sternum		20.6				22.3		~23.7	—/~34.5		~33/~33.5		35.4/34.6
Furcula	~16.1/~16.5	14.6							—/30.4				32.2/32.6
Coracoid		15.8/15.8	—/16.5		—/16.3			16.1/16.2	—/14.5		15.3/—	15.7/—	15.0/15.5
Scapula		23.3/21+											4.5/—
Humerus	27.4 /	~26/25.8	~28/~28	—/28.1	—/26.0	—/26.8		—/26.2	—/7.0		6.8/—		6.5/—
Ulna		30.8/—	33.8/—	34.7/33.7	—/32.5	—/~33		—/32.8	—/4.7		5.3/—		5.4/—
Radius		28.9/—	32.7/31.7	—/33.1		~30/—		—/31.6					
Carpometacarpus	~15.5	14.0/—	4.4/—	15.8/—		~14.5/—		15.2/14.5			~19/—		
Phalanx I-1		4.3/—	6.7/6.6	~4.5				4.5/—			26.7/—		
Phalanx II-1		6.5/—	5.0/4.9	—/7.1				7.1/7.0			~13.1/—		
Phalanx II-2				5.2/5.5	—/5.5			5.0/5.3					
Phalanx III-1			—/3.0										
Femur													
Tibiotarsus													
Tarsometatarsus													

When elements from both sides could be measured, values are presented in the format (right/left). No complete elements can be measured for FMNH PA733 or FMNH PA759.

