A RADIATION OF COLY-LIKE BIRDS FROM THE EOCENE OF NORTH AMERICA (AVES: SANDCOLEIFORMES NEW ORDER)

Peter Houde and Storrs L. Olson

ABSTRACT. A new order and family (Sandcoleiformes: Sandcoleidae) is erected for the Middle Eocene genera *Eobucco* Feduccia and Martin 1976, *Uintornis* Marsh 1872, and *Botauroides* Shufeldt 1915 of Wyoming and three new genera, *Sandcoleus, Anneavis,* and *Chascacocolius* from the Lower Eocene of Wyoming. Sandcoleiforms were coly-like (Coliidae) in appearance, but they exhibited very different bill specializations. They were not closely related to any extant orders; nevertheless, they were probably closer to colies than to any other birds currently known.

Key words: Eocene, Wyoming, calcareous nodules, Coliiformes, Primobucconidae.

INTRODUCTION

The diversity of known Early Eocene avian fossils from North America has dramatically increased since 1980 with the discovery of abundant vertebrate "microfossils" in calcareous nodules in the Willwood Formation of Wyoming (Houde, 1988). Fossils from this formation were generally known from mudstone and channel-sand deposits (Bown, 1980); thus, these nodules are significant as an overlooked and unexploited resource of fossils in an area that has been the subject of intensive paleontological surveying for more than a century. In addition, they preserve the association and three-dimensional integrity of even extremely fragile fossil skeletons. By contrast, traditional surface collecting and screen-washing techniques typically yield unassociated, fragmentary elements. Non-avian bones are usually much more abundant than avian remains in nodules. The nodule avifauna fills a substantial gap because the species represented are almost completely different from those of the stratigraphically contiguous mudstones. Furthermore, faunal associations are often similar from one nodule to another, suggesting a nonrandom mode of concentration or formation within a distinctive microenvironment.

We have collected and prepared large numbers of bird fossils from calcareous nodules in the Sand Coulee area of the Clarks Fork Basin of Wyoming (Fig. 1) continuously since 1981. Paleognathous carinates (Lithornithiformes Houde 1988) are the most abundant birds in the calcareous nodules and were the first avian group from them to be reported. The next most commonly represented group in the nodule avifauna is an unnamed order, described herein, that includes the genus *Eobucco* Feduccia and Martin 1976 and, probably, *Uintornis* Marsh 1872

and *Botauroides* Shufeldt 1915. *Eobucco, Uintornis,* and *Botauroides* were known only from holotypical tarsometatarsi from the Middle Eocene Bridger Formation, southwestern Wyoming. These genera were previously placed in the Eocene family Primobucconidae Feduccia and Martin 1976. By preparing some of the holotypes of the Primobucconidae for the first time [i.e., *Neanis schuchertii* (Shufeldt 1913), "*Neanis*" *kistneri* (Feduccia 1973), and "*Primobucco*" *olsoni* Feduccia and Martin 1976], we discovered that this family is polyphyletic (Houde and Olson, 1989). Some genera are obligate zygodactyls belonging to the suborder Galbulae of the Coraciiformes (*sensu* Olson, 1985), whereas others are anisodactyl (or of unknown foot structure) and belong to at least three other higher taxa.

We collected numerous specimens of close relatives of *Eobucco* in the calcareous nodules of the Willwood Formation. A minimum of 10 individuals has now been prepared from six different nodules. Included as three-dimensional bones are every skeletal element except the prefrontal, vomer, maxilla, palatine, jugal arch, stapes, some vertebrae, metatarsal I, ribs, and phalanges. These are augmented by an articulated postcranial skeleton with feather impressions from the Lower Eocene Green River Formation, southwestern Wyoming (Fig. 1). It is this assemblage to which we address this paper.

Despite such good skeletal representation, it has proven very difficult to determine the phylogenetic relationships of the *Eobucco* assemblage because it has no close modern relatives. It shares some presumably primitive characters with several disparate orders of predominantly arboreal birds. The greatest number of similarities are shared with the family Coliidae (Coliiformes) (colies, or mousebirds) of Africa, an equally enigmatic group, whereas other characters suggest those of the suborder Pici (Piciformes) or even other orders. Our treatment of this fossil assemblage as a distinct order reflects our conclusion that these birds diverged from all other orders very early during the radiation of higher avian taxa.

MATERIALS AND METHODS

The following abbreviations of institutions are used in this paper: AMNH, American Museum of Natural History, New York; BMS, Buffalo Museum of Science, Buffalo, New York; UKVP, Museum of Natural History, University of Kansas, Lawrence; UM, Museum of Paleontology, University of Michigan, Ann

Arbor; UNSM, University of Nebraska State Museum, Lincoln; USNM, National Museum of Natural History, Washington, D.C.; UWGM, Geological Museum of the University of Wyoming, Laramie; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Anatomical terminology follows Baumel (1979) and Vanden Berge (1979). Measurements are given in millimeters (mm).

Calcareous nodules from the Willwood Formation found at or near the surface of the ground were examined for external evidence of vertebrate fossils. Those exhibiting no fossils were broken into successively smaller fragments until fossils were found or until it was determined that no fossils were present. Damaged fossils were repaired with polyvinyl acetate, cyanoacrylate, or polyester laminating resin. The fossiliferous carbonate rock was slowly dissolved in a 7–12 percent solution of acetic acid for 2 days at a time. The treatment was repeated until the fossils were entirely free of the nodule. Between etchings, the nodules were rinsed for several hours in water and then air-dried, and the fossils were painted with a dilute solution of polyvinyl acetate dissolved in acetone. Small fragments of fossil bone were recovered by passing all discarded acid through a 0.59-mm mesh screen. One tibiotarsus was embedded in epoxy and prepared as a ground lapidary thin section, as described by Houde (1987). A specimen from the Green River Formation was prepared with a carbide needle under a dissecting microscope. Parts of this specimen were also repaired with polyester laminating resin and preserved with polyvinyl acetate. Fossil specimens were compared with the modern osteological material listed later. All specimens were drawn with the aid of a dissecting microscope. Most were drawn "free-hand" with the aid of measurements taken with dial calipers but not with a camera lucida. Drawings of paleotaxa are composites, made with reference to all available specimens, and usually are not of individual specimens, unless otherwise specified in the figure captions. No attempt was made to draw fractures or imperfections unless some aspect of the anatomy was entirely unknown. All appendicular elements illustrated are either from the right side or transposed so that they appear to be from the right side to facilitate comparisons.

COMPARATIVE OSTEOLOGICAL MATERIAL

All specimens are from the collection of the Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM). Falconidae: *Falco sparverius* 555743; Opisthocomidae: *Opisthocomus hoazin* 344065; Glareolidae: *Rhinoptilus cinctus* 490230, *Cursorius coromandelicus* 432031; Psittacidae: *Forpus coelestis* 492387; Musophagidae: *Corythaeola cristata* 291079, *Tauraco livingstonii* 559413, *Tauraco persa* 291081; Cuculidae: *Clamator glandarius* 552920, *Urodynamis taitensis* 559589, *Eudynamys scolopacea* 490637, 292057, *Crotophaga major* 430932, *Piaya cayana* 558792, 492313, *Cuculus canorus* 490368, *Saurothera vieilloti* 501735, *Rhamphococcyx curvirostris* 559826, *Rhopodytes tristis* 431312, *Ceuthmochares aereus* 347410, *Coccyzus erythrophthalmus* 553126, *Guira guira* 345884, *Surniculus lugubris* 488329, *Morococcyx erythropygus* (partial skeleton) 361662, *Dromococcyx phasianellus* (partial skeleton) 347717, *Tapera naevia* 19221, *Geococcyx californicus* 555729, *Neomorphus geoffroyi* (partial skeleton) 347797, *Coua ruficeps* 432195, *Centropus senegalensis* 347407; Tytonidae: *Tyto alba* 553901; Strigidae: *Phodilus badius* 20310, *Ciccaba woodfordii* 491216, *Pseudoscops grammicus* 559185, *Pulsatrix perspicillata* 345889, *Rhinoptynx clamator* 347339, *Otus*

Figure 1. Map of the United States of America showing collecting localities in Wyoming (square). **A.** Localities of calcareous nodules in the Willwood Formation Sand Coulee area of the Bighorn Basin, Park County. **B.** Localities in the Green River Formation near Kemmerer, Lincoln County.

flammeolus 554125, *Surnia ulula* 289974, *Asio otus* 554126, *Bubo virginianus* 559803, *Glaucidium brasilianum* 500519, *Ketupa ketupu* 559828, *Micrathene whitneyi* 555314, *Nyctea scandiaca* 491639, *Ninox novaeseelandiae* 492459, *Strix aluco* 559072, *Speotyto cunicularia* 501317, *Aegolius acadicus* 502238; Steatornithidae: *Steatornis caripensis* 560206; Podargidae: *Podargus strigoides* 492451; Nyctibiidae: *Nyctibius griseus* 555945; Aegothelidae: *Aegotheles cristatus* 227841; Caprimulgidae: *Podager nacunda* 344117, *Chordeiles acutipennis* 555588, *Nyctiprogne leucopyga* 429368, *Eurostopodus macrotis* 431310, *Nyctiphrynus ocellatus* 345891, *Caprimulgus carolinensis* 501321, *Phalaenoptilus nuttalli* 553912; Apodidae: *Streptoprocne semicollaris* 489351, *Cypseloides cherriei* 491750, *Cypseloides niger* 555770, *Hirundapus caudacutus* 500799, *Collocalia inexpectata* 489009, *Chaetura pelagica* 322320, *Cypsiurus parvus* 347445, *Tachornis phoenicobia* 553772, *Panyptila cayennensis* 431346, *Apus affinis* 431472, *Aeronautes andecolus* 227503; Hemiprocnidae: *Hemiprocne comata* 559923, *Hemiprocne longipennis* 226196; Trochilidae: *Glaucis hirsuta* 560156; Coliidae: *Urocolius macrourus* 499815, *Urocolius indicus* 558550, *Colius striatus* 558544, 558545; Trogonidae: *Priotelus temnurus* 429735, *Temnotrogon roseigaster* 318891, *Trogon melanurus* 347109, *Apaloderma narina* 430539, *Harpactes erythrocephalus* 557505, *Pharomachrus mocinno* 489405; Alcedinidae: *Alcedo quadribrachys* 291797, *Ceryle guttulata* 292776, *Dacelo novaeguineae* 344389, *Halcyon funebris* 557210, *Tanysiptera galatea* 557230; Todidae: *Todus todus* 559190; Momotidae: *Momotus momota* 289783, *Electron platyrhynchum* 321526, *Baryphthengus ruficapillus* 559416; Meropidae: *Merops apiaster* 593064, *Nyctyornis amicta* 18766; Coraciidae: *Coracias caudata* 431907, *Eurystomus glaucurus* 430541; Leptosomidae: *Leptosomus discolor* 291845; Upupidae: *Upupa epops* 343282; Phoeniculidae: *Phoeniculus purpureus* 322395, *Rhinopomastus cyanomelas* 431715; Bucerotidae: *Tockus birostris* 347342, *Penelopides panini* 291383, *Anorrhinus galeritus* 18758, *Aceros cassidix* 224805; Galbulidae: *Jacamerops aurea* 430890, *Galbula galbula* 500436; Bucconidae: *Chelidoptera tenebrosa* 492224, *Nystalus chacuru* 321611, *Malacoptila panamensis* 432163, *Nonnula rubecula* 555954, *Monasa nigrifrons* 491483, *Notharchus macrorhynchos* 500432; Capitonidae: *Trachyphonus darnaudii* 320830, *Lybius torquatus* 558561, *Psilopogon pyrolophus* 558259, *Capito niger* 428698,

Tricholaema leucomelan 430550, *Megalaima virens* 431611, *Semnornis ramphastinus* 430761, *Calorhamphus fuliginosus* 344510, *Pogoniulus duchaillui* 291795, *Eubucco bourcierii* 560025, *Gymnobucco calvus* 347446; Indicatoridae: *Indicator indicator* 430329, *Prodotiscus insignis* 429686, *Melichneutes robustus* (partial skeleton) 430771; Ramphastidae: *Ramphastos vitellinus* 430217, *Pteroglossus torquatus* 346642, *Baillonius bailloni* 429862, *Aulacorhynchus sulcatus* 344099, *Selenidera maculirostris* 344870; Jyngidae: *Jynx torquilla* 603675; Picidae: *Dryocopus lineatus* 562567, *Dinopium benghalense* 346830, *Colaptes auratus* 554428, *Picus vittatus* 321099, *Dendropicos namaquus* 430385, *Melanerpes carolinus* 502631, *Veniliornis spilogaster* 558001, *Sphyrapicus varius* 502575, *Campephilus guatemalensis* 562569; Eurylaimidae: *Smithornis sharpei* 292424; Pittidae: *Pitta maxima* 557243; Scytalopodidae: *Rhinocrypta lanceolata* 227512; Formicariidae: *Thamnophilus punctatus* 428225, *Conopophaga castaneiceps* 559994; Cotingidae: *Ampelion rubrocristatus* 428910.

SYSTEMATIC PALEONTOLOGY
Sandcoleiformes new order

INCLUDED FAMILY. Sandcoleidae new family, the only known family in this order.

DIAGNOSIS. Distinguished from all sufficiently known orders of birds except Colliformes (colies) by the following combination of osteological characters.

Skull. Nostril holorhinal; postorbital and zygomatic processes very small; mandible with small symphysis.

Sternum. Carina shallow; posterior margin with four deep notches.

Vertebrae. Stout; many cervicals with osseous bridge connecting transverse process with posterior articular process, forming lateral accessory foramen; posterior cervicals and anterior thoracics with large pneumatic foramen in lateral surface of body; pygostyle very large, ventral process very large, and horizontal lumina projecting laterad from base.

Coracoid. Narrow except at sternal extremity.

Scapula. Acromion simple, without projections.

Humerus. Short and robust; large shallow depression for coracobrachialis muscle; bicipital crest pronounced and narrow; deltopectoral crest angular at midcrest, tapering distad to shaft, not angular distally; tricipital fossa single, without pneumatic foramen; lateral epicondylar process small but distinct; medial epicondyle pronounced medially, approximately equal in length to condyles.

Radius. Distal condyle large.

Ulna. Short, curved, without pronounced olecranon process or raised papillae for attachment of remiges.

Carpometacarpus. First metacarpal short; minor metacarpal bowed; intermetacarpal space wide; distal end truncate.

Femur. Head large; trochanteric crest low; condyles compressed obliquely forming a concavity on medial side, possibly for origin of m. femorotibialis internus; tuberosity for attachment of m. gastrocnemius lateralis and ansa of m. iliofibularis large and distinct.

Tibiotarsus. Cnemial crest low, broad, and pronounced proximomedially, anterior surface deeply concave, anterior crest continuing distad as pronounced ridge on medial aspect of shaft for origin of m. peroneus longus; condyles widely spaced, anteroposteriorly compressed, and well rounded in lateral view.

Tarsometatarsus. Approximately equal in length or slightly shorter than femur; shaft flattened proximally, cotylae widely separated; intercotylar eminence small and indistinct; hypotarsus very small and simple, very large, centrally positioned canal and a more medial tendinal groove, which may be divided in two; medial infracotylar foramen large; articular facet for metatarsal I facing mediad, trochleae II and IV narrow, elevated equally, and splayed outward; trochlea III wide and deeply grooved.

Pedal Phalanges. Robust; interphalangeal articulations very deeply grooved; claws sharply curved.

