

The Eocene Zygodactyl Birds of North America (Aves: Piciformes)

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ABSTRACT

Recent discoveries of zygodactyl birds in the Eocene of Wyoming, along with reinterpretation of previously described taxa, show that these forms belong to an extinct family, affiliated with the Bucconidae, for which we here propose the name Primobucconidae. The genera *Primobucco*, *Neanis*, *Uintornis*, *Botauroides*, and a new genus, *Eobucco*, are assigned to this family, and three new species, *Primobucco olsoni*, *Uintornis marionae*, and *Eobucco brodkorbi* are described. Primobucconids appear to have been the dominant small perching birds of the Eocene of North America.

Introduction

Recent discoveries of piciform zygodactyl birds from the lower Eocene Green River Formation of Wyoming brought to light an entirely new element in the avifauna of the North American Tertiary. Brodkorb (1970a) described the first of these forms as a new genus and species of the Bucconidae, which is structurally the most primitive family of the Piciformes. This species, *Primobucco mcgrewi*, provided the earliest record of the order Piciformes and the only fossil record of the Bucconidae. In addition to describing *Primobucco mcgrewi*, Brodkorb (1970a) suggested that *Uintornis lucaris* Marsh (1872), from a much higher level in the Eocene than *P. mcgrewi*, might also be referable to

the Bucconidae. Later, Feduccia (1973) described a new zygodactyl bird, *Primobucco kistneri*, from the same formation as *P. mcgrewi*. While *P. mcgrewi* was based on a right wing, the type of *P. kistneri* included much of the skeleton on a slab. Although the bones were poorly preserved, the zygodactyl condition of the toes could be clearly discerned for the first time in any known fossil. Few useful osteological characters were present in this fossil, but by using ratios of the hindlimb elements it was at least possible to show that *P. kistneri* was a "perching" piciform bird, closely resembling the Bucconidae and Capitonidae in proportions. Being from the same approximate horizon and locality as *P. mcgrewi*, it seemed reasonable to assume that the two were related, although *P. mcgrewi* was larger than the modern bucconids *Notharchus tectus* or *Malacoptila panamensis* (Brodkorb, 1970a:14), whereas *P. kistneri* was much smaller, being approximately the size of some of the modern African capitonids of the genus *Pogoniulus*, which are about 100–130 mm long.

Feduccia (pp. 95–99, herein) examined the type of *Neanis schucherti* (Shufeldt, 1913), also from the lower Eocene of Wyoming, which was originally described as belonging to the Rhinocryptidae, thus supposedly representing the earliest record of the order Passeriformes. He found, however, that this species is not a passerine, but a piciform, probably congeneric with *P. kistneri*. Because both these species are much smaller than *P. mcgrewi*, *P. kistneri* was removed to the genus *Neanis*, and the genus *Primobucco* was reserved for larger lower Eocene forms the size of *P. mcgrewi*.

The problematical genus *Uintornis* was originally affiliated with the woodpeckers (Picidae) by Marsh (1872). Shufeldt (1915:51) stated emphat-

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ically that this assignment was erroneous, but left the question of the true affinities of the genus unsettled. Cracraft examined the type and agreed with Shufeldt that it was not from a woodpecker, suggesting instead that it belonged with the Cuculiformes (Cracraft and Morony, 1969:6). On Cracraft's suggestion, Brodkorb (1970b; 1971) placed *Uintornis* in the Cuculidae. Our present studies of the type of *Uintornis lucaris* show that it is not a cuculid and that Brodkorb's (1970a) original assignment of it to the Bucconidae was more nearly correct. We found three other tarsometatarsi, also from middle Eocene deposits in North America, to be affiliated with *Uintornis* at the family level. One of these was originally described by Shufeldt (1915) as a new genus and species of heron, *Botauroides parvus*; the second represents an undescribed species of *Uintornis*; while the last represents a new genus.

Two species of piciform birds from the Miocene of Europe have been placed in an extinct family Zygodactylidae (Brodkorb, 1971), based on the genus *Zygodactylus* (Ballman, 1969a; 1969b). These forms are distinctly different from the above species and further study of them will be necessary in order to clarify their affinities with other groups of modern and Tertiary zygodactyl birds. Meanwhile, the morphology of the Eocene forms precludes their assignment to any known family of the Piciformes and the erection of a new family is therefore made necessary.

ACKNOWLEDGMENTS.—We are greatly indebted to S. W. Shannon of the Geological Survey of Alabama for bringing to our attention the type of *Primobucco olsoni* and placing it at our disposal for study. P. O. McGrew of the University of Wyoming, Department of Geology, kindly lent the types of *Primobucco mcgrewi* and *Neanis kistneri*. Skeletons of modern species were made available through the courtesy of Pierce Brodkorb (University of Florida), R. W. Storer (University of Michigan Museum of Zoology), and R. L. Zusi (National Museum of Natural History, Smithsonian Institution). C. B. Schultz made the University of Nebraska specimen available. D. Adams and D. Bennett rendered the illustrations. Abbreviations are as follows: Geological Survey of Alabama Type Collection (GSATC), University of Kansas Museum of Natural History (KUVN), University of Nebraska State Museum (UNSM), University of

Wyoming Geological Museum (UWGM), and Yale Peabody Museum (YPM).

Order PICIFORMES

Suborder GALBULAE

PRIMOBUCCONIDAE, new family

INCLUDED GENERA.—*Primobucco*, *Neanis*, *Uintornis*, *Botauroides*, *Eobucco*.