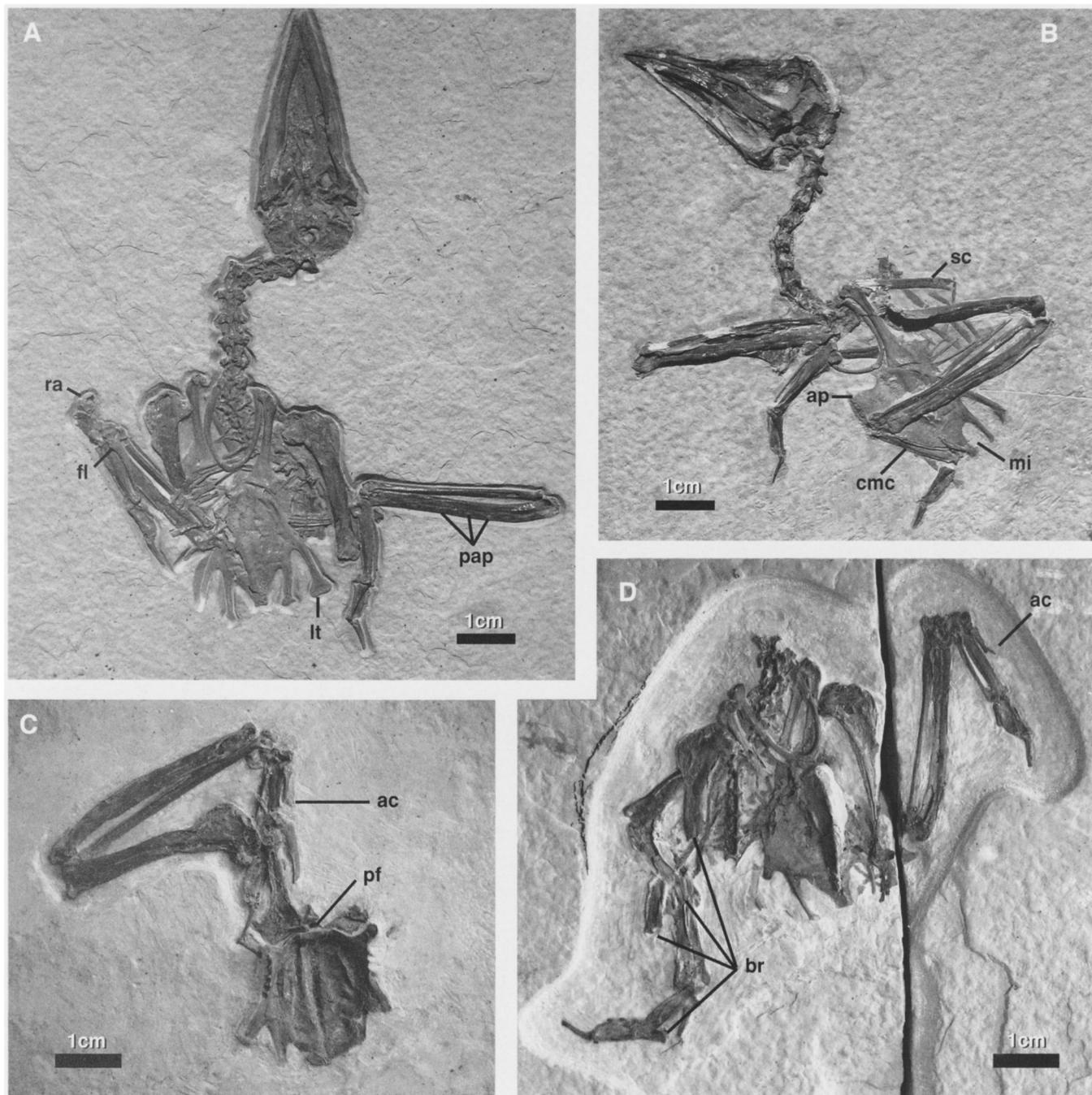


FIGURE 2. Specimens of *Primobucco mcgrewi* from locality H. **A**, FMNH PA 758; **B**, FMNH PA 724; **C**, FMNH PA 735; **D**, FMNH PA 738. **Abbreviations:** ac, alular claw; ap, apex of sternal keel; br, broken bones; cmc, carpometacarpus (partially overlain by sternum); fl, ventral flange on metacarpal III (see text); lt, lateral trabecula; mi, medial incisure; pap, feather papillae; pf, pneumatic foramen at base of external spine; ra, radiale; sc, scapula.

lip (FMNH PA 735), in agreement with extant Coraciidae and Brachypteraciidae.

The dorsal tubercle of the humerus is worn but appears to have been caudally oriented in FMNH PA 735. A shallow depression is present on the anterior face of the ulnar condyle as noted by Mayr et al. (2004). This feature is variably developed in extant Coracii and is seen in some other 'higher land bird' clades (e.g., Alcedinidae). Other details of the humerus were described by Mayr et al. (2004). Feather papillae are very weak or indistinguishable on the ulna in most specimens. Six secondary insertion

sites can be counted in FMNH PA 758, with a seventh possibly present but obscured by breakage. In FMNH PA 738, the left ulnare is free and overlies the ulna; the ulnare is also exposed in FMNH PA 346. The length of the crus longus of the ulnare slightly exceeds the length of the crus brevis in both specimens, in agreement with *Primobucco perneri*.

As previously noted by Mayr et al. (2004), the proximal portion of metacarpal III bears a ventrally projected flange considered synapomorphic for Coracii. In some extant Coracioidea, there is a foramen perforating this flange; however, this feature