All members for which a given structure is known may be distinguished from the Coliiformes by having the following characters.

Skull. Internasal septum absent; quadrate without dorsally projecting process of lateral mandibular condyle; mandible more gracile, mandibular fenestra small or lacking.

Vertebrae. Thoracics without long ventral spines; pygostyle with horizontal lamella more ventral and not as pronounced.

Sternum. Sternocoracoid process shorter; spina externa of manubrium lamellate in midsagittal plane; intermediate trabecula arises from lateral trabecula and points caudomediad.

Furcula. Articulation of coracoid narrow.

Coracoid. Articulation of furcula larger, curved ventrally; sternal extremity wide, medial and lateral angles flared.

Humerus. Deltopectoral crest longer, broader, and more lamellate.

Radius and Ulna. Approximately equal in length to humerus.

Ulna. Dorsal cotylar process rounder; insertion of ventral collateral ligament smaller.

Carpometacarpus. Lacks intermetacarpal process.

Pelvis. Caudal iliac spine well developed; ischium longer, more slender.

Tibiotarsus. Anterior cnemial crest more pronounced; origin of m. femorotibialis internus elevated on distinct crater-shaped papilla; tendinal groove (extensor canal) positioned more medially; condyles smaller, widely separated).

Tarsometatarsus. Wider, flatter; without ossified extensor retinaculum; medial canal of hypotarsus enclosed (or imperfectly enclosed) with additional smaller groove posterolateral to it; facet for metatarsal I large and concave; trochleae II and IV more elevated and more splayed.

Pedal Phalanges. Claws strongly curved and robust, with large insertion of flexor tendon.

Sandcoleidae new family

INCLUDED GENERA. *Sandcoleus* new genus, *Anneavis* new genus, *Eobucco* Feduccia and Martin 1976, *Chascacocolius* new genus, and probably *Uintornis* Marsh 1872 and *Botauroides* Shufeldt 1915.

DIAGNOSIS. As for order.

DISTRIBUTION. Clarkforkian, Wasatchian and Bridgerian Land Mammal Ages, Early to Middle Eocene; Wyoming.

DESCRIPTION. In general, the species of the Sandcoleidae were small, arboreal, stocky, muscular birds. The foot was anisodactyl, facultatively zygodactyl, and possibly even facultatively pamprodactyl. The head was small, the wings and legs short, and the tail long. They probably resembled colies superficially, but they were larger and had a longer bill, such as that of a thrush (*Turdus* Linnaeus 1758). The following descriptions are made with reference to members of the higher landbirds (Olson, 1985), to which comparison is implied if not specified (e.g., "the head is small," meaning compared with the higher landbirds the head is small).

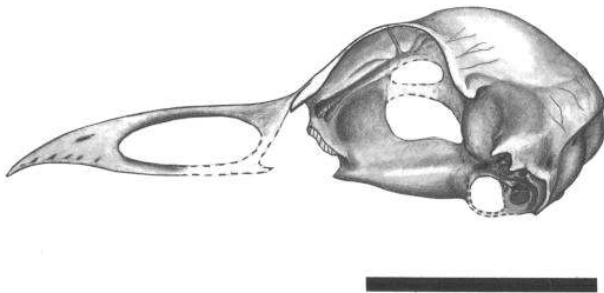**Skull (Fig. 2).** The bill is of generalized proportions, neither

Figure 2. Reconstructed composite skull of *Sandcoleus copiosus* n. gen., n. sp., without palatal elements, left lateral aspect. Scale = 2 cm.

Figure 4. Reconstruction of the mandible of the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913, left side reconstructed from right). Upper: dorsal view; lower: left lateral aspect. Scale = 2 cm.

long nor short, heavy nor thin; the premaxillary symphysis is short; the nostril is large and holorhinal; the internarial septum and intranarial ossifications are absent; the cranium is nearly spherical; the pseudotemporal fossa is very shallow, the postorbital process very small, and the zygomatic process very small and conical, not flattened laterally, being just large enough to accept the lateral cotyla of the quadrate, as in *Tauraco* Kluk 1779. In the tympanic cavity, the osseous canal of the occipital ramus of the external ophthalmic artery is very large and conspicuous, extending between the two articular cotylae for the quadrate and across the middle of the dorsal pneumatic foramen, as in *Falco* Linnaeus 1758. The canal is a groove that does not appear to have been enclosed as an osseous tube in the tympanic cavity. The groove for the olfactory nerve is large and the medial orbitonasal foramen is paired, penetrating the ectethmoid medially as in *Falco*. The prefrontals are not fused with the frontals. The supraorbital region of the frontals is narrow and diverges anteriad to end in bilateral conical projections (that presumably articulate with the prefrontals and are not the prefrontals themselves). These projections are juxtaposed to a large
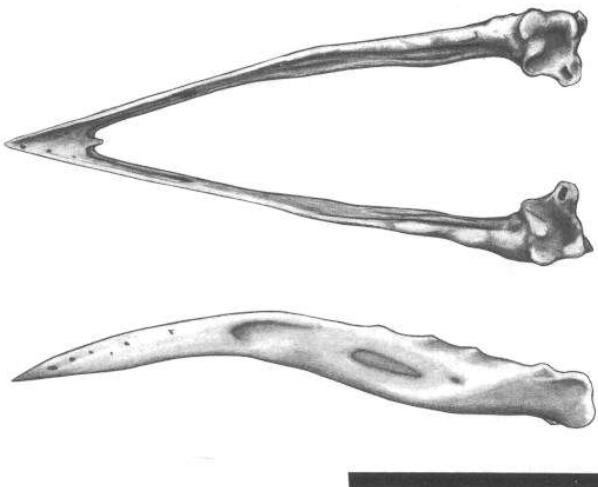
lateral orbitonasal foramen. Basipterygoid processes are absent. The pterygoid has flanges along its length, as in the Indicatoridae, and it is not cylindrical as in *Colius* Brisson 1760. The quadrate is similar to that of *Indicator* Stephens 1815, being stocky, with three well-defined mandibular condyles. The prootic and squamosal condyles are poorly separated and the orbital process is short. There are two large foramina on the medial surface of the quadrate that are separated by a well-defined ridge that connects the medial otic condyle with the medial mandibular condyle. The cotyla for the attachment of the quadratojugal includes a pit and a very small process projecting dorsad.

The mandible (Figs. 3, 4) is of medium length, with a very short mandibular symphysis, as in the Indicatoridae. The medial mandibular process is well developed but not long. The retroarticular process is developed to strikingly different degrees in different genera. Even when it is small, no more than a small ridge caudal to the lateral mandibular condyle, it is at least present, unlike in the Galbulae and Coraciiformes. The mandibular fenestra is small or absent. The dentary is slightly curved ventrally except at the rostral tip where the curvature is slightly dorsad. The mandible is superficially similar to that of the cuckoo *Eudynamys* Vigors and Horsfield 1826, except for the long retroarticular process in *Chascacocolius* new genus, which is described later.

The basihyal bone is short, broad, and basically hexagonal in dorsoventral view, with the apexes pointing laterad and with a ridge running anteroposteriad along the ventral surface.

Vertebrae. The vertebrae are stout, being similar overall to those in the Coliidae. Many of the cervicals have a tenuous osseous bridge connecting the transverse process with the posterior articular process, forming a lateral accessory foramen. The posterior cervicals and anterior thoracics have a large pneumatic foramen in lateral surface of body and lack long ventral spines. The caudal vertebrae have very long lateral and ventral spines. The pygostyle (Fig. 5) is very large, as in the Coliidae, but, unlike that of the Coliidae, the ventral process is very large

Figure 3. Reconstruction of the mandible of *Sandcoleus copiosus* n. gen., n. sp. (drawn from complete specimen in USNM 433973–434025 series). Upper: dorsal view; lower: left lateral aspect. Scale = 2 cm.
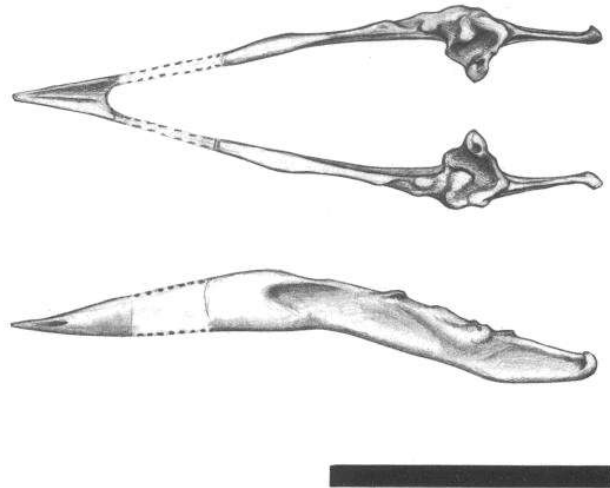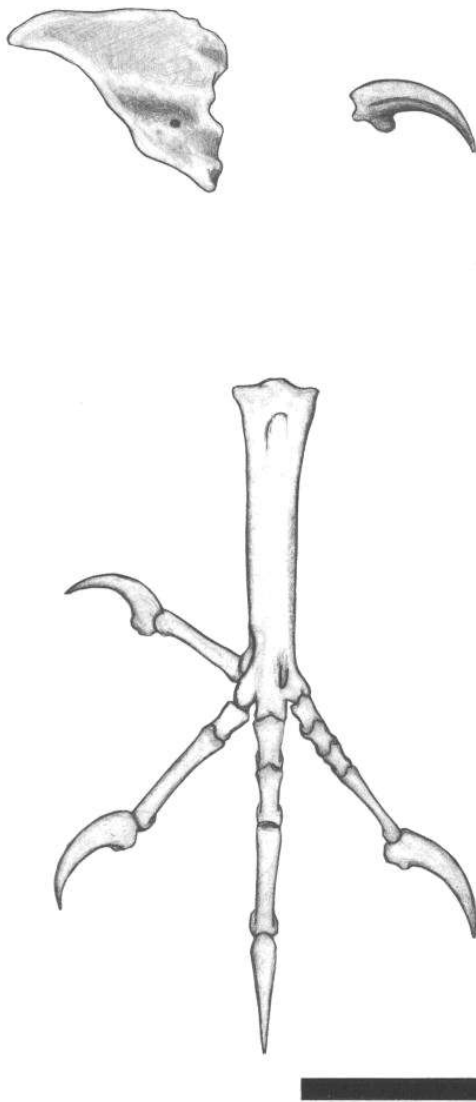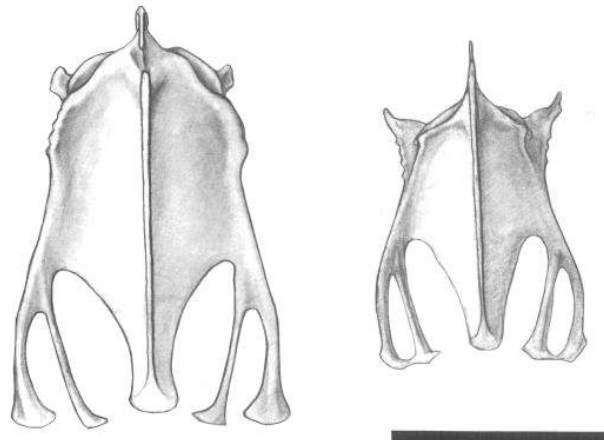
Figure 6. Reconstruction of the ventral aspect of the sternum. Left: holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912); right: *Indicator indicator* (USNM 430329). Scale = 2 cm.

The costal margin is short and the caudal border has four deep notches, with the medial trabeculae originating from the lateral trabeculae, as in the Indicatoridae.

Furcula. The furcula is thin. Unlike most landbirds, it lacks a hypocleideum and the coracoidal articulation is small, without an articular facet.

Coracoid. The coracoid (Fig. 7) has a long, thin shaft. The cotyla for the scapula and the scapular extremity are very small and the procoracoid process is relatively small or absent, as in the Todidae and Momotidae. The furcular articulation is hooked ventromediad. The foramen of the supracoracoid nerve is inconspicuous. The sternal extremity is broad and curved, with a shallow depression in the region of m. sternocoracoideus and a very small depression medial to the line of m. supracoracoideus on the ventral surface of the sternal extremity. There is a distinct

Figure 5. Upper left: right lateral aspect of the pygostyle of the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912); upper right: right lateral aspect of a terminal pedal phalanx of *S. copiosus*; lower: outline of the left pedal elements of the holotype of *Anneavis anneae* n. gen., n. sp. (BMS E 25337), showing the short proximal phalanges. Note that metatarsal I is unknown. Scale = 2 cm.

and the base is flat, as in a number of other families, e.g., Musophagidae.

Sternum. The sternum (Fig. 6) is longer than wide and is more expanded caudally, strongly resembling that in *Indicator* except for the manubrium. The manubrium is a well-developed single blade, rather than being bifid, and it protrudes anteriad from the carina, rather than being continuous with the carina as it is in *Indicator*. The carina is very shallow, the sternocoracoid processes are short, and the coracoidal sulci cross at the midline.
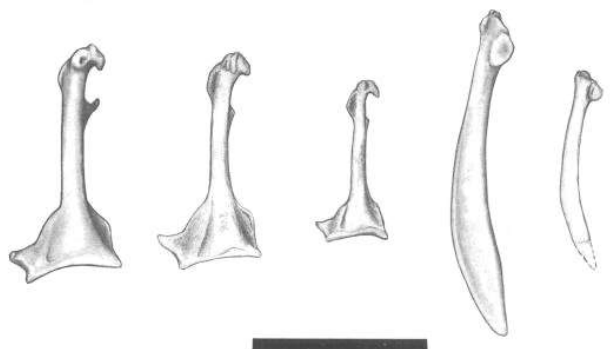

Figure 7. Reconstructions of the ventral aspects of the right coracoids and the dorsal aspect of the right scapulae of, from left to right, the coracoid of the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912), the coracoid of *Anneavis anneae* n. gen., n. sp. (composite reconstruction), the coracoid of the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913), the scapula of the holotype of *S. copiosus*, and the scapula of the holotype of *C. oscitans*. Scale = 2 cm.
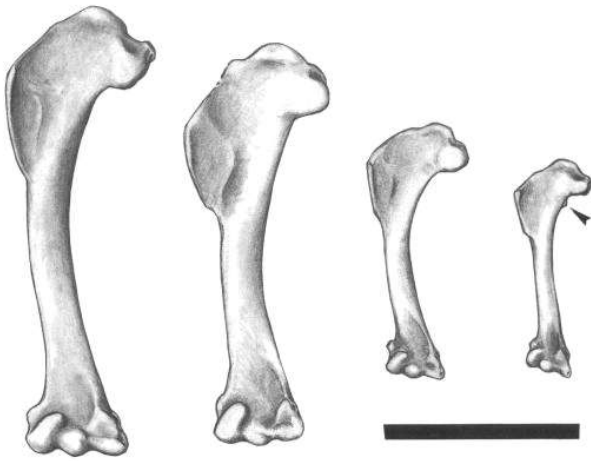
Figure 8. Reconstructions of the anterior aspects of the right humeri of, from left to right, respectively: the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912; reconstructed from right and left sides), *Anneavis anneae* n. gen., n. sp. (composite reconstruction), the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913; reconstructed from right and left sides), and *Colius striatus* (USNM 558544). Arrow: process, or "spur," of tricipital fossa; see text for details. Scale = 2 cm.

flange on the medial border of the sternal extremity. The lateral process is pronounced as in the Coraciidae and Musophagidae. The sternal articulation is not noticeable on the ventral surface.