DIAGNOSIS.—Small perching birds with the following combination of characters: (1) humerus (Figure 1a) with shaft curved, the head inflected medially, and the deltoid crest low, slightly rounded and proximally located; (2) radius and ulna (Figure 1a) slender and elongate; (3) metacarpals II

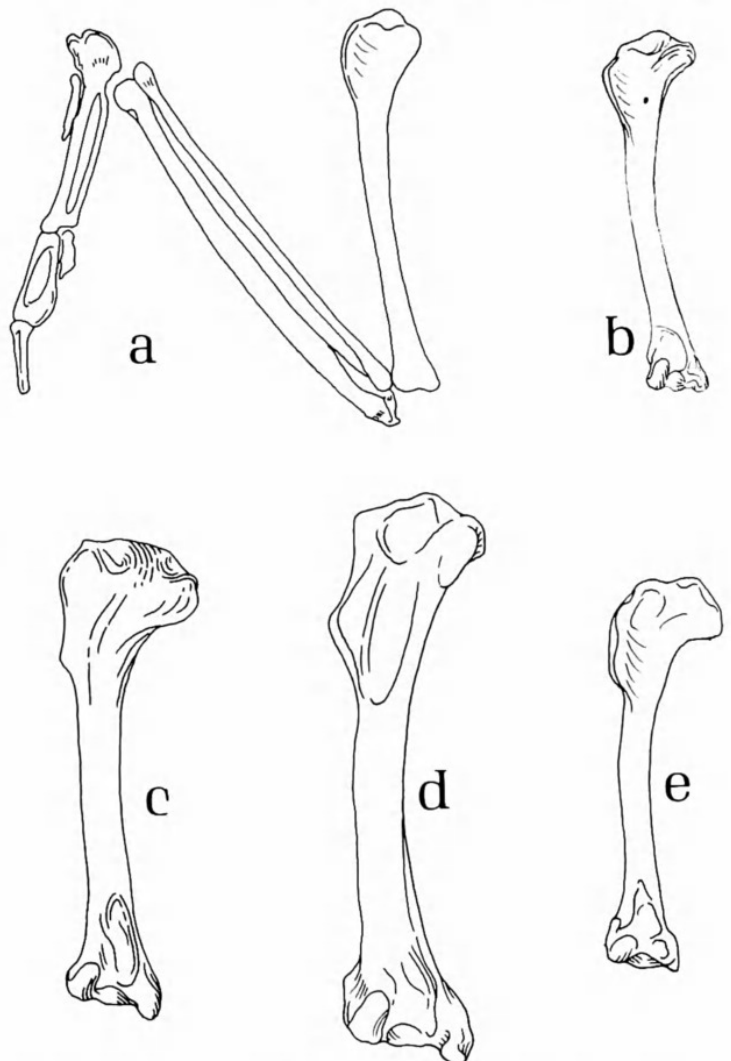


FIGURE 1.—a, Restoration of the right wing of *Primobucco olsoni*, palmar view. Palmar views of right humeri: b, *Chelidoptera tenebrosa* (Bucconidae); c, *Megalaima lineata* (Capitonidae); d, *Tauraco* sp. (Musophagidae); e, *Tapera naevia* (Cuculidae).

and III (Figure 1a) nearly parallel to each other, with only a narrow intermetacarpal space; (4) phalanx I digit II of manus (Figure 1a) broader proximally than in most other Piciformes; (5) tarsometatarsus (Figure 2e, f) relatively short, broad, and flat; (6) hypotarsus with a square lateral block of bone and a low ridge leading distally from it (Figure 6), probably with only a single tendinal canal (not clearly determinable in any known specimen); (7) papilla for tibialis anticus on the extreme internal margin of the tarsometatarsus (Figure 2e, f); (8) tarsometatarsus with a single proximal foramen (Figure 6); (9) distal end of tarsometatarsus flared, with large intertrochlear spaces and trochleae lying in the same anterior-posterior plane (Figures 2e,f,k; 5; 6); (10) middle trochlea the most distad, with the inner and outer trochleae about subequal (Figures 2e,f; 5; 6); (11) facet for metatarsal I entirely medial (Figures 5, 6); (12) inner trochlea grooved distally and posteriorly, middle trochlea deeply grooved (Figures 5, 6); (13) outer trochlea inflected inwards, with-

tarsus (Figure 2e, f); (8) tarsometatarsus with a single proximal foramen (Figure 6); (9) distal end of tarsometatarsus flared, with large intertrochlear spaces and trochleae lying in the same anterior-posterior plane (Figures 2e,f,k; 5; 6); (10) middle trochlea the most distad, with the inner and outer trochleae about subequal (Figures 2e,f; 5; 6); (11) facet for metatarsal I entirely medial (Figures 5, 6); (12) inner trochlea grooved distally and posteriorly, middle trochlea deeply grooved (Figures 5, 6); (13) outer trochlea inflected inwards, with-