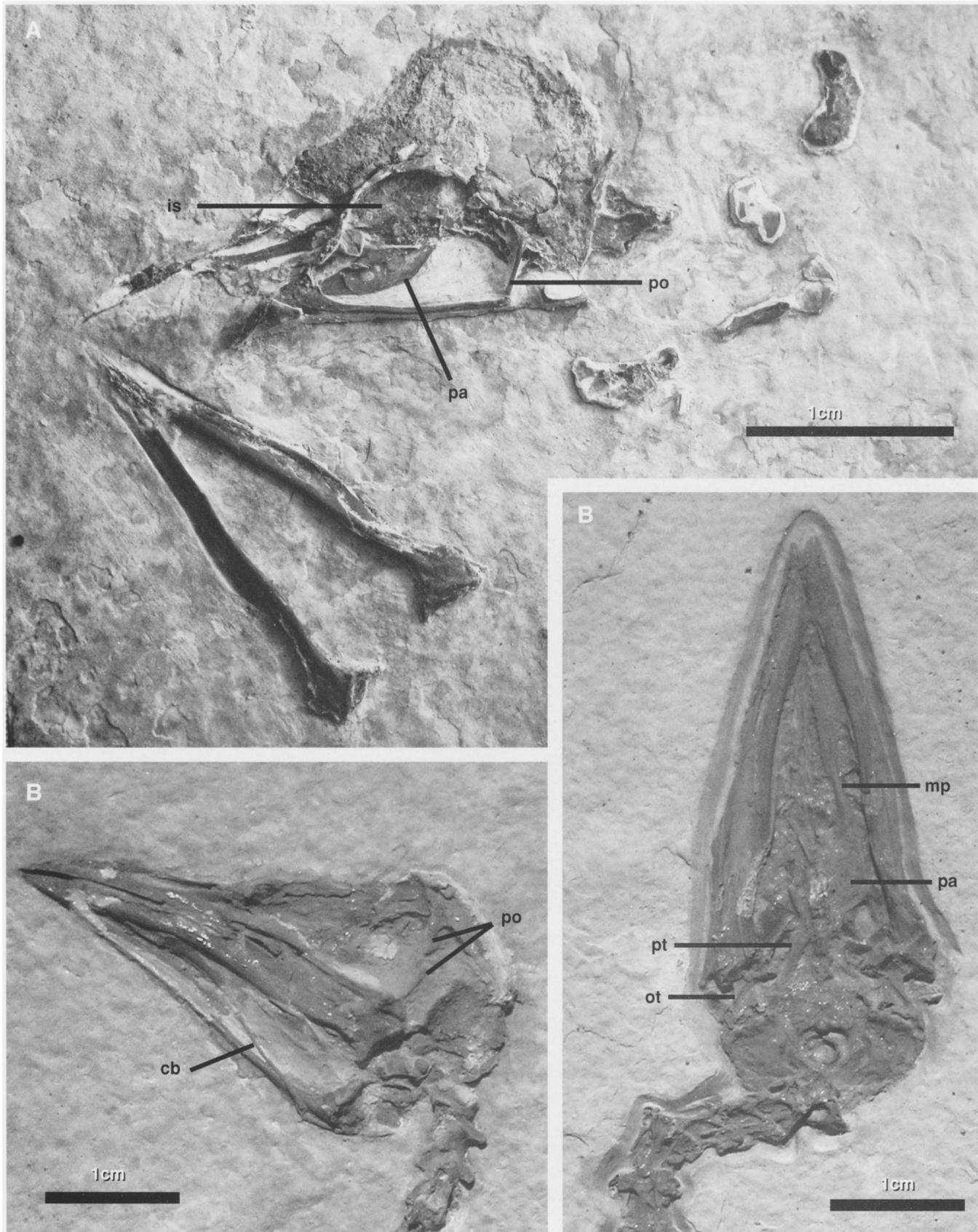


FIGURE 3. Skulls of *Primobucco mcgrewi* from locality H. **A**, FMNH PA 733; **B**, FMNH PA 724; **C**, FMNH PA 758. **Abbreviations:** **cb**, ceratobranchial; **is**, interorbital septum; **mp**, maxillary process of palatine; **ot**, otic process of quadrate; **pa**, palatine; **po**, postorbital process (broken in FMNH PA 724).