Scapula. The scapula (Fig. 7) is simple and narrow. As in the Bucconidae and Trogonidae, there is no enlargement or process for an articulation with the furcula.

Humerus. The humerus (Fig. 8) is robust. The pectoral crest is large, pronounced, triangular, and lamellate, and it is nearly 30 percent as long as the entire bone. The coracobrachial depression is broad and shallow. The bicipital crest is very short, pronounced, and bulbous. The tricipital fossa is single, small, and deep, and it is not pneumatized. The shaft is robust and curved. The condyles and the medial epicondyle are bulbous, well rounded, and of approximately equal distal extent. The lateral epicondyle is a well-defined bump, positioned close to the radial condyle. The brachial depression is shallow, with an indistinct lateral border. The tricipital grooves are shallow. The humerus is most similar overall to that in the Coliidae except that the pectoral crest is more lamellate and lacks the process in the tricipital region of the coliid humerus (see Figs. 8, 9; this process has not been named to the best of our knowledge). There is also some resemblance to the humerus in the Trogonidae because of the long pectoral crest and short bicipital crest.

Ulna. The ulna (Fig. 10) is short, with a short, bulbous olecranon process. The shaft is curved in the proximal one-third to one-half, and its diameter may increase gradually from the midpoint to the distal end. There are no papillae for the attachment of secondary remiges.

Radius. The radius (Fig. 10) is short, straight, and robust, with a fairly large condyle.

Carpometacarpus. The carpometacarpus (Fig. 10) is short, with a pronounced extensor process and very short alular process. The intermetacarpal space is moderately wide as it is in *Coracias* Linnaeus 1758 and not as wide as in the Trogonidae.

The intermetacarpal process is small or nearly absent. The minor metacarpal is slightly bowed, but not so extensively as in the Cuculidae, and the minor metacarpal often possesses a facet or buttress on the ventral surface for articulation with the ulnare. The articular facets for the digits are approximately equal in distal extent. The articular facet for the minor digit is a small, raised papilla.

Pelvis. The pelvis (Fig. 11) is wide, with the anterior and posterior portions of the ilium approximately equal in length. The anterior ala of the ilium does not meet the dorsal midline ridge of the synsacrum, and the terminal process of the ilium is present. The ala of the ischium, not including the terminal process, is approximately equal in length to the ilioischiadic foramen. The terminal process of the ischium is similar to that in *Indicator,* being very long, thin, and bent and ending in a large pedestal-like articulation with the pubis. The ischiopubic fenesetra is very large, and the obturator foramen is also large, about equal in size to the acetabulum.

Femur. The femur (Fig. 12) is long, with a large head and low trochanteric crest. The cranial intermuscular line begins medial to the trochanteric crest, rather than on the crest. The lateral condyle is very large, and the medial condyle is small, with a concave medial surface. The tuberosity for the attachment of m. gastrocnemius lateralis and the ansa of m. iliofibularis are distinctly large, a diagnostic feature of the Sandcoleidae and Coliidae. The patellar groove is moderately deep, being very similar overall to the femur in *Colius,* except that the lateral condyle and associated structures are larger, and the condyles are compressed obliquely and rotated mediad relative to the shaft.

Tibiotarsus. The tibiotarsus (Fig. 13) is similar to that in the Coliidae and similar, but less so, to that in some of the Pici. The anterior cnemial crest is positioned far to the medial side. The lateral cnemial crest is large but not acute. The anterior and lateral cnemial crests are connected by a ridge that is exaggerated anteriorly but not proximally and that circumscribes a broad, concave intercristal "sulcus." The anterior cnemial crest is continuous distally with a ridge opposite the fibular crest. The origin of m. femorotibialis internus is elevated on a distinct papilla that has a concavity in it. The fibular crest is equal to or greater than one-third the length of the shaft and is more pronounced distally. The shaft curves mediad, especially at the level of the distal end of the fibular crest. The shaft diameter is narrowest at a level approximately two-thirds distad. The origin and insertion of the extensor retinaculum are pronounced. The extensor canal is positioned medially. The condyles are low, well rounded, and widely separated. The sulcus of the tibial cartilage is wide and shallow.

Tarsometatarsus. The tarsometatarsus (Figs. 14–16) is short, broad, and flat, with the cotylae widely separated. The intercotylar eminence is very low. The profile of the shaft becomes gradually narrower distally throughout its length until the level of the facet for the hallux. The hypotarsus is very small and low, being superficially similar to that in *Forpus* Boie 1858. There are three hypotarsal canals, two side by side and one behind, all centrally positioned between the cotylae. The lateral canal is the largest, and the medial and posterior canals may be connected as an imperfectly closed groove. The plantar surface of the shaft is relatively flat and does not form a large ridge as it meets the hypotarsus. The tuberosity of m. tibialis cranialis is large and positioned mediad, at a point distad one-third the length of the shaft. The infracotylar region is quite concave, with two large proximal vascular foramina. The facet for the hallux (=metatarsal I) is very large and faces mediad, not plantad.
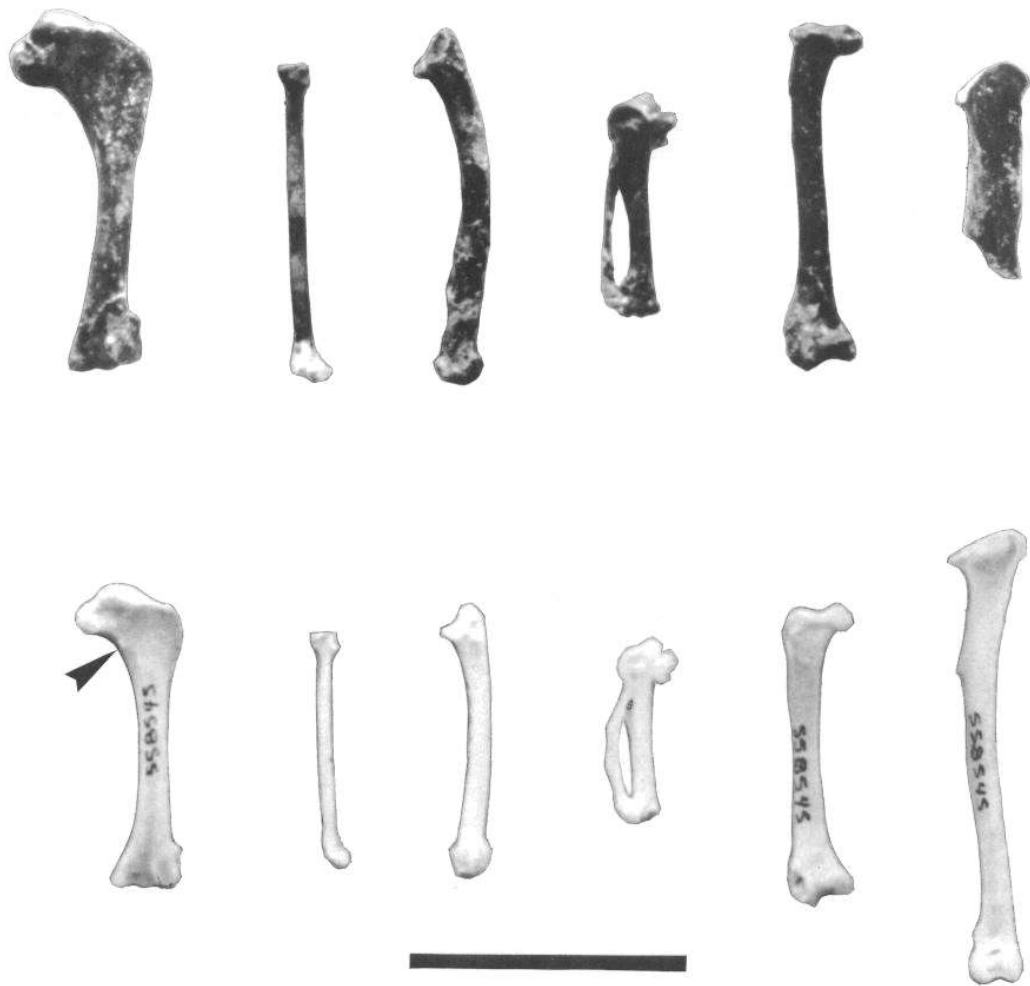
Figure 9. Selected elements of the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913), above, compared with *Colius striatus* (USNM 558545), below. Left to right: posterior aspect of right humerus, posterior aspect of right radius, ventral aspect of right ulna, ventral aspect of left carpometacarpus, posterior aspect of left femur, and anterior aspect of right tibiotarsus (distal end of *Chascacocolius oscitans* not shown). Arrow: process, or "spur," of tricipital fossa; see text for details. Scale = 2 cm.

The interosseous foramen may be large or small. The distal (intertrochlear) foramen is large. Trochleae II and IV are elevated approximately equally and are splayed widely from trochlea III, so that the intertrochlear incisures are very wide. The trochleae lie in the same dorsoplantar plane. The collateral processes of trochleae II and IV are very large, particularly so in the latter, extending plantad to form a deep flexor trough, as in the Coliidae but more exaggerated. There is no sehnenhalter. Trochlea II is small and bulbous; trochlea III has a deep groove, and the medial ridge is smaller than the lateral ridge; and the medial ridge of trochlea IV in distal view forms a semicircle around the distal tendinal foramen, as in the Coliidae but more semicircular. The medial ridge of trochlea IV protrudes anteriad to form a groove medial to the trochlea on the anterior surface of bone distal to the interosseous foramen, as in the Coliidae.

Phalanges. The phalangeal formula is complete, and the pha-

langes are robust (Fig. 5). The three proximal phalanges of digit IV are extremely short as in the Coliidae, Apodidae, and Strigidae. The interphalangeal articular surfaces are highly convoluted as in the Strigidae. The plantar surfaces of the phalanges have bilateral ridges for the attachment of a ligamentous retinaculum. As in the Apodidae, the ungual phalanges are large and strongly hooked and have a large flexor tubercle; they are not bilaterally compressed.

Sandcoleus new genus

TYPE SPECIES. *Sandcoleus copiosus* new species, the type and only known species of this genus (see Fig. 19).

DIAGNOSIS. Placed in family by having the suite of characters listed previously for the Sandcoleidae.
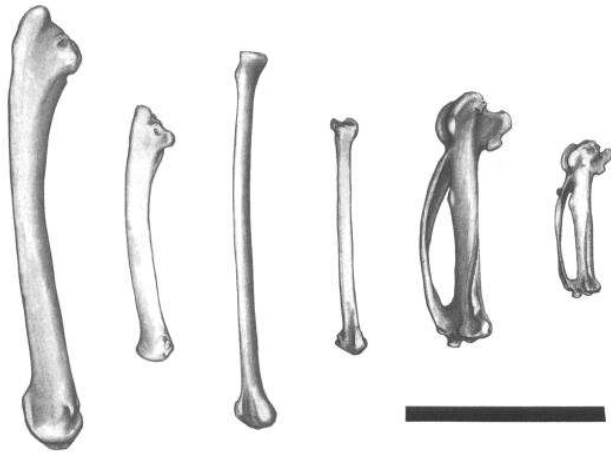
Differs from *Anneavis* new genus by having: sternum with

Figure 10. Reconstructions of the dorsal aspects of the right ulnae, the anterior aspects of the right radii, and the dorsal aspects of the right carpometacarpi, respectively. In each pair, right: *Sandcoleus copiosus* n. gen., n. sp. (composite reconstruction); and left: the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913; the left radius and carpometacarpus are reversed to appear to be the right side). Scale = 2 cm.

Figure 12. Reconstructions of the right femora of, from left to right: the dorsal aspect of *Sandcoleus copiosus* n. gen., n. sp. (composite reconstruction), the ventral aspect of the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913; left femur reversed to appear to be the right side), and the ventral aspect of *Colius striatus* (USNM 558544). Scale = 2 cm.

curved lateral margins; coracoid with long procoracoid process; humerus with narrower bicipital crest, longer medial epicondyle, pectoral crest pointing more palmad than laterad; preacetabular portion of pelvis longer; tibiotarsus with fibular crest not as pronounced distally, shaft of more uniform diameter throughout length; tarsometatarsus with larger distal vascular foramen, trochlea IV raised anteriorly with a groove medial to it on the anterior surface, trochlea III deeply grooved.
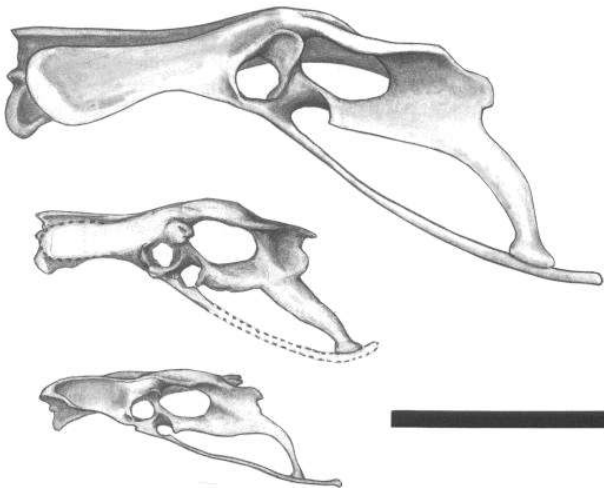

Figure 11. Reconstructions of the left aspects of pelves of, upper: the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912); middle: the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913); and lower: *Jynx torquilla* (USNM 603675). Scale = 2 cm.

Differs from *Eobucco* by having: tarsometatarsus with more bulbous trochleae II and IV in anterior view, trochlea III more nearly bilaterally symmetrical, lateral intertrochlear notch narrower, collateral flange of trochlea IV pointing plantad and not curved plantad–mediad around flexor tendons.

Differs from *Uintornis* by having: tarsometatarsus without ridge along medial margin of shaft, trochlea II and IV more elevated and bulbous in anterior view, trochlea III more bilaterally symmetrical.

Differs from *Chascacocolius* by having: tip of bill broader; mandible with a short, rather than long, retroarticular process; scapula with elongate glenoid facet; humerus with shorter pectoral crest and medial and lateral epicondyles shorter; radius with one groove in condyle, not two; carpometacarpus with very small intermetacarpal process, buttress for ulnare on minor metacarpal small or absent; pelvis with long anterior ala of ilium, no terminal iliac process, and terminal process of ischium more arched to create a wider ischiopubic fenestra; tibiotarsus with apex of proximal margin of cnemial crest more medial, fibular crest not as pronounced distally, distal aperture of extensor canal positioned in center of shaft in anterior view, no groove on anterior aspect of shaft medial to extensor canal.

ETYMOLOGY. A latinization of Sand Coulee, a river in the Clarks Fork Basin (northern Big Horn Basin), which is the namesake of both the fossiliferous Clarkforkian Sand Coulee beds of the Willwood Formation and the area from which all of the specimens of this genus have been collected. Coulee is a term widely used in western North America for a streambed, whether wet or dry. It is derived from French *couler*, to flow, and ultimately from Latin *colare*, to strain or sieve (cf. *colum*, a sieve). When thus latinized, the ending becomes a homophone of *Colius*, the living genus to which these birds are most similar. The generic name is to be treated as masculine in gender.
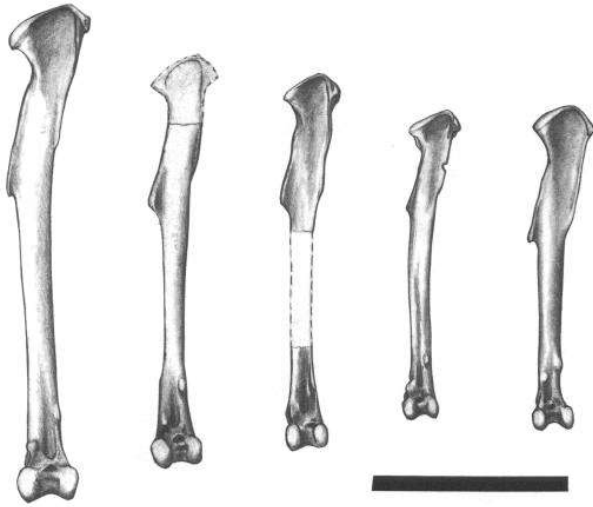
Figure 13. Reconstructions of the anterior aspects of the right tibiotarsi of, from left to right: *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912), *Anneavis anneae* n. gen., n. sp. (composite reconstruction), the holotype of *Chascacocolius oscitans* n. gen., n. sp. (USNM 433913), *Colius striatus* (USNM 558544), and *Melanerpes carolinus* (USNM 502631). Scale = 2 cm.