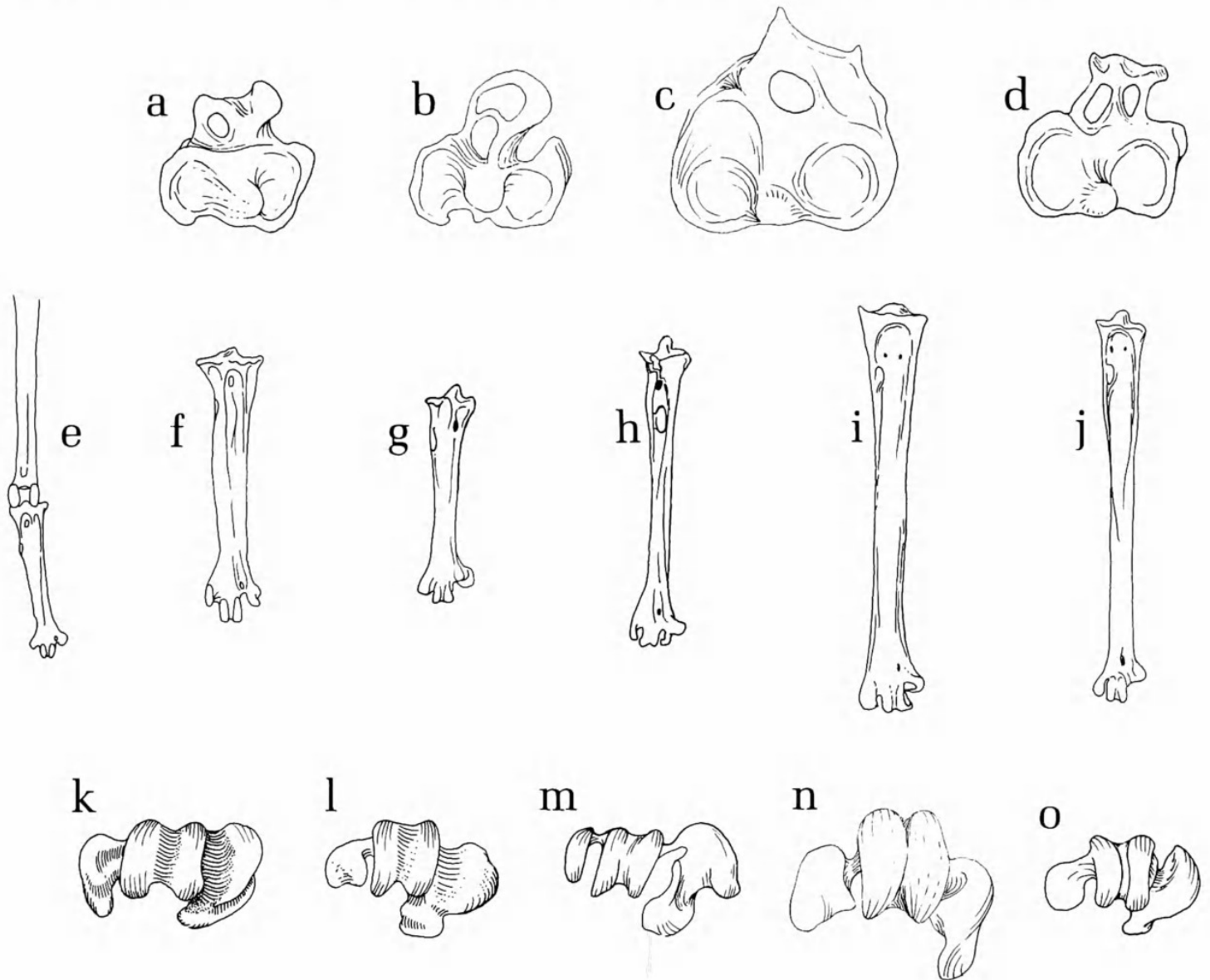


FIGURE 2.—Proximal views of left tarsometatarsi: a, *Notharcus macrorhynchos* (Bucconidae); b, *Megalaima lineata* (Capitonidae); c, *Tauraco* sp. (Musophagidae); d, *Piaya cayana* (Cuculidae). Restoration of the distal end of the left tibiotarsus and tarsometatarsus: e, *Primobucco olsoni*. Anterior (f-j) and distal (k-o) views of left tarsometatarsi: f, k, *Eobucco brodkorbi* (Primobucconidae); g, l, *Notharcus macrorhynchos* (Bucconidae); h, m, *Megalaima lineata* (Capitonidae); i, n, *Tauraco* sp. (Musophagidae); j, o, *Piaya cayana* (Cuculidae).

out a well-developed sehnenhalter, but with a distinct groove separating the posterior portion of the trochlea from the remainder.

REMARKS.—Characters 1, 6, and 13 of the diagnosis eliminate all families of the Piciformes except the Bucconidae. In the other piciformes, the bill is long (except in indicatorids and capitonids), the shaft of the humerus tends to be straight with the deltoid crest parallel to it (Figure 1c), there are two or more hypotarsal canals arranged one behind the other (Figure 2b), and the sehnenhalter is well developed (Figure 2m). The fossils tend to be buconid-like in characters 1, 2, 3, 5, 6, 7, 8, and 13. They differ from the Bucconidae, however, in having a shorter mandibular symphysis, and in characters 4, and 9 through 12. The buconids and the other piciforms differ from the Primobucconidae in that phalanx I digit II of the manus is narrower, especially at its proximal end; the inner and middle trochleae of the tarsometatarsus are placed closer together and the outer trochlea is elevated; the anterior face of the middle trochlea is not deeply grooved; and the facet for the first metatarsal is posteriorly situated.

Because *Uintornis* was suggested as being culculiform (Cracraft and Morony, 1969), we have compared all members of the Primobucconidae with nine genera of Cuculidae and three genera of Musophagidae. The Primobucconidae differ from both of these families in all but character 10 in the above diagnosis. The musophagids and cuculids differ from the Primobucconidae in that the ulna is short, strongly curved, and has large feather papillae; metacarpal III is strongly curved so that there is a large intermetacarpal space; the supratendinal bridge is much above the proximal margin of the condyles of the tibiotarsus; the tarsometatarsus is elongate (Figure 2i,j); the inner and middle trochleae are close to each other, and the outer trochlea is elevated and inflected inwards, with no separation of the posterior portion from the rest of the trochlea (Figure 2n,o); the facet for metatarsal I is located posteriorly and the inner trochlea is not prominently grooved. The anterior face of the tarsometatarsus is often deeply excavated in culculiforms and there are usually two proximal foramina. The cuculids always have two large enclosed hypotarsal canals (Figure 2d), a feature that is certainly absent in the only primobucconid in which it can be checked. Also, musophagids have a very triangu-

lar and distally situated deltoid crest (Figure 1d).

Clearly the Primobucconidae belong in the Piciformes and are most closely related to the Bucconidae. We can find no substantive evidence for a relationship between *Uintornis* (or any of the other forms of Primobucconidae) and any group of the Cuculiformes.

The family Primobucconidae includes five genera. The species of two of these genera, *Primobucco* and *Neanis*, are preserved as crushed specimens on slabs and represent medium-sized and small forms, respectively, of lower Eocene age. Three genera, *Uintornis*, *Botauroides*, and *Eobucco*, are medium to large in size and are middle Eocene in age; all are represented by fairly well-preserved tarsometatarsi only. Obviously, distinguishing the lower from the middle Eocene forms is difficult because the material is not strictly comparable. Nevertheless, size differences and such characters of the tarsometatarsus as can be discerned in the lower Eocene genera will permit them to be distinguished from most, if not all, of the middle Eocene forms. For this reason, and because of the time element involved, we believe it is best to recognize five genera in the Primobucconidae.