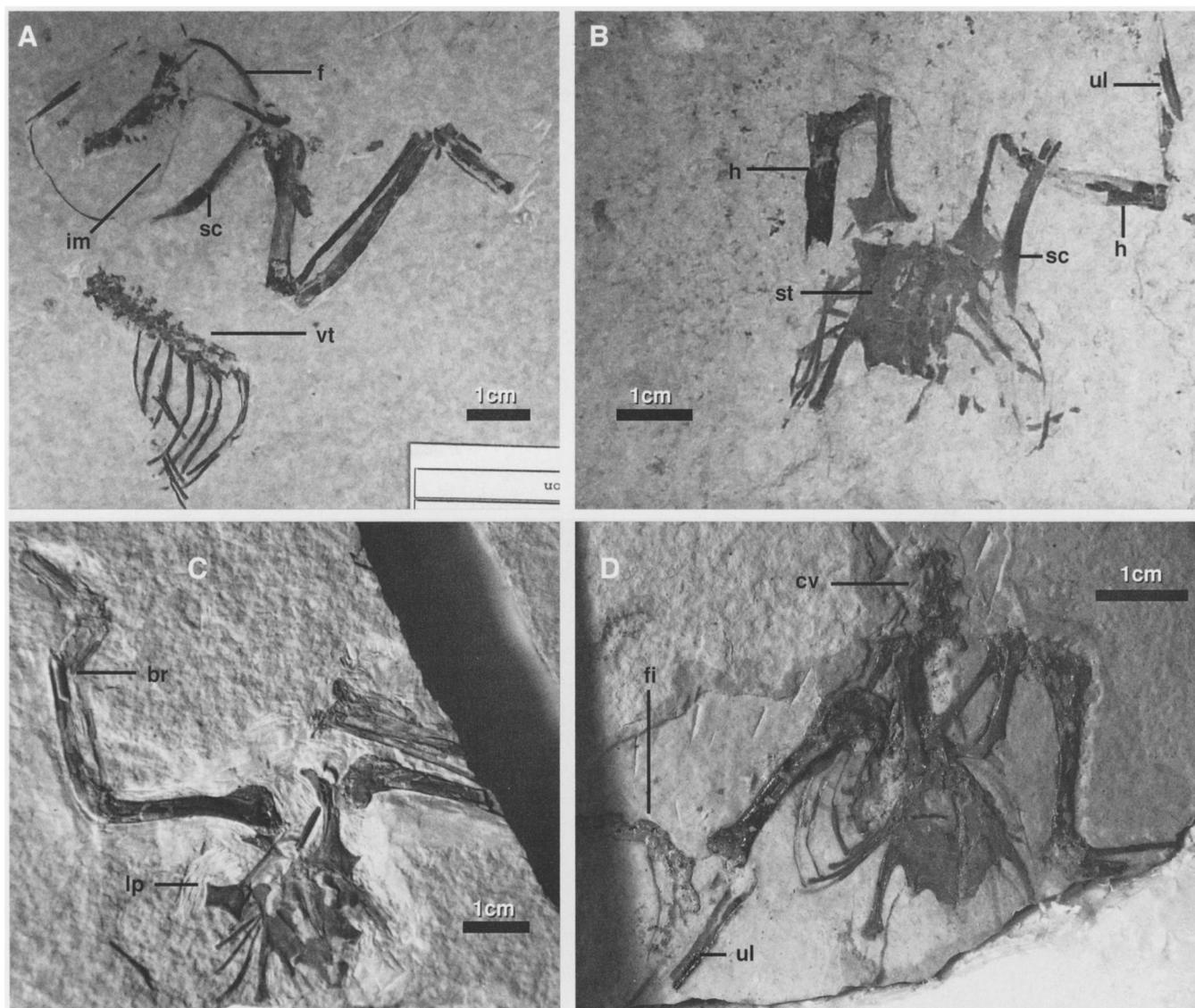


FIGURE 4. Specimens of *Primobucco mcgrewi*. **A**, UWGM 14563 (locality E); **B**, FMNH PA 759 (locality H); **C**, FMNH PA 345 (locality A); **D**, UWGM 12545 (locality H). **Abbreviations:** br, broken bones; cv, cervical vertebrae; f, furcula; fi, fish vertebrae; h, humerus; im, impression of lateral trabecula of sternum; lp, lateral process of coracoid; sc, scapula; st, sternum; ul, ulna; vt, articulated cervical and thoracic vertebra. Note that portions of UWGM 14563 and FMNH PA 759 are preserved as impressions and were lost in the splitting of the slab, not by perimortem/postmortem breakage.

is unambiguously absent in multiple specimens of *Primobucco mcgrewi* (FMNH PA 346, FMNH PA 735, FMNH PA 758). The intermetacarpal process is very weak and the pisiform process is spike-like. In FMNH PA 758, a depression separates the extensor process and the pisiform process. A similarly placed but deeper depression occurs in *Geranopterus alatus*, another extinct representative of Coracii (Mayr and Mourer-Chauviré, 2000). Metacarpal III projects slightly beyond the distal margin of metacarpal II. In all specimens where the hand is articulated, the alular phalanx bears a small claw. An alular claw is also present in *Primobucco perneri* (Mayr et al., 2004). Phalanx II-1 has a very weakly projected internal indicus process. In this respect, *Primobucco mcgrewi* resembles Brachypteraciidae but differs from Coraciidae and the stem species *Eocoracias brachyptera*. The latter taxa have an internal indicus process that is more distally projected and distinct. Phalanx II-2 is quite narrow and rod-like throughout its length, differing from the more tapering phalanx II-2 of extant rollers.