Sandcoleus copiosus new species

HOLOTYPE. USNM 433912 (Figs. 17, 18), formerly articulated partial skeleton preserved in a calcareous nodule, lacking only the palatal elements, mandibular symphysis, some vertebrae and ribs, right carpometacarpus, right innominate, left tarso-
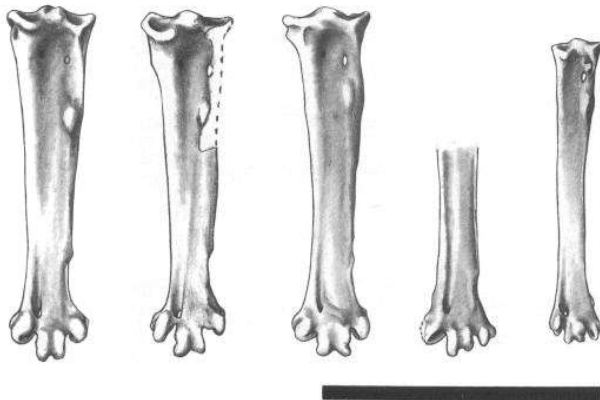

Figure 15. Tarsometatarsi. Upper row: proximal aspect; lower row, anterior aspect of trochleae; from left to right: *Anneavis anneae* n. gen., n. sp. (composite reconstruction), *Colius striatus* (USNM 558544), *Notharchus macrorhynchus* (USNM 500432), and *Forpus coelestis* (USNM 492387). Scale = 1 cm.

metatarsus, and some phalanges. Collected by A. Houde and P. Houde in July 1983.

DIAGNOSIS. As for the genus.

TYPE LOCALITY. NW¼ of SE¼ Sec. 7, T56N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W.

TYPE HORIZON. *Plesiadapis cookei* zone, Middle Clarkforkian (lowermost Eocene), Sand Coulee beds, Willwood Formation, Clark's Fork Basin.

REFERRED SPECIMENS. USNM 433973–434025, 53 elements representing a minimum of three individuals, including: complete crania (2), pterygoid, quadrate, mandible, coracoids (2), scapula, humerus, ulnae (2), carpometacarpus, femur and tarsometatarsi (2), incomplete cranium, quadrate, mandibles (2), sternum, coracoids (5), scapula, humeri (2), radii (2), ulnae (2),

Figure 14. Anterior aspects of the tarsometatarsi of, from left to right: *Sandcoleus copiosus* n. gen., n. sp. (composite reconstruction), the holotype of *Eobucco brodkorbi* Feduccia and Martin (UNSM 20046; left tarsometatarsus reversed to appear to be the right side), *Anneavis anneae* n. gen., n. sp. (composite reconstruction), *Uintornis lucaris* Marsh (referred specimen AMNH 8400; left tarsometatarsus reversed to appear to be the right side), and *Colius striatus* (USNM 558544). Scale = 2 cm.
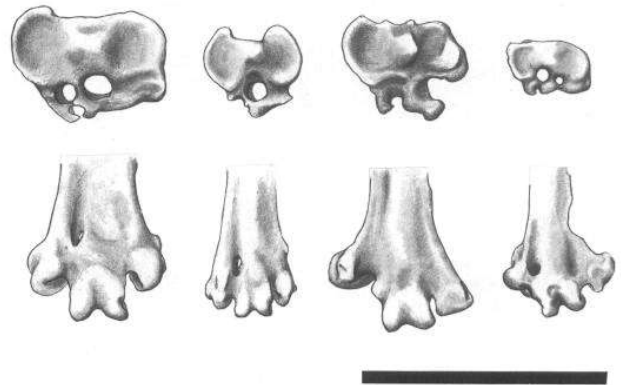

Figure 16. Reconstructions of the distal aspects of the tarsometatarsi of, upper row, from left to right: *Sandcoleus copiosus* n. gen., n. sp. (composite reconstruction), the holotype of *Eobucco brodkorbi* Feduccia and Martin (UNSM 20046), and *Anneavis anneae* n. gen., n. sp. (composite reconstruction); and lower row, from left to right: *Uintornis lucaris* Marsh (referred specimen AMNH 8400; left tarsometatarsus reversed to appear to be the right side), *Colius striatus* (USNM 558544), *Notharchus macrorhynchus* (USNM 500432), and *Forpus coelestis* (USNM 492387). Note that trochlea IV of *E. brodkorbi* is partially reconstructed; see text for details. Scale = 1 cm.

Figure 17. Selected elements of the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912), coated with ammonium chloride, compared with *Trogon* sp. (no data); from left to right: anterior aspect of right humerus of *S. copiosus*, right humerus of *Trogon* sp., left humerus of *S. copiosus*, and left humerus of a trogon, and dorsal aspect of: right carpometacarpus of *S. copiosus* and right carpometacarpus of a trogon. Scale = 2 cm.
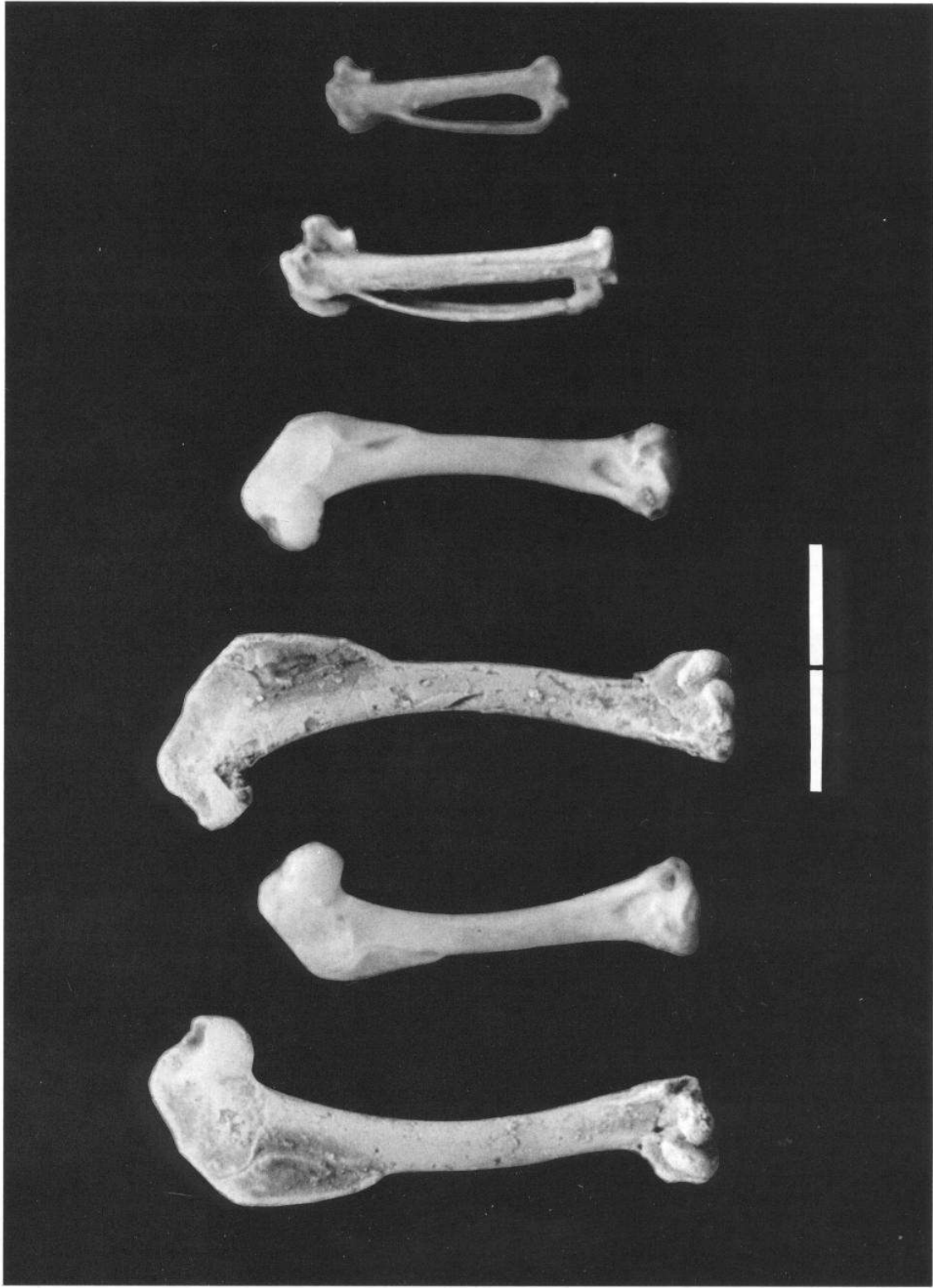
Figure 18. Selected elements of the holotype of *Sandcoleus copiosus* n. gen., n. sp. (USNM 433912), coated with ammonium hydroxide, compared with *Colius striatus* (USNM 558545); from left to right: anterior aspect of left tibiotarsus of *S. copiosus*, left tibiotarsus of *C. striatus*, right tarsometatarsus of *S. copiosus*, and right tarsometatarsus of *C. striatus*. Scale = 2 cm.

carpometacarpus, femur and tibiotarsus, and assorted tracheal rings, vertebrae, a pygostyle, phalanges, and fragments all preserved in one calcareous nodule, collected by A. Houde and P. Houde from NE¼ of SE¼ Sec. 7, T56N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Middle Clarkforkian Land Mammal Age.

UM 83893, formerly articulated partial skeleton, including: partial quadrate, humerus, radius and ulna, pelvis, femora, tibiotarsi, tarsometatarsus, and assorted vertebrae and fragments preserved in a calcareous nodule, collected by A. Houde and P. Houde from NE¼ of SE¼ Sec. 7, T56N R101W, Clark Quadrangle,

Park County, Wyoming; 44°46′N, 109°23′W; Middle Clarkforkian Land Mammal Age.

USNM 433914–433917, four elements representing a minimum of one individual, including: coracoid, the distal end of a humerus, carpometacarpus, and the proximal end of a tibiotarsus, all preserved in one calcareous nodule, collected by A. Houde and P. Houde from NE¼ of NE¼ Sec. 5, T56N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Early Wasatchian Land Mammal Age.

USNM 433971 and 433972, carpometacarpus and proximal end of a femur preserved in a calcareous nodule, collected by

Figure 19. Hypothetical restoration of *Sandcoleus copiosus* n. gen., n. sp., an abundantly preserved species in calcareous nodules from the Early Eocene Willwood Formation of Wyoming.

A. Houde and P. Houde from NW¼ of SE¼ Sec. 23, T56N R102W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Early Wasatchian Land Mammal Age.

ETYMOLOGY. Latin, *copiosus*, abundant, in allusion to the frequency of occurrence of this species in calcareous nodules in the Sand Coulee area.

DISTRIBUTION. Clarkforkian and Wasatchian Land Mammal Ages of the Willwood Formation in Clark's Fork Basin, Wyoming.

COMMENTS. All referred material was collected in and near the type locality. There is remarkable heterogeneity in morphology, even among individuals from the type locality. In particular, two tarsometatarsi from the same nodule differ from one another in the sizes of the proximal and distal vascular foramina, the degree of concavity of the plantar surface, and the width of the shaft. A tarsometatarsus from a different nodule is morphologically similar to one of the two, but it is somewhat

larger. We attribute these differences to individual, rather than interspecific, variation.

Numerous referred specimens (USNM 433973–434025) representing a minimum of three individuals were recovered from the same calcareous nodule as the holotypes of *Lithornis promiscuus* Houde 1988 and *Lithornis plebius* Houde 1988. These specimens of *Sandcoleus* were mistakenly referred to as *Eobucco* sp. in the description of *L. promiscuus* (Houde, 1988:37).

Sandcoleus copiosus was synchronous and sympatric with *Anneavis anneae* in the Early Wasatchian of the Clark's Fork Basin.

Sandcoleus copiosus is larger than all other known members of this family except *Eobucco brodkorbi*, which it equals in size.

MEASUREMENTS (mm) OF HOLOTYPE. Left and right, respectively, are given for paired elements when both are present.

Skull. Length, 52.0; width of premaxillae at anterior margin of nostril, 6.0; breadth across zygomatics, 20.1; supraorbital width, 7.6.

Mandible. Length of internal process from lateral cotyla, 7.3, 7.3; width of cotylae, 5.5, 5.5; depth of mandible, 5.0, 4.8.

Sternum. Length, 41.2; width at costal margin, 19.4; width at caudolateral process, 26.1; depth of carina from coracoidal sulci, 11.6.

Coracoid. Length, 24.4, 24.7; width of sternal articulation, —, 10.4; length of procoracoid, 4.4, 4.3; width of glenoid facet, 2.7, 2.7; width of midshaft, 2.2, 2.3.

Scapula. Length, 38.1, 37.7; width of shaft, 3.0, 3.3; width of glenoid facet, 2.6, 2.6.

Humerus. Length, 46.3, 45.6; length of pectoral crest from caput, 20.5, 20.4; length of bicipital crest from caput, —, 9.7; diameter of midshaft, 4.1, 4.0; distal width, 10.0, —; depth of condyles, 5.1, —.

Radius. Length, 41.2, 41.6; proximal width, 3.7, 3.7; diameter of midshaft, 1.9, 1.7; distal width, 4.7, 4.6.

Ulna. Length, 45.2, 45.4; maximum proximal width, 6.6, 6.8; diameter of midshaft, 3.5, 3.4; width of condyle, 4.9, 5.0; depth of condyle, 5.5, 5.6.

Carpometacarpus (Left). Length, 25.9; width of trochlea, 4.2; length from alular process to extensor process, 4.4; height of extensor process from trochlea, 7.6; anteroposterior width of midshaft of major metacarpal, 2.3; intermetacarpal width, 2.3; width of articular facet for major digit, 3.0.

Pelvis. Length of synsacrum, 35.6; width of body of synsacrum, 6.0; estimated width across antitrochanters, 25.4; length of anterior ala of ilium from acetabulum, 20.5; length of posterior ala of ilium from acetabulum, 17.9; length of ischium from acetabulum, 24.0.

Femur. Length, 36.7, 36.5; length of head from trochanteric crest, 7.6, 7.8; diameter of head, 3.4, 3.4; height of trochanteric crest, 5.2, 4.7; diameter of midshaft, 3.1, 3.1; distal width, 7.7, 7.8; height of medial condyle, 4.3, 4.4; height of lateral condyle and tibiofibular crest, 5.9, 5.8.