Primobucco Brodkorb, 1970a

TYPE-SPECIES.—*Primobucco mcgrewi* Brodkorb, 1970a.

INCLUDED SPECIES.—*P. mcgrewi*, *P. olsoni*.

AMENDED DIAGNOSIS.—Medium-sized primobucconids, larger than *Neanis* and probably smaller than *Uintornis*, *Botauroides*, or *Eobucco*.

Primobucco mcgrewi Brodkorb, 1970a

HOLOTYPE.—Right wing, UWGM 3255.

TYPE-LOCALITY AND HORIZON.—From fish quarries in SE $\frac{1}{4}$ of Sec 18, T21N, R117W, near Fossil, Lincoln County, Wyoming; lower beds of Green River Formation, lower Eocene (Late Wasatchian) (Brodkorb, 1970a).

Primobucco olsoni, new species

FIGURES 1a, 3, 4

HOLOTYPE.—Two slabs containing a nearly complete skeletal impression and counterimpression,

Geological Survey of Alabama Type Collection, GSATC 217 (Figures 3, 4).

TYPE-LOCALITY AND HORIZON.—The "first bluff" north of US Highway 30 north, across from Nugget, Lincoln County, Wyoming; Green River Formation, lower Eocene. Collected by Mr. George Moravec.

DIAGNOSIS.—Smaller than *Primobucco mcgrewi* but larger than *Neanis*. Wing more slender and humerus longer than in *Primobucco mcgrewi*. Middle trochlea of tarsometatarsus extending farther distally than the other trochleae.

DESCRIPTION.—Skeleton preserved on two slabs with numerous feather impressions; mandible

broad with a short symphysis; humerus with a low, gently curved deltoid crest almost parallel to shaft (Figure 1a); head of humerus inflected medially; radius and ulna slender, straight, and elongate, the ulna with no evidence of feather papillae; carpometacarpus long and slender with a large, straight process for metacarpal I and a narrow intermetacarpal space; phalanx 1 digit II of the manus broad (narrower proximally in most bucconids); tibiotarsus short and robust with the supratendinal bridge straight, lying just above the condyles; tarsometatarsus broad, short, and flat with a high intercotylar prominence, anterior face of shaft with a low medial ridge, a single medial

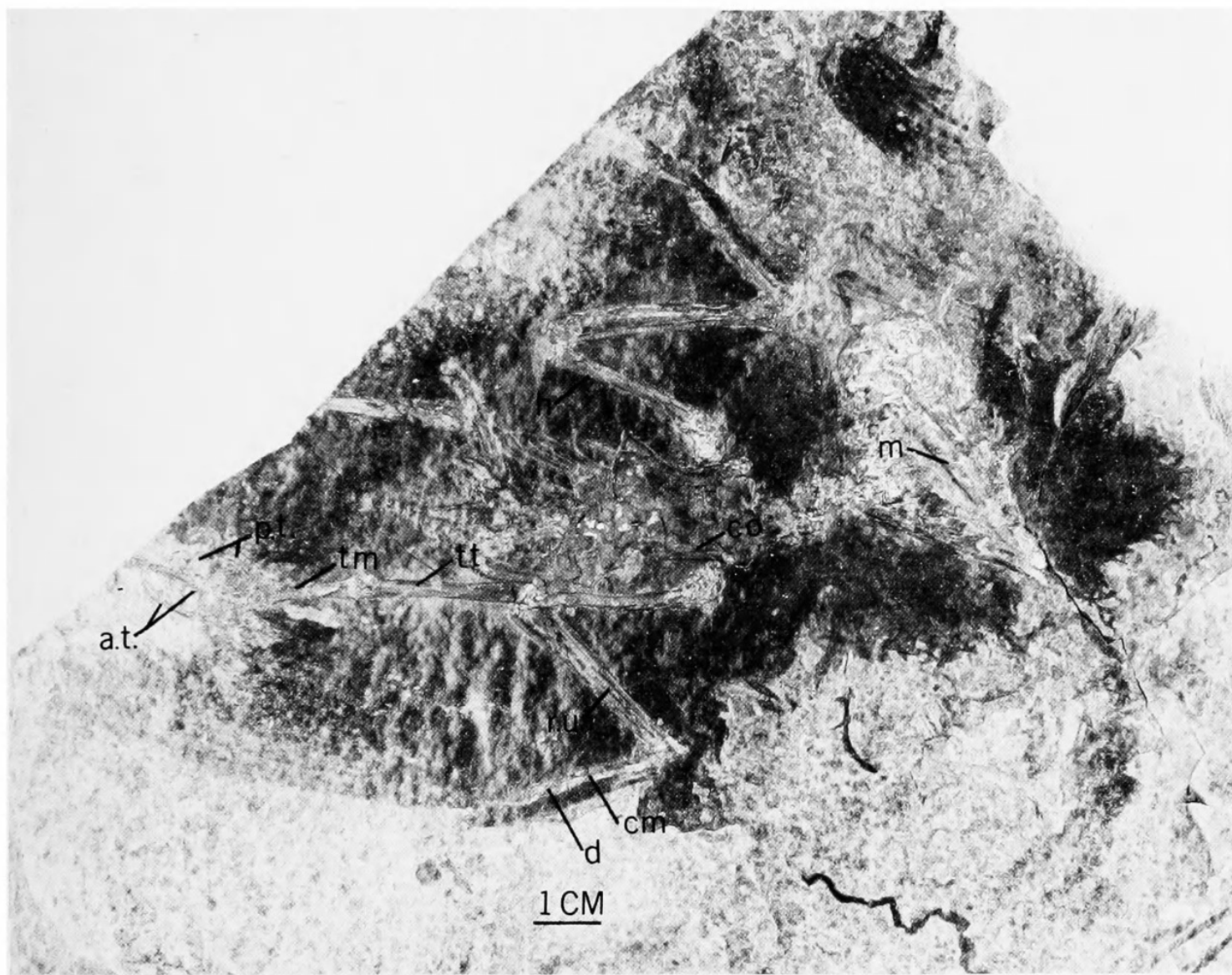


FIGURE 3.—Holotype slab of *Primobucco olsoni*, new species (GSATC 217), viewed ventrally. (a.t. = anterior toes, co = coracoid, cm = carpometacarpus, d = digit II, h = humerus, m = mandibular ramus, p.t. = posterior toes, r.u. = radius and ulna, tm = tarsometatarsus, tt = tibiotarsus)