## DISCUSSION

FBM records of *Primobucco mcgrewi* place the earliest phylogenetically and temporally constrained occurrence of stem Coracii at  $51.66 \pm 0.09$  Ma (Smith et al., 2008). A second stem roller from the Green River Formation cannot currently be assigned to a specific horizon (Clarke et al., 2009). The tarsometatarsus from Condé-en-Brie assigned to Primobucconidae indet. by Mayr et al. (2004) is also from the early Eocene. The age range of this fossil (MP zones 8–9; Schmitdt-Kittler, 1987) indicates it could be contemporaneous with or slightly older than the FBM *P. mcgrewi* specimens. Regardless, more substantial material is desirable to confirm the affinities of this tarsometatarsus to Coracii. Slightly younger records include the Messel taxa *Primobucco frugilegus*, *Primobucco perneri*, and *Eocoracias brachyptera*. These are dated to approximately 47 Ma based on a  $47.8 \pm 0.2$   $^{40}\text{Ar}/^{39}\text{Ar}$  age obtained from the basalt chimney below Lake Messel (Mertz et al., 2004) and

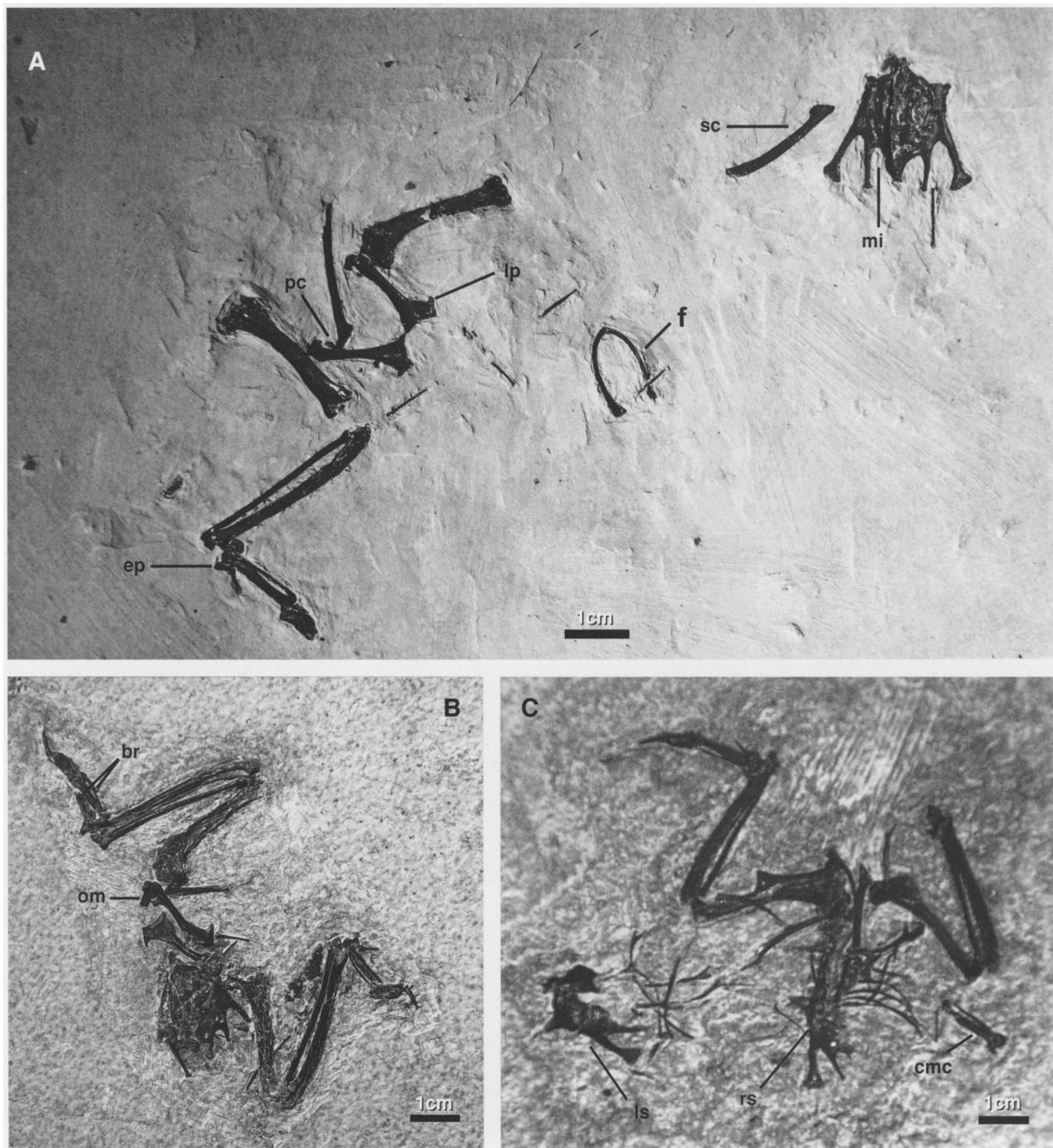


FIGURE 5. Specimens of *Primobucco mcgrewi*. **A**, FMNH PA 346 (locality K); **B**, FMNH PA 611 (locality B); **C**, WSGS U-93-1A (locality E). **Abbreviations:** **br**, broken bone; **cmc**, carpalometacarpus; **ep**, extensor process of carpalometacarpus; **f**, furcula; **lp**, lateral process of coracoid; **ls**, left half of sternum; **mi**, medial incisure of sternum; **om**, omal end of scapula; **pc**, procoracoid process; **rs**, right half of sternum; **sc**, scapula.

accounting for sedimentation rate (Franzen, 2005). Previously reported occurrences of Primobucconidae from the early Eocene London Clay appear to be erroneous (see Taxonomic Remarks above). The unpublished, privately held London Clay specimens mentioned by Mayr et al. (2005) were noted as early Eocene, and

if confirmed would be nearly contemporaneous with the FBM *Primobucco mcgrewi* specimens.