Tibiotarsus. Length (from articular surfaces, not cnemial crest), 50.1, 50.9; width of cnemial crest, 8.0, —; width of proximal articular surface, 6.1, 6.0; proximal depth (cnemial crests to condyles), 7.7, —; length of fibular crest from proximal condyles, 18.2, —; height of fibular crest, 4.6, —; maximum width of midshaft, 3.0, 3.0; distal width, 6.2, 6.1; depth of medial condyle, 4.8, —; depth of lateral condyle, —, 4.8.

Tarsometatarsus (Right). Length, 28.1; proximal width, 6.8; proximal depth, 5.2; width of midshaft, 3.3; depth of midshaft, 2.1; depth of trochlea II, 2.7; depth of trochlea III, 2.9; width of trochlea III, 2.8; depth of trochlea IV, 4.0.

Pygostyle. Maximum length, 17.7; maximum width, 5.4.

Anneavis new genus

TYPE SPECIES. *Anneavis anneae* new species, the type and only known species of this genus.

DIAGNOSIS. Placed in family by having the suite of characters listed previously for Sandcoleidae.

Differs from *Sandcoleus* by having the characters mentioned for *Anneavis* in the diagnosis of the former genus.

Differs from *Eobucco* by having: tarsometatarsus with more bulbous trochleae II and IV in anterior view, trochlea III more nearly bilaterally symmetrical, lateral intertrochlea notch narrower, collateral flange of trochlea IV pointing plantad and not curved plantad–mediad around flexor tendons.

Differs from *Uintornis* by having: tarsometatarsus without ridge along medial margin of shaft, with trochlea II and IV more elevated and bulbous in anterior view, trochlea III more bilaterally symmetrical.

Differs from *Chascacocolius* by having: tip of bill broader; scapula with elongate glenoid facet; humerus with shorter pectoral crest, and medial and lateral epicondyles shorter; radius with one tendinal groove, not two; carpometacarpus with very small intermetacarpal process, buttress for ulnare on minor metacarpal smaller; tibiotarsus with distal aperture of extensor canal positioned in center of shaft in anterior view, and no groove on anterior aspect of shaft medial to extensor canal.

ETYMOLOGY. *Anne,* plus Latin, *avis,* a bird. The genus and type species are dedicated to Anne E. Houde, for assisting in the discovery and collection of every specimen from the Willwood Formation included in this paper. The generic name is feminine in gender.

Anneavis anneae new species
Figures 20, 21

HOLOTYPE. BMS E 25337, postcranial skeleton with feather impressions on a marlstone slab. Collected by Verl and Rick Hebdon.

DIAGNOSIS. As for genus.

TYPE LOCALITY. Warfield fossil quarries at Warfield Springs, near Kemmerer, Lincoln County, Wyoming, NW¼ Sec. 5, T19N R117W; 41°44′N, 110°31′W.

TYPE HORIZON. Upper Wasatchian (Lower Eocene), Fossil Butte Member of the Green River Formation, from a "blue layer" about 30–45 cm thick underlying a thick layer of cream-colored calcareous sediment. This is one of the "F-2" localities in the Eocene Fossil Lake mentioned by Grande (1984:13, fn.).

REFERRED SPECIMENS. USNM 336571, 433934–433970, 38 elements representing a minimum of three individuals, including: complete quadrate, coracoids (2), scapula, humerus, ulna, and tarsometatarsi (2), incomplete premaxilla, cranium, sternum, scapulae (2), humeri (5), radius, synsacrum, femur, tibiotarsi (3), and assorted vertebrae, phalanges, and fragments all preserved in one calcareous nodule, collected by A. Houde and P. Houde, from NW¼ of SE¼ Sec. 23, T56N R102W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Early Wasatchian Land Mammal Age.

USNM 433918–433933, 16 elements representing a minimum of two individuals, including: coracoids (2), humeri (2), carpometacarpi (2), synsacrum and tarsometatarsi (3), and incomplete sternum, femur, tibiotarsus, and phalanges, all preserved in one calcareous nodule, collected by A. Houde and P. Houde from NE¼ of NE¼ Sec. 5, T56N R101W, Clark Quadrangle, Park County, Wyoming; 44°46′N, 109°23′W; Early Wasatchian Land Mammal Age.

UWGM 20312, a partial articulated skeleton from the Split Fish layer, Fossil Butte Member, Green River Formation, Lincoln County, Wyoming.

DISTRIBUTION. Early to Late Wasatchian; Willwood and Green River Formations, Wyoming.

COMMENTS. The clearly visible feather impressions of the holotype reveal that *Anneavis anneae* possessed short remiges and a very long, tapered tail, like that of the Coliidae (Fig. 21). The long rectrices may have been present in all members of the family. The only other genus of this family in which the pygostyle is known is *Sandcoleus,* in which it is large. From this it is assumed that its rectrices were long.

Numerous referred specimens of *Anneavis anneae* (USNM 336571, 433934–433970) were recovered from a calcareous nodule that also contained specimens of lithornithids, a flightless predatory bird, an artiodactyl and other mammals, and a lizard. The midshaft of the tibiotarsus of one of these referred specimens (USNM 336571) was embedded in epoxy and prepared as a polished lapidary thin section by Houde (1987:126), who erroneously referred to the specimen as "*Eobucco* sp."

This species is most similar to *Sandcoleus copiosus* and *Eobucco brodkorbi* among known sandcoleids and was sympatric with the former in the Early Wasatchian in the Clark's Fork Basin, Wyoming.

This species is smaller than *Eobucco brodkorbi* or *Sandcoleus copiosus* and larger than *Uintornis lucaris* or *Chascacocolius oscitans.*

MEASUREMENTS (mm) OF HOLOTYPE. Left and right, respectively, are given for paired elements when both are present.

Sternum. Length, ca. 39; width at costal margin, 19.1; width at caudolateral process, ca. 31.

Coracoid. Length, 23.2, 22.8; length of sternal articulation, —, ca. 9.7; width of midshaft, ca. 2.4, —.

Humerus. Length, 41.7, 40.1; length of pectoral crest from caput, 18.8, 18.8; length of bicipital crest from caput, 8.1, 8.1; diameter of midshaft, 3.8, 4.6; distal width, —, ca. 7.5.

Radius. Length, 37.0, 38.2; diameter of midshaft, 1.9, 1.6.

Ulna. Length, —, 41.5; diameter of midshaft, 3.8, 4.4.

Carpometacarpus. Length, 21.6, 22.8; length from alular process to extensor process, 4.4, 4.9; height of extensor process from trochlea, 7.3, 7.7; anteroposterior width of midshaft of major metacarpal, 2.0, 1.6; intermetacarpal width, 1.9, 2.1.

Pelvis. Length of synsacrum, 26.9; width of body of synsacrum, 7.7; width through acetabula, 20.7; length of ischium from acetabulum, ca. 17.5, 16.

Femur. Length, 27.7, 33.4; diameter of midshaft, 2.8, 2.8.

Tibiotarsus. Length (cnemial crest–condyles), 43.3, 40.4; width of cnemial crest, 6.5, —; height of fibular crest (diameter of shaft plus elevation of ridge), 4.1, —; maximum width of midshaft, 2.7, —; distal width, 5.3, —; depth of medial condyle, —, 3.7.

Tarsometatarsus. Length, 23.7, 23.5; proximal width, 5.8, 5.9; width of midshaft, 3.1, 3.3; depth of trochleae, 6.2, 4.8; width of trochlea III, 2.2, —.

Pygostyle. Maximum length, 15.1.

Eobucco Feduccia and Martin 1976

INCLUDED SPECIES. *Eobucco brodkorbi;* the type and only known species of this genus.

EMENDED DIAGNOSIS. Placed in order by having the suite of tarsometatarsal characters listed previously for Sandcoleiformes. Differs from all sufficiently known members of the family in which the tarsometatarsus is known by having: wider lateral

Figure 20. Holotype of *Anneavis anneae* n. gen., n. sp. (BMS E 25337), from the Lower Eocene Green River Formation of Wyoming. The specimen consists of the postcranial skeleton. It is coated with ammonium chloride to enhance details of the bones, but this obscures the feather impressions.
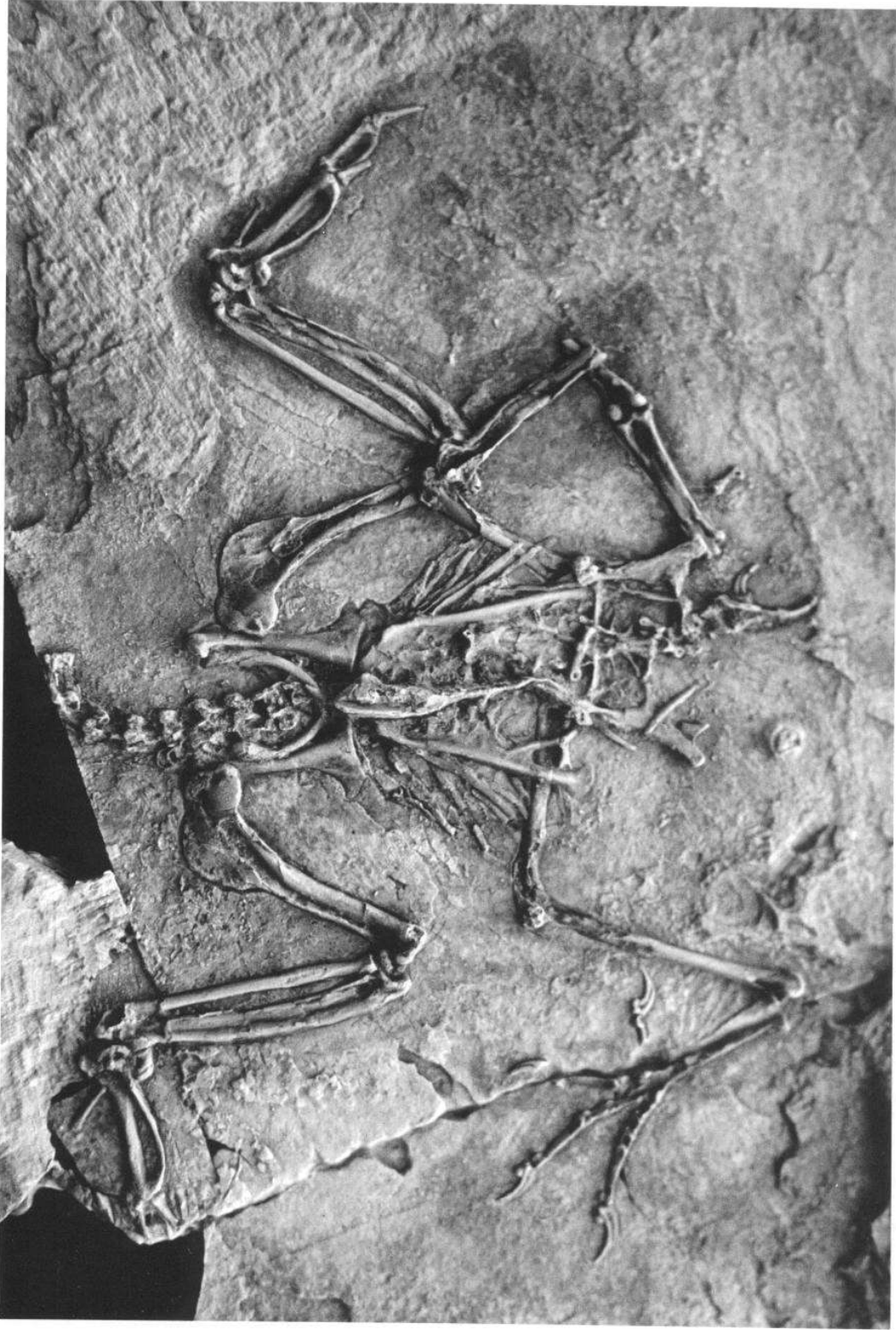
Figure 21. Holotype of *Anneavis anneae* n. gen., n. sp. (BMS E 25337), from the Lower Eocene Green River Formation of Wyoming, showing impressions of the feathers. The pencil points to the lateral margin of the tail feathers.

intertrochlear notch and collateral flange of trochlea IV bent more mediad around flexor tendons.

Differs from *Sandcoleus* and *Anneavis* by having: tarsometatarsus with less concave plantar surface, narrower trochleae II and IV, and trochlea III asymmetrical with medial ridge smaller than lateral ridge. Also differs from *Anneavis* by having: trochlea IV raised anteriad and with groove medial to it on anterior surface of shaft.

Differs from *Uintornis* by having: tarsometatarsus without ridge along medial border of shaft, trochleae II and IV more elevated, and with narrower lateral intertrochlear notch.

Eobucco brodkorbi
Feduccia and Martin 1976
Figures 14, 16

HOLOTYPE. UNSM 20046, left tarsometatarsus.
EMENDED DIAGNOSIS. As for genus.
TYPE LOCALITY. "56 km north of Green River, Sweetwater County, Wyoming" (Feduccia and Martin, 1976).
TYPE HORIZON. "Bridger Formation, Middle Eocene" (Feduccia and Martin, 1976).
REFERRED SPECIMENS. None
COMMENTS. We find certain inaccuracies in the original description of this species by Feduccia and Martin (1976:109), which reads as follows: "... intercotylar eminence high and large; hypotarsus damaged but with a large lateral square of bone, which may have included a closed canal (the two closed canals, such as found in cuculids, could not have been present) ... tubercle for tibialis anticus very small and distally situated along the medial edge of shaft ..." Compared to birds that possess a high and large intercotylar eminence, such as in the Pici, the eminence of *Eobucco* is very low. The hypotarsus in the holotype of *E. brodkorbi* is indeed broken; nonetheless, we believe that it possessed two or three closed canals as in the other members of the family. A large proximomedial fragment of the holotype is missing, including everything medial to the insertion of m. tibialis anticus and the medial proximal vascular canal. In their illustration of the holotype, Feduccia and Martin (1976: fig. 6) included a dashed line from the intact medial margin of the shaft proximad to the damaged tubercle for m. tibialis anticus and incorrectly indicated this to be the medial border of the tarsometatarsus. The tubercle for insertion of m. tibialis anticus is large, not small, and is not positioned on the medial edge of the shaft. Our illustrations (Figs. 14, 16) correct this and two other matters of reconstruction. The anterior surface of trochlea IV is damaged and probably would have been similar to that of *Sandcoleus* or *Colius*. The lateral flange of trochlea IV is cracked and flattened against the shaft but probably would have been positioned more plantad, as shown in our drawing.

Eobucco brodkorbi is larger than all other sufficiently known members of the family except *Sandcoleus copiosus*, to which it is equal in size.

Uintornis Marsh 1872

INCLUDED SPECIES. *Uintornis lucaris* Marsh 1872, type species, and *Uintornis marionae* Feduccia and Martin 1976 (this species was not examined).
EMENDED DIAGNOSIS. Placed in order by having the suite of tarsometatarsal characters listed previously for Sandcoleiformes.

Differs from all sufficiently known members of the family by having: tarsometatarsus with narrower shaft, ridge along medial edge of shaft, trochlea III markedly asymmetrical with lateral ridge much larger than medial ridge and lateral intertrochlear notch very wide anteriorly.