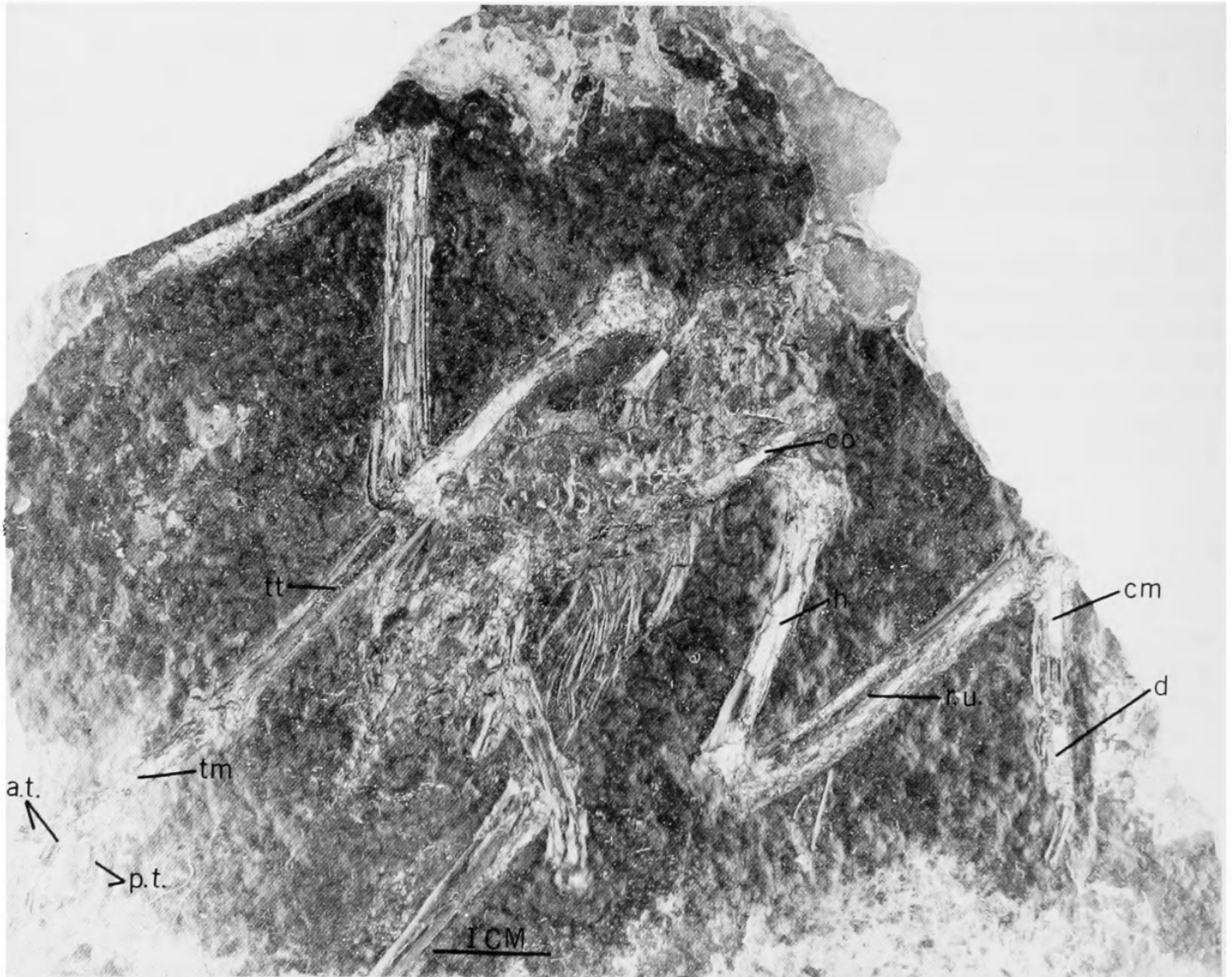


FIGURE 4.—Holotype counterslab of *Primobucco olsoni*, new species, viewed dorsally. (Abbreviations as in Figure 3.)

proximal foramen, the papilla for tibialis anticus along the medial edge, the facet for metatarsal I situated medially, the middle trochlea situated distally, and the trochleae deeply grooved. Compared to *Primobucco mcgrewi* the humerus of *P. olsoni* is longer (28.8 vs. 26.7 mm), the shaft more slender (least width c. 2.2 vs. 3.0 mm), the proximal width greater (c. 7.5 vs. 6.7 mm), the ulna shorter (c. 32.0 vs. 34.2 mm), and phalanx I digit II of manus shorter (c. 6.7 vs. 7.0 mm). The approximate length of the coracoid is c. 15.0 mm and that of the mandibular ramus c. 34.5 mm. The estimated toe lengths measured (in mm) through the arc are: digit I, 11.0; digit II, 16.4; digit III, 18.8; and digit IV, 13.3. Equivalent estimates of the toe arcs for *Neanis kistneri* are 6.8, 7.4, 8.6, and 8.2,

respectively. The chord of the left wing of *P. olsoni* is estimated at 92 mm; of the species of *Bucconidae* listed in Ridgway (1914), the Barred Puffbird, *Nystalus radiatus*, is the nearest in size, with the wing chord of males averaging about 92 mm.