The 12 new specimens treated in this paper are identified to mid-lake or nearshore FBM deposits and can further be assigned to specific quarries by collection records and lithological

comparisons (L. Grande, pers. comm.). Moreover, two of the three previously reported specimens of *P. mcgrewi* can now be identified to specific quarries for the first time.

The FBM preserves a rich flora and fauna (e.g., MacGinitie, 1969; Feldman et al., 1981; Grande, 1984; Cushman, 1999; Carvalho et al., 2004; Conrad et al., 2007; Simmons et al., 2008) that indicates a tropical to subtropical forested environment surrounded Fossil Lake during the Eocene (MacGinitie, 1969; Grande, 1994; Buchheim, 1998). A freshwater environment is strongly supported by the biota recovered from the fossiliferous layers of the middle unit of the FBM, though more saline conditions may have predominated at other periods in the history of Fossil Lake (Buchheim, 1994b; Grande, 1994; Buchheim, 1998).

A map showing the distribution of specimens referenced in this paper is presented in Fig. 1. Ten *Primobucco mcgrewi* specimens are from nearshore environments (Table 1; F-2 of Grande and Buchheim, 1994). Nine of these are from the Thompson Ranch locality (locality H of Grande and Buchheim, 1994) situated in the northeastern region of Fossil Lake, and the 10th specimen was collected from nearshore F-2 equivalent deposits from the Warfield Springs locality in the southern part of the lake (locality K of Grande and Buchheim, 1994).

The remaining five *Primobucco mcgrewi* specimens were collected from mid-lake (F-1) deposits (Fig. 1). One specimen was recovered from Lewis Ranch site 1 (locality A of Grande and Buchheim, 1994) and one from Lewis Ranch site 2 (locality B of Grande and Buchheim, 1994). Two specimens were collected from Wyoming State commercial site 1 (locality E of Grande and Buchheim, 1994). Unfortunately, the holotype (UWGM 3299) cannot be assigned to a particular quarry, though the lithology indicates it is derived from F-1 deposits (L. Grande, pers. comm.)