Uintornis lucaris Marsh 1872

HOLOTYPE. YPM 617, distal end of right tarsometatarsus.
DIAGNOSIS. As for genus; *Uintornis marionae* not examined; see Feduccia and Martin (1976).
TYPE LOCALITY. Henry's Fork, Sweetwater County, Wyoming.
TYPE HORIZON. Bridger Formation, Middle Eocene.
REFERRED SPECIMENS. AMNH 8400 (Figs. 14, 16), distal end of left tarsometatarsus.
COMMENTS. *Uintornis* has been treated as a woodpecker, a puffbird, a cuckoo, and a primobucconid (taxonomic history reviewed by Feduccia and Martin, 1976). Because this species is known from only a fragment of a single element, we cannot be certain that it is properly included in the Sandcoleidae. It is consistent with other members of the family by having: tarsometatarsus with facet for metatarsal I facing mediad, not plantad, inner ridge of trochlea IV roughly semicircular in distal view, lateral flanges of trochlea II and especially trochlea IV exaggerated posteriorly, all of which suggest that *Uintornis* was facultatively zygodactyl and pamprodactyl, as were other sandcoleids.

Uintornis marionae
Feduccia and Martin 1976

HOLOTYPE. UKVP 26906, distal end of right tarsometatarsus.
DIAGNOSIS. Not examined; see Feduccia and Martin (1976).
TYPE LOCALITY. Sage Creek, Sweetwater County, Wyoming.
TYPE HORIZON. Bridger Formation, Middle Eocene.
REFERRED SPECIMENS. None.
COMMENTS. Although we have not examined this species, it appears to have been correctly identified by Feduccia and Martin (1976) as a congener of *U. lucaris*.

Chascacocolius new genus

TYPE SPECIES. *Chascacocolius oscitans* new species, the type and only known species of the genus.
DIAGNOSIS. Placed in family by having the suite of characters listed previously for the Sandcoleidae. Differs from all members of the family for which a given structure is known by having: mandible with narrow symphysis and long retroarticular process; scapula with rounder glenoid facet; humerus with larger pectoral crest, long medial and lateral epicondyles; radius with two tendinal grooves, one in dorsal edge of distal extremity; carpometacarpus with pronounced buttress for ulnare located on ventral surface of minor metacarpal, larger intermetacarpal process, minor metacarpal less bowed; pelvis with well-developed terminal iliac process, large ilioischiadic foramen, smaller ilioischiadic lamina, obturator foramen large and nearly enclosed, and straighter terminal process of ischium; femur with larger papilla for attachment of m. gastrocnemius lateralis and ansa of m. iliofibularis, and more excavated medial aspect of medial condyle; tibiotarsus with proximal apex of profile of cnemial crest more lateral, intercristal sulcus shallower, groove medial to extensor canal on anterior surface of distal end, distal aperture of extensor canal more medial. Also differs from *Sandcoleus* by having: coracoid with short procoracoid process.

ETYMOLOGY. Greek *chaskax, chaskakos*, a gaper, plus the generic name *Colius,* which is supposed to derive ultimately (see Newton, 1896:101) from Greek *kolios,* a jackdaw. The name is masculine in gender and refers to the strong gaping adaptations evident in the mandible.

Chascacocolius oscitans new species

HOLOTYPE. USNM 433913 (Fig. 9), formerly articulated partial skeleton, including the mandible, right quadrate, basihyal, several cervical and thoracic vertebrae, furcula, right and left coracoid, right scapula, right and left humerus, right ulna, left radius and distal half of right radius, left carpometacarpus, pelvis lacking right innominate, left femur, right tibiotarsus, and a few phalanges. Collected in a calcareous nodule by A. Houde and P. Houde in July 1985.

DIAGNOSIS. As for genus.

TYPE LOCALITY. NW¼ of NE¼ Sec. 4, T55N R101W, Clark Quadrangle, Park County, Wyoming; 44°46'N, 109°23'W.

TYPE HORIZON. Lower Wasatchian (Lower Eocene), Gray Bull beds, Willwood Formation, Clark's Fork Basin.

REFERRED SPECIMENS. None.

ETYMOLOGY. Latin, *oscitans,* gaping, yawning, again in reference to the gaping adaptation of the species.

DISTRIBUTION. Early Wasatchian Land Mammal Age of the Willwood Formation in Clark's Fork Basin, Wyoming.

COMMENTS. Both this genus and *Uintornis* are widely divergent from the other members of the family (*Botauroides* is excluded from consideration here) and also include the smallest species yet discovered. *Uintornis* is known only from the tarsometatarsus, which is unfortunately the only major appendicular element that remains unknown for *Chascacocolius.* Thus, it is possible that *Chascacocolius* may eventually prove to be a junior synonym of *Uintornis.* Because the Early Eocene genera *Sandcoleus* and *Anneavis* apparently have their closest affinities with the Middle Eocene genus *Eobucco,* rather than the contemporary genus *Chascacocolius,* it seems equally plausible that *Uintornis* may be a Middle Eocene relative of *Chascacocolius,* although such a relationship is not implied here.

In its postcranial skeleton, this species is the most coly-like of the Sandcoleiformes yet known. The narrow bill and extremely large retroarticular process of the mandible suggest that it was highly specialized for foraging by gaping, unlike the Coliidae (Fig. 4). Similar adaptations are widespread among the Passeriformes, especially in the Sturnidae, Icterinae, and Drepanidini. Gaping adaptations have evolved within each of these groups and of themselves are not diagnostic at any taxonomic level above the genus. By contrast, gaping adaptations are rare in non-passerine birds, occurring only in the Upupidae, Phoeniculidae, Haematopodidae, and some Scolopacidae. *Chascacocolius* shows that primitive coly-like landbirds had already radiated into some passerine "niches" by the Early Eocene.

The holotype of this species was preserved in the same nodule as articulated partial skeletons of marsupials, primates, an insectivore and a lizard.

This species is smaller than other known members of the family.

MEASUREMENTS (mm) OF HOLOTYPE. Left and right, respectively, are given for paired elements when both are present.

Quadrate (Right). Length of otic process from intercondylar notch, 6.1; width of condyles of otic process, 3.7; width of mandibular condyles, 4.9.

Mandible. Minimum length, 35.6; length of internal process from lateral cotyla, —, 5.2; width of cotylae, —, 4.1; length of

retroarticular process from internal process, —, 8.6; depth of mandible, —, 3.9.

Coracoid. Length, —, 17.8; width of sternal articulation, 7.0, 6.7; length of procoracoid, 1.9, 1.7; width of glenoid facet, 1.7, 1.8; width of midshaft, —, 1.6.

Scapula (Right). Length, >20; width of shaft, 1.9; width of glenoid facet, 1.7.

Humerus. Length, 26.5, 26.5; length of pectoral crest from caput, 12.2, 12.9; length of bicipital crest from caput, 6.5, 6.1; diameter of midshaft, 2.5, 2.5; distal width, 6.1, 6.3; depth of condyles, 3.4, 3.4.

Radius. Length, 23.8, —; proximal width, 2.5, —; diameter of midshaft, 1.4, 1.2; distal width, 2.9, 2.9.

Ulna (Right). Length, 26.3; maximum proximal width, 4.1; diameter of midshaft, 2.3; depth of dorsal condyle, 3.6.

Carpometacarpus (Left). Length, 15.9; width of trochlea, 2.8; length from alular process to extensor process, 2.7; height of extensor process from trochlea, 4.9; anteroposterior diameter of midshaft of major metacarpal, 1.3; intermetacarpal width, 1.4; width of articular facet for major digit, 2.3.

Pelvis. Length of synsacrum, 21.7; width of body of synsacrum, 5.0; estimated width across antitrochanters, 15.2; length of posterior ala of ilium from acetabulum, 17.7; length of ischium from acetabulum, 18.2.

Femur (Left). Length, 25.1; length of head from trochanteric crest, 5.1; diameter of head, 2.4; height of trochanteric crest, 3.4; diameter of midshaft, 2.1; distal width, 4.9; height of medial condyle, 2.7; height of lateral condyle and tibiofibular crest, 3.9.

Tibiotarsus (Right). Width of cnemial crest, 5.8; width of cotylae, 4.3; proximal depth (cnemial crests to cotylae), 4.5; distance from proximal articular surface to distal end of fibular crest, 11.6; height of fibular crest (diameter of shaft plus elevation of ridge), 3.9; maximum width of shaft, 2.5; distal width, 3.9.

Botauroides Shufeldt 1915

INCLUDED SPECIES. *Botauroides parvus* Shufeldt 1915, the type and only known species of this genus.

DIAGNOSIS. Not examined; see Feduccia and Martin (1976).

Botauroides parvus Shufeldt 1915

HOLOTYPE. YPM 1030, distal end of left tarsometatarsus.

DIAGNOSIS. Not examined; see Feduccia and Martin (1976).

TYPE LOCALITY. Spanish John Meadow, Wyoming.

TYPE HORIZON. Bridger Formation, Wyoming.

REFERRED SPECIMENS. None

COMMENTS. *Botauroides* was thought by Shufeldt (1915) to be a heron (Ardeidae), only to be transferred later by Feduccia and Martin (1976) to the Primobucconidae, the supposed relatives of puffbirds (Bucconidae). We cannot be certain that this genus is properly included in the Sandcoleidae, because we have not examined the only known specimen.

SYSTEMATIC COMPARISONS

This section surveys the major similarities between sandcoleiforms and a diversity of modern arboreal birds. Our purpose here is to justify the ordinal status of the Sandcoleiformes and to justify its placement somewhat near the Piciformes, but nearest to the Coliiformes.

When describing a new taxon, it is necessary only to make comparisons to existing taxa that belong to the next inclusive unit of categorical hierarchy, usually within a genus, family, or

order. Because we describe the Sandcoleiformes as a new order, it is necessary to make comparisons with a wide variety of birds, representing many different orders. In the Description and Diagnosis sections of this paper, we limited comparisons to those taxa of extant birds that we believe are most similar in appearance to sandcoleiforms as a "best guide" to the recognition of sandcoleiform fossils. However, in this section we outline the similarities between sandcoleiforms and representatives of many orders to illustrate that they share some characters with a wide variety of arboreal birds.

We compared Sandcoleiformes with members of Olson's (1985) higher landbird assemblage, to which we believe the Sandcoleiformes belong, as well as some members of Olson's basal landbird assemblage. Based on our general knowledge of comparative avian anatomy, we believe that the relationships of the Sandcoleiformes do not lie among Olson's waterbird assemblage or among the terrestrial members of the basal landbird assemblage.

We did not summarize the comparisons in the form of a table or a cladogram because most shared characters differ qualitatively in as many ways as the number of different birds that possess them. Moreover, we are not presently confident of our ability to distinguish between primitive and derived states of characters in the Sandcoleiformes, given the relatively poor consensus on the interordinal relationships among the higher landbirds.

In the paragraphs that follow, the descriptions refer to the taxon named in each heading. Similarities always refer to characters of the taxon specified at the beginning of each paragraph, and they are comparative to characters of the Sandcoleiformes.

GLAREOLIDAE. This family is mentioned only because the osseous canal of the external ophthalmic vessels passes between the facets for the articulation with the quadrate, directly across the dorsal pneumatic recess, as in sandcoleiforms. The osseous canal in glareolids, however, is very small and is otherwise not similar in morphological details to the fossils.

FALCONIDAE. The only strong similarities of falcons to sandcoleids are the following: the zygomatic process is short, and the tympanic cavity is similar in its detailed structure, especially the osseous canal of the occipital ramus of the external ophthalmic vessels and the very large lateral orbitonasal foramen of the duct of the nasal gland. There is also a superficial similarity in the humerus because of its robustness, curvature, and flared pectoral crest and in the tarsometatarsus because it is flattened.

PSITTACIDAE. Similarities of parrots to sandcoleids are only superficial and include the following: the carpometacarpus has a blunt distal end; the femur is similar in proportions to that of the fossils, especially in the large head; the tarsometatarsus (Figs. 15, 16) is flattened and has widely spaced cotylae and a low intercotylar eminence; the hypotarsus has three canals (or two canals and one groove); and the trochleae are splayed.

MUSOPHAGIDAE. The most notable similarities of the touracos to sandcoleids are the following: the lateral orbitonasal foramen of the duct of the nasal gland is large and positioned laterally; the sternum has four notches in the posterior margin, a shallow carina, crossed coracoidal sulci, and a flat manubrium; and the pygostyle is large, with a broad ventral surface. Other similarities include the following: the zygomatic and postorbital processes are small; the mandibular symphysis is small; the cervical vertebrae have pneumatic foramina and sometimes an accessory osseous bridge that connects the transverse process with the posterior articular process to form a lateral accessory foramen; the coracoid has a large lateral angle; the humerus has a pronounced bicipital crest and a broad, shallow coracobrachial depression; the radius is short and has a large condyle; the ulna is short and has a short, rounded olecranon and large, rounded dorsal process; the carpometacarpus has a blunt distal end; and the tarsometatarsus has a large scar for the articulation of the hallux, is thin in the region of the medial proximal vascular canal, and has an elongated collateral flange of trochlea IV.

CUCULIDAE. Similarities of certain cuckoos (e.g., *Eudynamys*) to sandcoleids include the following: the mandibular symphysis is small; the bill is superficially similar in shape; the sternum has caudomedial trabeculae that converge toward the midline distally; the carpometacarpus has a blunt distal end, a wide intermetacarpal space, and no intermetacarpal process; the ulna is short, with a short, rounded olecranon; the radius has a large distal condyle; and the tarsometatarsus is flattened and has a large, strongly inflected collateral flange of trochlea IV.

STRIGIDAE AND TYTONIDAE. The only notable similarities of owls to sandcoleiforms are the following: the proximal three phalanges of digit IV of the pes are extremely reduced in length, with the relief of the interphalangeal articular surfaces (i.e., notch and groove) being much exaggerated. As in the Falconidae, the osseous canal of the external ophthalmic vessels is large and passes between the facets for articulation with the quadrate, but in owls this is connected to the pila prootica rather than passing directly across the dorsal pneumatic recess. In owls, the sternum has four notches in the posterior margin (except *Tyto* Billberg 1828), the carpometacarpus has a blunt distal end, and the tarsometatarsus is flat and concave posteriorly, but these elements are otherwise not morphologically similar to those of sandcoleids.

CAPRIMULGIDAE, PODARGIDAE, NYCTIBIIDAE, AND STEATORNITHIDAE. These share no important similarities with sandcoleids except that the cervical vertebrae of *Podargus* have an accessory process connecting the transverse and posterior articular processes and the pygostyle is superficially similar.

AEGOTHELIDAE. Similarities of owlet-frogmouths to sandcoleids include the following: the sternum in general, particularly the pattern of the sternal notches, and the ischium and ilium have long terminal processes. Other interesting similarities include the following: the skull, which has less pneumatization than in other caprimulgiform families, has a small zygomatic process; the cervical vertebrae have pneumatic foramina; the humerus, similar in its curvature and robustness to the fossils, with a pronounced bicipital crest, and a well-rounded radial condyle; the femur with a tubercle (although small) for the attachment of m. gastrocnemius lateralis and ansa m. iliofibularis; and the pygostyle in general.

APODIDAE. The most notable similarities of swifts to sandcoleids are the following: the proximal three phalanges of digit IV of the pes are extremely reduced in length, and the terminal phalanges of the pes are large. Other similarities are the following: the carpometacarpus has a blunt distal end; the tibiotarsus has a crest opposite the fibular crest; and the tarsometatarsus is flattened, has widely spaced cotylae, a low intercotylar eminence, and a concave plantar surface.