ETYMOLOGY.—The specific name is in honor of Storrs L. Olson for his contributions to avian paleontology.

REMARKS.—No accurate measurements of the tibiotarsus were possible but by comparing the two sides we were able to estimate the total length of the tibiotarsus very roughly as 28.5 (± 3) mm. The tarsometatarsus measures c. 15.5 mm, giving a ratio of tarsometatarsus to tibiotarsus of approximately 0.54. This rules out an affinity with the

Picidae (average ratio of 8 species, 0.67) or the Cuculidae (average of 7 species, 0.69). The same ratio for *Neanis kistneri* is 0.56; the average for 6 species of Bucconidae, 0.58; 3 species of Galbulidae, 0.51; five species of Capitonidae, 0.58; and 2 species of Indicatoridae, 0.59 (Feduccia, 1973). These ratios indicate only that the fossil does not belong to either the Cuculidae or the Picidae, but is a "perching" piciform bird. In woodpeckers, the different ratio results from the tibiotarsus being proportionately reduced. Comparative measurements of bucconids are given in Brodkorb (1970a).

The holotype of *Primobucco olsoni* is especially important because it permits us to associate the skeleton of *Primobucco* with those primobucconids known only from the tarsometatarsus. Features in which *Primobucco* resembles *Eobucco* and *Uintornis* are the short, broad tarsometatarsus with a high intercotylar prominence, the single lateral proximal foramen, the small and very medially situated tubercle for the tibialis anticus, and the medially situated facet for metatarsal I.

Neanis Brodkorb, 1965

SYNONYM.—*Hebe* Shufeldt, 1913 (preoccupied).

TYPE-SPECIES.—*Hebe schucherti* Shufeldt, 1913.

INCLUDED SPECIES.—*N. schucherti*, *N. kistneri*.

AMENDED DIAGNOSIS.—Wing relatively shorter than in *Primobucco*; tarsometatarsus with large hypotarsus.

REMARKS.—Better preserved material is needed for a full diagnosis of the very small zygodactyl birds referred to *Neanis*.

Neanis schucherti (Shufeldt, 1913)

HOLOTYPE.—YPM 1233, partial skeleton on a slab and impression on counterslab.

TYPE-LOCALITY AND HORIZON.—Fish cut of the railroad, 8 km west of Green River City, Wyoming; Green River Formation, lower Eocene.

Neanis kistneri (Feduccia, 1973)

HOLOTYPE.—UWGM 3196, partial skeleton on a slab.

TYPE-LOCALITY AND HORIZON.—N $\frac{1}{2}$, NW $\frac{1}{4}$, Sec 6, T23N, R104W, Sweetwater County, Wyom-

ing; Tipton Tongue Member of the Green River Formation, lower Eocene (Wasatchian).

AMENDED DIAGNOSIS.—Smaller than *N. schucherti* or any of the other primobucconids.

Uintornis Marsh, 1872

TYPE-SPECIES.—*Uintornis lucaris* Marsh, 1872.

INCLUDED SPECIES.—*U. lucaris*, *U. marionae*.

AMENDED DIAGNOSIS.—Zygodactyl birds with the outer trochlea of the tarsometatarsus not as strongly rotated as in other primobucconids; middle trochlea situated distally; distal foramen located above the outer trochlea.

Uintornis lucaris Marsh, 1872

HOLOTYPE.—YPM 617, distal end of right tarsometatarsus (Figure 5f,g).

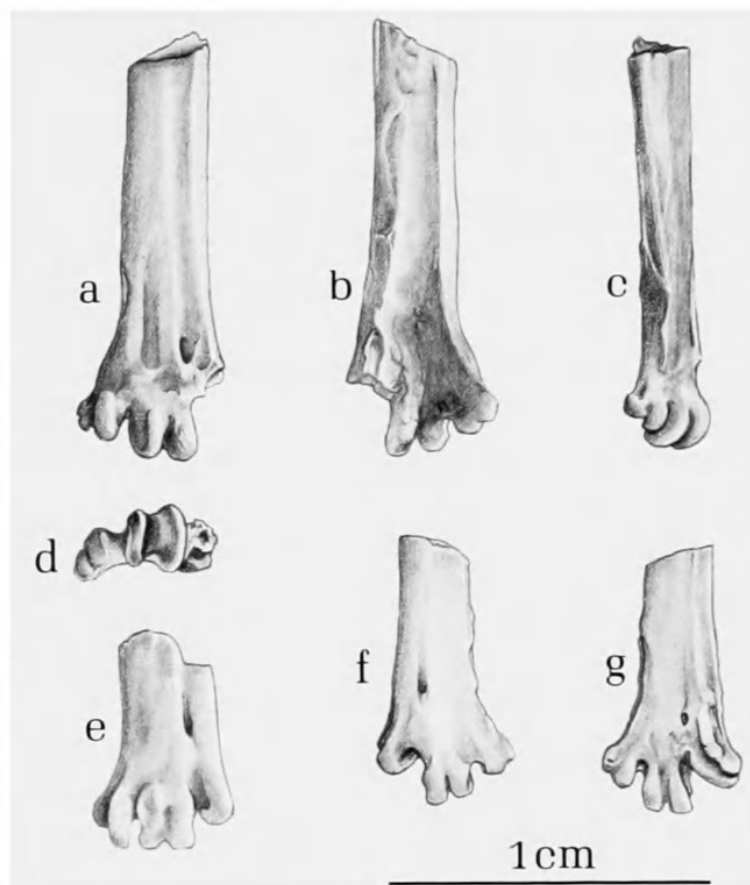


FIGURE 5.—Tarsometatarsi of *Uintornis* and *Botauroides*: a-d, holotype partial left tarsometatarsus of *Uintornis marionae*, new species (KUVF 26906), anterior, posterior, medial, and distal views; e, holotype, partial left tarsometatarsus of *Botauroides parvus* (YPM 1030), anterior view; f-g, holotype partial right tarsometatarsus of *Uintornis lucaris* (YPM 617), anterior and posterior views.