*Primobucco mcgrewi* specimens are thus distributed throughout Fossil Lake, but more common in nearshore deposits. Elements preserved and pattern of disarticulation are broadly similar in nearshore and mid-lake deposits. The most complete specimens, including all known skulls, are from nearshore F-2 deposits. The level of articulation for all reported *Primobucco mcgrewi* specimens is summarized in Table 1. Broken bones are common in specimens from both nearshore and mid-lake facies. Eight of the 15 specimens show such breakage. Because all individuals are missing at least some elements, broken bones could represent perimortem or postmortem damage. Pectoral elements are disproportionately represented. We found a single isolated skull and identified no isolated pelvic elements assignable to *Primobucco mcgrewi* in our survey of 148 avian fossils from the FBM. Because the tarsometatarsus of *Primobucco* is distinct from other known Green River species, it is unlikely these observations are biased by a failure to identify less complete specimens, though collecting bias remains a possibility.

Actualistic studies of avian taphonomy have indicated that the skull is typically one of the first elements to separate from the remainder of the carcass (Oliver and Graham, 1994; Davis and Briggs, 1998). The contrasting degradation pattern in *P. mcgrewi* suggests strong connections between the cervical vertebrae and skull, and the cervical and thoracic vertebrae, perhaps in relation to the relatively large heads of these birds. Three of the six reported specimens of *Primobucco* from the Eocene Messel Lake deposits are complete (Mayr et al., 2004). Two specimens of *Primobucco perneri* (SMF Me 516, SMF Me 3546) preserve the skull and neck in articulation with the pectoral girdle and wing but lack the pelvis and hindlimb, and one otherwise complete specimen of *Primobucco frugilegus* lacks most parts of the hindlimbs (SMF Me 3507). When interpreting taphonomy in the fossil record, it is important to consider not only transport and scavenging effects, but also anatomy. Recognition of a similar sequence of disarticulation in *Primobucco* specimens from Messel provides additional support for the influence of anatomy on the observed degradation pattern.

## CONCLUSIONS

Extant Coraciidae hunt in open environments (Fry et al., 1992; Fry, 2001), whereas most Brachypteraciidae forage on the forest floor (Langrand, 2001). The flora and fauna of the middle unit of the FBM are consistent with Fossil Lake being immediately surrounded by a humid, taxonomically diverse, paratropical lowland forest environment (Buchheim, 1998; Cushman, 1999) similar to that inferred for the fossiliferous deposits of the Grube Messel (Schaal and Ziegler, 1992; Lenz et al., 2005). Some open areas must have been associated with local deltaic environments near the southern part of the lake at Warfield Springs (locality K) (Buchheim, 1994a). Given current sampling, only one of the 15 *Primobucco mcgrewi* specimens is known from those southeastern lake deposits, which along with evidence from wing-shape and diet is consistent with a preference for more closed forested environments for *Primobucco*.

With the addition of 12 specimens of *Primobucco mcgrewi* from multiple localities within Fossil Lake, it is clear that this species was a significant component of the avifauna. Preliminary tallies suggest that this species accounts for >10% of FBM avian specimens, but this may be a slight underestimate. Several FBM additional specimens are represented by single elements that cannot be assigned to a particular clade or species because of their incompleteness, but are consistent in size with *Primobucco mcgrewi*. Today, rollers remain locally abundant in some environments, although their numbers have been impacted significantly by human degradation of the forests that they require for cavity nesting (Fry, 2001) or foraging (Langrand, 2001). Stem rollers from FBM deposits are so far referable to only one species, suggesting appreciable abundance but low diversity for Coracii in the FBM avifauna. Because *Primobucco mcgrewi* is a relatively small bird with a delicate skeleton (as indicated by frequent bone breaks), abundance of this taxon in the FBM more likely reflects true abundance than increased anatomical preservation potential relative to other FBM species. One other species of roller is known from the Green River Formation. *Paracoracias occidentalis* is phylogenetically much closer to the roller crown clade (Clarke et al., 2009), but the exact provenance of the fossil is unknown. Based on lithological comparison, however, it does not appear to have been from FBM deposits (L. Grande, pers. comm.). The current study improves our understanding of one important component of the FBM avifauna. Increased taxonomic sampling and taphonomic evaluation are required to further resolve patterns of diversity and identify potential preservational artifacts.

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