COLIIDAE. Of all families of modern birds, the colies are the most similar to sandcoleids in general proportions as well as in morphological details, especially of the humerus and hindlimb (see Figs. 8, 9, 12–17, Diagnosis of the Sandcoleiformes, and Description of the Sandcoleidae). Yet, significant differences exist between colies and sandcoleids, in which the latter are more like other families described in this section. The *differences* of colies include the following: the bill is short; the tympanic cavity does not have the large canal of the external ophthalmic vessels passing centrally across the dorsal pneumatic recess; the

quadrate and zygomatic process have flattened lateral surfaces; the quadrate has a process projecting dorsad from the lateral mandibular condyle; the pterygoids are cylindrical; the sternum has a different pattern of sternal notches and a short sternocoracoid process; the furcula has a hypocleideum; the scapula has a process for the articulation of the furcula; the carpometacarpus has a well-developed intermetacarpal process; the pelvis has neither a large ischiopubic fenestra nor a broad terminal process of the ischium; and the pygostyle has Picidae-like transverse processes.

TROGONIDAE. Similarities of the trogons to sandcoleids are superficial and include the following: the sternum has four notches in the posterior margin; the scapula does not have a large process for the articulation of the furcula; the proportions of forelimb elements; the humerus has a long pectoral crest, a pronounced, narrow bicipital crest, and a broad, shallow coracobrachial region; and the carpometacarpus has a blunt distal end (Fig. 18).

ALCEDINIDAE, TODIDAE, MOMOTIDAE, MEROPIDAE, AND CORACIIDAE. Similarities to sandcoleiforms are few, but include the following: the sternum with four notches in the posterior margin; the furcula has no hypocleideum; and the coracoids of todids and coraciids have combinations of characters such as the well-developed medial angle, lateral process, narrow shaft, small procoracoid (not Coraciidae), and a small scapular extremity.

LEPTOSOMIDAE. In addition to the few similarities for other families of Coraciiformes listed earlier, cuckoo-rollers are similar to the fossils because of the following: in the tympanic cavity, the osseous canal of the external ophthalmic vessels passes between the facets for the articulation with the quadrate and the lateral facet is nestled into the zygomatic process; some cervical vertebrae have an accessory process connecting the transverse process and posterior articular process; the scapula is without a large articular process for the furcula; the humerus has a long, flared pectoral crest that comes to an angle approximately at midlength of the crest; the tarsometatarsus is broad and has widely spaced cotylae, a low intercotylar eminence, and a flattened shaft; and the collateral flange of trochlea IV is exaggerated posteriorly.

UPUPIDAE AND PHOENICULIDAE. Hoopoes and woodhoopoes exhibit only a few similarities to the fossils, including the following: the mandible with a long retroarticular process (among sandcoleids, only *Chascacocolius* new genus, described previously, is known to have an elongated retroarticular); the cervical vertebrae have an accessory process connecting the transverse and posterior articular process; the carpometacarpus has a blunt distal end; and the ischiopubic fenestra is large.

GALBULIDAE. The only similarities of jacamars to sandcoleids are the following: the zygomatic process is small; the cervical vertebrae have pneumatic foramina and an accessory process connecting the transverse and posterior articular processes; the sternum has four notches in the posterior margin (although the pattern is like that of coliids, not like sandcoleids); the tarsometatarsus is short and flattened; and the pygostyle is generally similar.

BUCCONIDAE. The only similarities of puffbirds to sandcoleids are the following: the cervical vertebrae have accessory processes connecting the transverse and posterior articular processes; the scapula has no large articular process for attachment of the scapula; and the sternum has four notches in the posterior margin (although the pattern is like galbulids and coliids, not like sandcoleids) (see Figs. 15, 16).

CAPITONIDAE. Similarities of barbets to sandcoleids are restricted to the following: the sternum because of the configuration of the caudal trabeculae (e.g., *Calorhamphus* Lesson 1839, *Gymnobucco* Bonaparte 1850, and *Lybius* Hermann 1783); the furcula has no hypocleideum; the tibiotarsus has a broad cnemial region (intercristal sulcus; e.g., *Trachyphonus* Ranzani 1821, not *Tricholaema* Verreaux and Verreaux 1855); and the ischium has a long, bent terminal process (e.g., *Tricholaema*).

INDICATORIDAE. Among the Pici, the honeyguides are the most similar to the fossils because of the following: the cranium is well rounded; the supraorbital region is narrow; the frontal bones diverge anteriorly and are not incised by the prefrontals; the lateral orbitonasal foramen is large and positioned very laterally; the zygomatic process is small; the pterygoid has ridges along its entire length; the mandibular symphysis is small; the cervical vertebrae have pneumatic foramina; the pygostyle has no transverse processes; the sternum (Fig. 6) is similar in general, except that the spina externa of the manubrium (which is bifid in *Prodotiscus* Sundevall 1850, unlike the fossils) forms a continuous ridge with the procumbent anterior margin of the carina; the furcula has no hypocleideum; the coracoid is narrow, although narrower than in sandcoleids; the pelvis is similar in all details, especially the large obturator and ilioischiadic foramina and the large ischiopubic fenestra with a long, bent terminal ischial process; and the tibiotarsus as in the Capitonidae.

RAMPHASTIDAE. The only similarities of toucans to sandcoleids are the following: the lateral orbitonasal foramen is positioned laterally in *Baillornis* Cassin 1867, *Selenidera* Gould 1837, and *Aulacorhynchus* Gould 1834, and the cervical vertebrae with pneumatic foramina.

JYNGIDAE. Wrynecks are almost as similar to the fossils as are the indicatorids. Typically of the Pici, similarities include the following: the sternum because of the morphology of the sternal notches; the tibiotarsus in general; and the ischium with a long, bent terminal process (Fig. 11).

PICIDAE. Similarities of the diverse woodpecker family to sandcoleids include the following: the orbitonasal foramen is positioned laterally; the cervical vertebrae have an accessory process connecting the transverse and posterior articular processes (e.g., *Picus* Linnaeus 1758); the sternum has a shallow carina and a configuration of the caudal trabeculae similar to that of the fossils; the furcula has no hypocleideum; the humerus has a well-developed lateral epicondyle and bulbous capitulum; the pelvis has a large ischiopubic fenestra and a long, bent terminal process of the ischium (especially *Picus*), although shorter than in sandcoleids; the femur has a tubercle for the attachment of m. gastrocnemius lateralis and ansa iliofibularis, although small; the tibiotarsus because of the configuration of the cnemial crests (although they are more symmetrical in anterior view than in sandcoleids) and a crest opposite the fibular crest (Fig. 13).

PASSERIFORMES. Similarities of perching birds to sandcoleiformes are rare and include the following: a skull that is well rounded in some species; a long retroarticular process of mandible in some (e.g., *Sturnella* Vieillot 1816 and *Sturnus* Linnaeus 1758); a sternum with four notches in the posterior margin (i.e., some scytalopodids); a pelvis with a large ischiopubic fenestra and long terminal process of the ischium (e.g., *Ampelion* Tschudi 1845); and the tibiotarsus with a crest on the tibiotarsus opposite the fibular crest.

DISCUSSION

The order Sandcoleiformes represents an archaic group with no close relationships among modern birds. Most similarities are

with the Coliidae, but there are also very close similarities to the Pici, particularly the Indicatoridae. Even among more disparate orders of landbirds, there are families or genera that share similarities with sandcoleids that the coliids and Pici do not. Such characters are likely primitive, if not evolved convergently. This suggests a very early origin and divergence of the Sandcoleiformes from all known orders of birds. Sibley et al. (1988) suggested that the Pici are the sister-group of Coliidae plus other higher landbirds. If this were so, then the strong similarities of Sandcoleiformes to the Coliidae and Pici and weaker similarities to other groups could indeed be shared primitive characters, retained since the early divergence of the lineages leading to the Pici, Coliiformes, Sandcoleiformes, and other higher landbirds.

The ecology of Sandcoleiformes, like most birds, is best reflected by the specializations of their bills and feet. The bill of *Sandcoleus* is similar in overall proportions to that of *Eudynamys* or *Turdus*. *Sandcoleus* could have been a generalist, eating anything from berries, fruits, and seeds to hard- and soft-bodied invertebrates. The bill of *Chascacocolius* is perhaps as specialized as that of any living bird for gaping as a mode of foraging. Gaping in landbirds is typically associated with an insectivorous diet, and modern gapers may forage either on the ground or in trees.

All sandcoleiformes appear to have been both facultatively zygodactyl and pamprodactyl. We believe that, like all zygodactyl or facultatively zygodactyl birds, sandcoleiforms could oppose digit IV to digits II and III. This is because trochlea IV of the tarsometatarsus is relatively narrow and the lateral flange is very large and extends caudad or caudomediad in the manner of a sehnenhalter. Moreover, there is a large distal foramen, and to varying degrees there is a groove medial to trochlea IV on the anterior aspect of the shaft.

In their description of the hindlimb myology of the Coliidae, Berman and Raikow (1982) could identify only a few myological traits that might be directly associated with pamprodactyly; however, because they did not specifically discuss or illustrate any of the muscular origins and insertions on the pelvic skeleton itself, we could not ascertain whether or not any of these adaptations are present in the Sandcoleidae. Sandcoleiforms possess particularly large processes and ridges for the origins and insertions of the distal musculature of the pelvic appendage and in general closely resemble colies in these respects. Moreover, the coly-like location of the large facet for the articulation of metatarsal I on the medial surface of the tarsometatarsus, rather than on the plantar surface, would facilitate rotation of digit I mediad and anteriad. The most significant difference in the condition of the feet between the Coliidae and Sandcoleidae is that in the Coliidae the facet for metatarsal I is positioned more distad on the tarsometatarsus, and the tarsometatarsal trochleae are more closely spaced and none are significantly elevated proximad above the others. Although the Sandcoleidae possessed feet superficially similar to those of raptorial birds, they were probably not similarly adapted behaviorally. The bill of *Sandcoleus* was too weak to have been used efficiently in predation on anything other than small invertebrates, and the bill of *Chascacocolius* clearly indicates that its mode of food-fathering was bill-oriented rather than foot-oriented. The foot of sandcoleiforms was therefore probably specialized for climbing and creeping in trees.

The long rectrices of sandcoleids had somewhat thickened shafts, but no more so than those of colies or the more long-tailed species of parrots. The pygostyles of sandcoleiforms lack the specializations of the transverse processes that anchor the retrices in most species of Pici and Coliidae. Hence, the tails of

sandcoleiforms would not have been structurally equivalent to those in these modern taxa.

One could imagine that the flight of sandcoleiforms might have been somewhat like that of species of the Pici or Coliidae. They were probably strong fliers, but they appear to have been poorly adapted for long periods of flight, because their wing was short and rounded and the carina of their sternum was shallow.

The order Sandcoleiformes is morphologically diverse and was probably much more speciose than is apparent from the relatively few fossil forms described here. Sandcoleiforms were probably numerically abundant as well, because they represent one of the two most commonly preserved orders of landbirds in the Lower Eocene of Wyoming (the other being the Lithornithiformes). Sandcoleiforms probably filled many of the niches similar to those later occupied by passerines. Replacement by modern orders of archaic early Tertiary groups, with no close living relatives, is a pattern also observed among mammals (Russell, 1982), where creodonts and condylarths, for example, were replaced by carnivores and ungulates.

Sandcoleiforms fit another pattern that is becoming increasingly familiar in avian paleontology: the occurrence of groups in North America whose closest living relatives are now geographically distant and often insular. Colies, if they are the nearest relatives of sandcoleiforms, are restricted to Africa, although their range once extended as far north as France (Mourer-Chauviré, 1982). Sandcoleiformes appear to fulfill Olson's (1985) prophecy of the discovery of coly-like birds elsewhere in the Tertiary outside of Africa. The closest similarities to Lithornithiformes are among the tinamous (Tinamidae) of Central and South America and the kiwis (Apterygidae) of New Zealand (Houde, 1988). Olson (1987) recently identified a primitive relative of the South American oilbird (Steatornithidae), and Houde and Olson (1989) identified fossils similar to the Madagascan ground-rollers (Atelornithidae), both from the Lower Eocene of Wyoming.

The known fossil record of the Sandcoleiformes is brief, lasting only from the Early to Middle Eocene. Although future discoveries may push their record back into the Paleocene, it appears unlikely that they persisted much after the Middle Eocene. No certain members of the Sandcoleiformes have been identified in the large avifaunas from the Middle Eocene excavations at Messel, Germany, and the Eo-Oligocene at Quercy, France. However, a single humerus (Paris Museum QU 17092) from an unknown level of the Phosphorites du Quercy that was designated the holotype of *Primocolius sigei* Mourer-Chauviré 1988 (Coliidae) is, in our opinion, more similar to *Chascacocolius* than it is to *Colius*, because the shaft is robust and curved, the medial epicondyle is short, the pectoral crest is large, and there is no bony spur in the tricipital fossa that is distinctive of colies. We have not had the opportunity to compare other specimens that were referred to *P. sigei*, which include a carpometacarpus in addition to humeri. An unpublished single tarsometatarsus (Basel Museum QO 596), also identified as a coly (C. Mourer-Chauviré, pers. comm.) and also from an unknown level of the Phosphorites du Quercy is intermediate between *Anneavis* and *Colius* with respect to its robustness and width, and splaying and elevation of trochleae II and IV.

The impracticality of identifying isolated elements from early Tertiary birds (Olson, 1977) is underscored by the discovery of this, yet another, group of birds with no close affinities to modern birds that combines a mosaic of characters similar to individual parts of various unrelated taxa of modern birds. The fact that *Uintornis* and *Botauroides* had been assigned to no fewer

than four families of modern birds attests to the riskiness of this practice. Harrison (1980:83) described "a small owl from the Lower Eocene of Britain," on the basis of a single proximal pedal phalanx of digit III. The specimen, he declared, "is sufficiently specialized to be recognised as that of an owl." Specifically, it is short and the distal articular surface extends onto the dorsal aspect of the bone. While we do not suggest that *Eostrix vincenti* Harrison 1980 is actually a member of the Sandcoleiformes, we do point out that much of the same condition of the pedal phalanges occurs in Sandcoleiformes as well as in Strigiformes and other groups.

Hoch (1975:552, fig. 6) referred a small humerus (Mineralogical Museum of Copenhagen specimen MNH. V.P. 1282) from the lowermost Eocene of the Mo Clay to the Falconiformes but wisely did not name the specimen. This humerus is sufficiently dissimilar from humeri of the Falconiformes and similar to humeri of the known Sandcoleiformes that it might be correctly included in the latter. It has a large, broad pectoral crest, a narrow bicipital crest, and proportions similar to those exhibited by *Sandcoleus*. It is not a member of any genus for which the humerus is known, however, and its inclusion in the Sandcoleiformes is unwarranted at this time.

SUMMARY AND CONCLUSIONS

The order Sandcoleiformes includes one family with seven species in six genera. The monotypic genera *Sandcoleus*, *Anneavis*, and *Chascacocolius* are described as new, with the previously described genera *Eobucco*, *Unitornis*, and *Botauroides* being referred to the family. The known distribution of the Sandcoleiformes is limited to Lower and Middle Eocene deposits of Wyoming.