TYPE-LOCALITY AND HORIZON.—Henry's Fork, Sweetwater County, Wyoming; Bridger Formation, middle Eocene.

AMENDED DIAGNOSIS.—Outer trochlea of tarsometatarsus inflected inwards but with inner and outer trochlear ridges not widely separated; middle trochlea located much farther distally than the others and distal foramen located more proximad.

DESCRIPTION.—Shaft of tarsometatarsus broad and flat; inner extensor grooves deep; distal foramen more proximal than the outer trochlea; distal end expanded with wide intertrochlear notches; trochleae deeply grooved; inner trochlea small, smooth anteriorly and grooved posteriorly, with a small medially directed posterior flange; middle trochlea deeply grooved, with high, thick, trochlear ridges, the inner trochlear ridge distal to the outer and with a short, thick neck; outer trochlea large, at the same level as the inner trochlea and inflected medially; outer trochlea grooved, with the outer ridge produced posteriorly as a flange or incipient sehnenhalter; facet for metatarsal I medially situated. Measurements (in mm) of type: width of distal end, 4.77; width of shaft at distal foramen, 3.3; depth and width of inner trochlea, 1.36 and 1.27; depth and width of middle trochlea, 2.00 and 1.90; depth of outer trochlea 2.90.

Uintornis marionae, new species

FIGURE 5a-d

HOLOTYPE.—KUVF 26906, distal end of right tarsometatarsus lacking outer trochlea (Figure 5a-d).

TYPE-LOCALITY AND HORIZON.—Sage Creek, Sweetwater County, Wyoming; Bridger Formation, middle Eocene.

DIAGNOSIS.—Resembles *Uintornis* and differs from *Botauroides* in having a more slender shaft, a small inner trochlea, and a distinct groove proximal to the outer trochlea. Differs from *Uintornis lucaris* in being about 25 percent larger, and in having the facet for metatarsal I less deeply impressed and the outer ridge of the outer trochlea more medially inclined and elongated.

DESCRIPTION.—Tarsometatarsus broad and flat; distal foramen lying proximal to outer trochlea in anterior view and not visible in posterior view; facet for metatarsal I situated laterally; inner

trochlea grooved posteriorly and smooth anteriorly; intertrochlear spaces wide; middle trochlea deeply grooved and situated distally; trochleae not arched. Measurements (in mm) of type: width of shaft at distal foramen, 4.18; depth and width of inner trochlea, 1.83 and 1.34; depth and width of middle trochlea, 2.25 and 2.02.

ETYMOLOGY.—Named for Marion A. Jenkinson, who has often assisted us in our work on fossil birds.

REMARKS.—The size difference and various qualitative features of the specimen separate it from *Uintornis lucaris*. After *Eobucco*, described later in this paper, it is the largest known member of the Primobucconidae. *Uintornis* seems to be the least specialized genus of the family in terms of toe rotation.

Botauroides Shufeldt, 1915

TYPE-SPECIES.—*Botauroides parvus* Shufeldt, 1915.

INCLUDED SPECIES.—*B. parvus*.

AMENDED DIAGNOSIS.—*Botauroides* differs from *Uintornis* in having a proportionately wider shaft, the notch for the facet of metatarsal I shallower and slightly more posterior, the inner trochlea at about the same level as the middle trochlea, and outer trochlea not as elevated. The inner ridge of the outer trochlea is slightly more rotated and does not project as far anteriorly as it does in *Uintornis*. The outer trochlea is proportionately smaller and the medial ridge of the middle trochlea swings farther medially. *Uintornis* has a shallow groove just proximal to the outer trochlea, and the inner trochlea is relatively smaller than in *Botauroides*.

Botauroides parvus Shufeldt, 1915

HOLOTYPE.—YPM 1030, distal end of left tarsometatarsus (Figure 5e).

TYPE-LOCALITY AND HORIZON.—Spanish John Meadow, Wyoming; Bridger Formation, middle Eocene.

DIAGNOSIS.—As for the genus.

DESCRIPTION.—Shaft very broad and flat, not expanded distally; distal foramen situated far proximally; inner trochlea larger and grooved posteriorly; inner and middle trochleae at same level;

outer trochlea relatively small, rotated medially and not very elevated; trochleae not arched.

REMARKS.—Cracraft (pers. comm.) directed our attention to the similarities between *Botauroides* and *Uintornis*. Shufeldt (1915), with his uncanny ability to err, had referred it to the Ardeidae, where it appears in Brodkorb's (1963) catalog.

Eobucco, new genus

TYPE-SPECIES.—*Eobucco brodkorbi*, new species.

DIAGNOSIS.—Largest known primobucconid; resembles *Uintornis* and differs from *Botauroides* in having the facet for metatarsal I deeply impressed and the middle trochlea located farther distally. Differs from *Uintornis* in having the ridges of the middle trochlea not extending as far proximally on the anterior side; in having the outer ridge of the outer trochlea inclined more medially and elongated until it extends past the outer ridge of the middle trochlea (it does not reach this trochlea in *Uintornis*); in having the outer ridge of the inner trochlea extending posteriorly as a distinct flange; and in the far distal position of the distal foramen.

Eobucco brodkorbi, new species

FIGURE 6

HOLOTYPE.—UNSM 20046 (Figure 6), left tarsometatarsus.

TYPE-LOCALITY AND HORIZON.—56 km north of Green River, Sweetwater County, Wyoming; Bridger Formation, middle Eocene.

DIAGNOSIS.—As for the genus.