The order Sandcoleiformes is not phylogenetically close to any other known order of birds; still, it may be closer to the order Coliiformes than it is to any other. Sandcoleiforms resemble colies postcranially, and, to a lesser degree, they also resemble members of the Pici and other groups. At least some had short remiges and long, tapered rectrices, like those of colies. However, sandcoleiforms were more diverse than known colies, because they were specialized for at least two very different modes of feeding. Some possessed a thrush-like bill, whereas one had a gaping bill like that of certain icterids. Thus, sandcoleiforms may have occupied niches that are currently exploited by passerines.
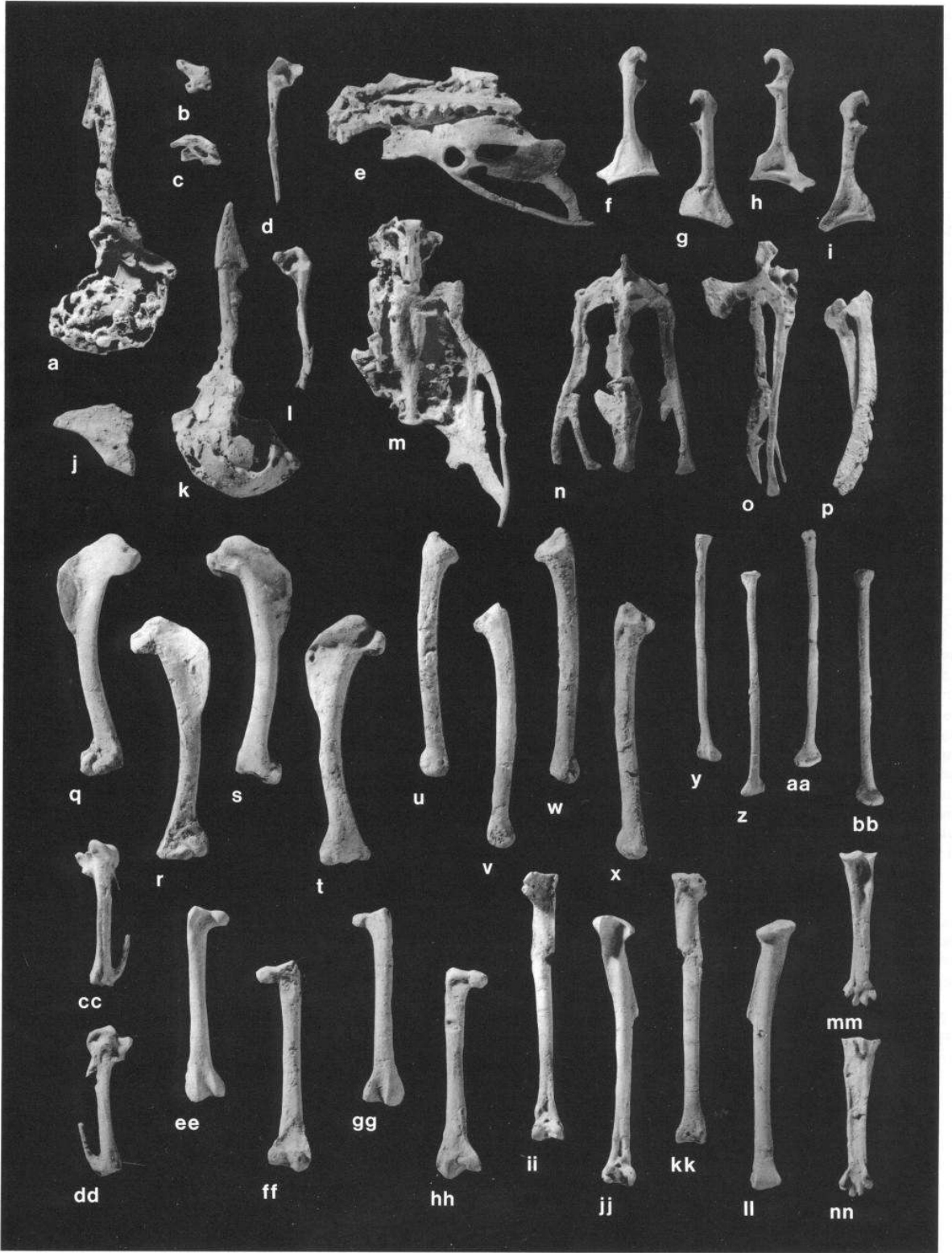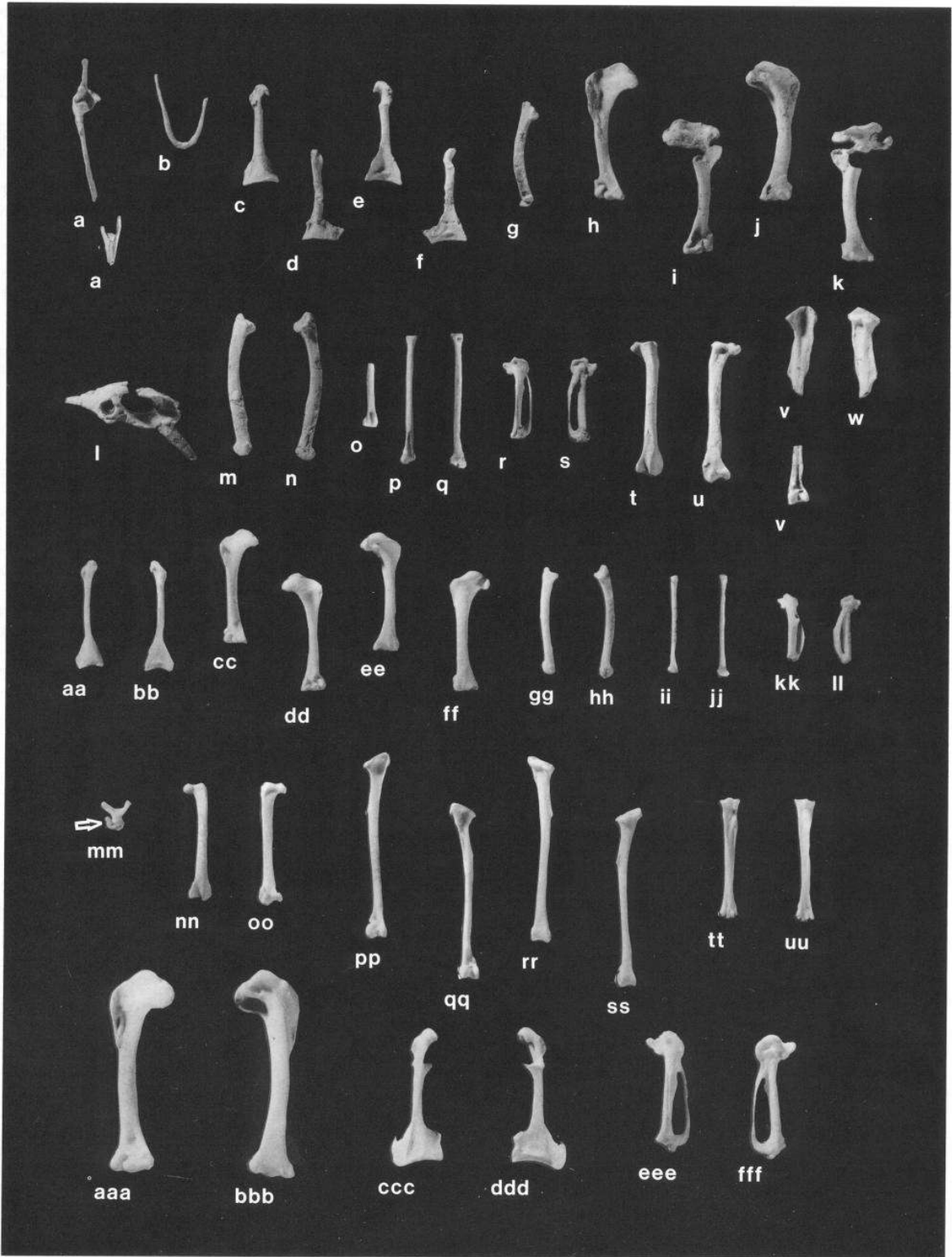
ADDENDUM

Plates I and II were not completed in time to be included in the text references in this paper. They were intended to replace several of the figures called out in the text and are presented to augment those figures.

Plate I. *Sandcoleus copiosus*, holotype specimen (USNM 433912): **a**, skull, ventral view; **b**, right quadrate, lateral view; **c**, cervical vertebra, right lateral view; **d**, right posterior portion of mandible, dorsal view; **e**, pelvis, dorsolateral view; **f**, right coracoid, ventral view; **g**, left coracoid, ventral view; **h**, right coracoid, dorsal view; **i**, left coracoid, dorsal view; **j**, pygostyle, right lateral view; **k**, skull, dorsolateral view; **l**, left posterior portion of mandible, dorsal view; **m**, pelvis, ventral view; **n**, sternum, ventral view; **o**, sternum, left lateral view; **p**, left and right scapulae, lateral and medial views, respectively; **q**, right humerus, cranial view; **r**, left humerus, cranial view; **s**, right humerus, caudal view; **t**, left humerus, caudal view; **u**, right ulna, caudal view; **v**, left ulna, caudal view; **w**, right ulna, cranial view; **x**, left ulna, cranial view; **y**, right radius, cranial view; **z**, left radius, cranial view; **aa**, right radius, caudal view; **bb**, left radius, caudal view; **cc**, left carpometacarpus, dorsal view; **dd**, left carpometacarpus, ventral view; **ee**, right femur, cranial view; **ff**, right femur, caudal view; **gg**, left femur, cranial view; **hh**, left femur, caudal view; **ii**, right tibiotarsus, cranial view; **jj**, left tibiotarsus, cranial view; **kk**, right tibiotarsus, caudal view; **ll**, left tibiotarsus, caudal view; **mm**, right tarsometatarsus, dorsal view; **nn**, right tarsometatarsus, plantar view; all approximately actual size; all treated with ammonium chloride.

Plate II. *Chascacocolius oscitans*, holotype specimen (USNM 433913), top two rows (a–w); *Colius striatus* (USNM 558544), third and fourth rows (aa–uu); and *Trogon viridus* (USNM 562749), bottom row (aaa–fff): **a**, symphysis and right posterior portion of mandible; **b**, furcula, cranial view; **c**, right coracoid, ventral view; **d**, left coracoid, ventral view; **e**, right coracoid, dorsal view; **f**, left coracoid, dorsal view; **g**, right scapula, lateral view; **h**, right humerus, cranial view; **i**, left humerus, cranial view; **j**, right humerus, caudal view; **k**, left humerus, caudal view; **l**, left innominate, lateral view; **m**, right ulna, caudal view; **n**, right ulna, cranial view; **o**, distal portion of right radius, cranial view; **p**, left radius, cranial view; **q**, left radius, caudal view; **r**, left carpometacarpus, dorsal view; **s**, left carpometacarpus, ventral view; **t**, left femur, cranial view; **u**, left femur, caudal view; **v**, proximal and distal portions of right tibiotarsus, cranial view; **w**, proximal portion of right tibiotarsus, caudal view; **aa**, right coracoid, ventral view; **bb**, right coracoid, dorsal view; **cc**, right humerus, cranial view; **dd**, left humerus, cranial view; **ee**, right humerus, caudal view; **ff**, left humerus, caudal view; **gg**, right ulna, caudal view; **hh**, right ulna, cranial view; **ii**, right radius, cranial view; **jj**, right radius, caudal view; **kk**, left carpometacarpus, dorsal view; **ll**, left carpometacarpus, ventral view; **mm**, right quadrate, lateral view; arrow indicates dorsal process of lateral mandibular condyle; **nn**, left femur, cranial view; **oo**, left femur, caudal view; **pp**, right tibiotarsus, cranial view; **qq**, left tibiotarsus, cranial view; **rr**, right tibiotarsus, caudal view; **ss**, left tibiotarsus, caudal view; **tt**, right tarsometatarsus, dorsal view; **uu**, right tarsometatarsus, plantar view; **aaa**, right humerus, cranial view; **bbb**, right humerus, caudal view; **ccc**, right coracoid, ventral view; **ddd**, right coracoid, dorsal view; **eee**, left carpometacarpus, dorsal view; **fff**, left carpometacarpus, ventral view; all approximately actual size; a–w treated with ammonium chloride.

Plate I

Plate II

Eocene Coly-like Birds ■ 159

LITERATURE CITED

Baumel, J.J. 1979. Osteologia. In *Nomina anatomica avium*, ed. J.J. Baumel, A.S. King, A.M. Lucas, J.E. Breazile, and H.E. Evans, 53–121. New York: Academic Press.

Berman, S.L., and R.J. Raikow. 1982. The hindlimb musculature of the mousebirds (Coliiformes). *Auk* 99:41–57.

Bown, T.M. 1980. Summary of latest Cretaceous and Cenozoic sedimentary, tectonic, and erosional events, Bighorn Basin, Wyoming. *University of Michigan Papers on Paleontology* 24:25–32.

Feduccia, A. 1973. A new Eocene zygodactyl bird. *Journal of Paleontology* 47:501–03.

Feduccia, A., and L.D. Martin. 1976. The Eocene zygodactyl birds of North America (Aves: Piciformes). *Smithsonian Contributions to Paleobiology* 27:101–10.

Grande, L. 1984. Paleontology of the Green River Formation, with a review of the fish fauna, 2nd ed. *Geological Survey of Wyoming, Bulletin* 63:1–333.

Harrison, C.J.O. 1980. A small owl from the Lower Eocene of Britain. *Tertiary Research* 3:83–87.

Hoch, E. 1975. Amniote remnants from the eastern part of the Lower Eocene North Sea Basin. *Colloque international CNRS* 218:543–62.

Houde, P. 1987. Histological evidence for the systematic position of *Hesperornis* (Odontornithes: Hesperornithiformes). *Auk* 104:125–29.

———. 1988. Paleognathous birds from the early Tertiary of the Northern Hemisphere, ed. R.A. Paynter, Jr. *Publications of the Nuttall Ornithological Club* 22:1–148.

Houde, P., and S.L. Olson. 1989. Small arboreal nonpasserine birds from the early Tertiary of western North America. In *Acta XIX Congressus Internationalis Ornithologici*, Vol. 2, ed. H. Ouellet, 2030–36. Ottawa: University of Ottawa Press.

Marsh, O.C. 1872. Notice of some new Tertiary and post-Tertiary birds. *American Journal of Science* 4:256–62.

Mourer-Chauviré, C. 1982. Les oiseaux fossiles des Phosphorites du Quercy (éocène supérieur à oligocène supérieur): Implications paléobiogéographiques. *Geobios mémoire spécial* 6:413–26.

———. 1988. Le Gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertebres de l'éocène superieur, II Oiseaux. *Palaeontographica Abteilung, A* 205:29–50.

Newton, A. 1896. *A dictionary of birds*. London: A. and C. Black, 1088 pp.

Olson, S.L. 1977. A Lower Eocene frigatebird from the Green River Formation of Wyoming (Pelecaniformes: Fregatidae). *Smithsonian Contributions to Paleobiology* 35:1–33.

———. 1985. The fossil record of birds. In *Avian biology*, Vol. 8, ed. D.S. Farner, J.R. King, and K.C. Parkes, 79–238. New York: Academic Press.

———. 1987. An Early Eocene oilbird from the Green River Formation of Wyoming (Caprimulgiformes: Steatornithidae). *Documents des laboratoires de géologie, Lyon* 99:56–70.

Russell, D.E. 1982. Tetrapods of the northwestern European Tertiary Basin. *Geologisches Jahrbuch A* 60:5–74.

Shufeldt, R.W. 1913. Fossil feathers and some heretofore undescribed fossil birds. *Journal of Geology* 21:628–52.

———. 1915. Fossil birds in the Marsh Collection of Yale University. *Transactions of the Connecticut Academy of Arts and Sciences* 19:1–110.

Sibley, C.G., J.E. Ahlquist, and B.L. Monroe, Jr. 1988. A classification of the living birds of the world based on DNA-DNA hybridization studies. *Auk* 105:409–23.

Vanden Berge, J.C. 1979. Myologia. In *Nomina anatomica avium*, ed. J.J. Baumel, A.S. King, A.M. Lucas, J.E. Breazile, and H.E. Evans, 175–219. New York: Academic Press.