DESCRIPTION.—Shaft of tarsometatarsus short, broad, and flattened; intercotylar prominence 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); a shallow groove rather than a ridge leads distally from the hypotarsus; anterior face of shaft grooved, with a high lateral ridge present; medial edge of shaft thin; a single large proximal foramen present near the midline; tubercle for tibialis anticus very small and distally situated along the medial edge of the shaft; facet for metatarsal I high and deeply impressed into the medial side of the shaft; distal

foramen small, level with the outer trochlea; trochleae widely spread, not arched; inner trochlea relatively large, anterior face smooth, posterior face grooved; proximal part of the outer rim of the outer trochlea produced into a large posterior flange; middle trochlea large with high trochlear ridges diverging posteriorly; middle trochlea more distal than other trochleae; large outer trochlea at the same level as the inner trochlea; outer trochlea rotated medially with its elongate outer ridge extending medially past the outer rim of the middle trochlea; outer trochlea grooved. Measurements (in mm) of type: total length, 26.95; width of proximal end, 6.75; width of distal end, 6.00; depth and width of the inner trochlea, 1.36 and 1.27; depth and width of middle trochlea, 2.00 and 1.90; depth and width of outer trochlea, 2.90 and 1.80.

ETYMOLOGY.—Named for Pierce Brodkorb, who

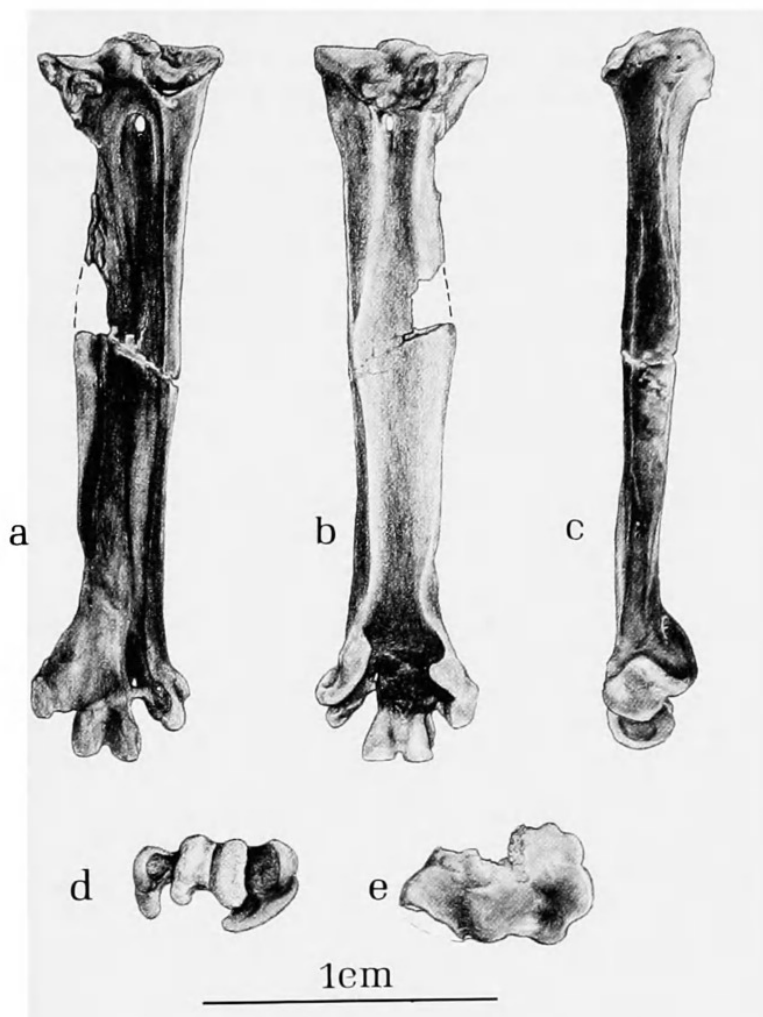


FIGURE 6.—Holotype left tarsometatarsus of *Eobucco brodkorbi*, new genus and species (UNSM 20046): a, anterior view; b, posterior view; c, lateral view; d, distal view; e, proximal view.

was the first to recognize the true affinity of the primobucconids.

REMARKS.—This is the largest and most advanced of the known primobucconids. It shares with *Uintornis* the distal position of the middle trochlea but has the outer trochlea much larger and more medially rotated. The single proximal foramen is remarkable for its large size and central position, thereby resembling the proximal foramen in *Galbula*. The medial side of the shaft is deeply indented under the internal cotyla where it is reduced to a thin blade. The tubercle for the tibialis anticus is extremely reduced. *Eobucco* possesses a combination of primitive and specialized characters that probably preclude its having given rise to any modern group of piciforms.

Conclusion

The allocation of *Neanis schucherti*, *Uintornis lucaris*, and *Botauroides parvus* to the Piciformes, and the description of the new forms *Primobucco olsoni*, *Uintornis marionae*, and *Eobucco brodkorbi*, brings the total number of species of North American Eocene zygodactyl birds to eight: two very small forms, *Neanis schucherti* and *Neanis kistneri*; two medium-size forms, *Primobucco mcgrewi* and *Primobucco olsoni*; two large forms,

Eobucco brodkorbi and *Uintornis marionae*, and two others, *Uintornis lucaris* and *Botauroides parvus*, slightly smaller than the last two.

The order Piciformes probably arose in the New World and its forms occupied the "perching" arboreal adaptive zone in the early Tertiary of North America when tropical and subtropical climates predominated. Later, the order spread to the Old World where the Miocene Zygodactylidae and the modern families Picidae, Capitonidae, and Indicatoridae are represented, the last named being the only modern piciform family not found in the New World. Probably through climatic change and competition with more advanced land birds, e.g., passerines, the piciforms retreated mainly to tropical zones of the New and Old Worlds. The most primitive living piciform families, the Bucconidae and Galbulidae, are presently confined to the New World tropics. The Bucconidae are structurally closest to the Eocene family Primobucconidae.

The preponderance of evidence now indicates that the typical "perching" birds of the early Tertiary of North America were primitive piciforms, rather than passerine birds. Thus, it was probably not until the mid-Tertiary that the passerines took over in North America as the predominant "perching" group.

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