A NEW BIRD (FAMILY CRACIDAE) FROM THE EARLY OLIGOCENE OF SOUTH DAKOTA

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THE FAMILY CRACIDAE, including the curassows, guans, and chachalacas, ranges in the present day from the lower Rio Grande Valley in Texas south to Argentina. The modern distribution of the family gives no clue to the considerable radiation once enjoyed by the group in what is now temperate North America. Fossil species are known from Tertiary deposits in Florida, Nebraska, and South Dakota. This paper describes a new fossil cracid, older than any previously discovered, from the top of the Chadron formation, lower Oligocene of South Dakota.

The fossil is preserved in fine-grained, fresh-water limestone. Preparation of the specimen in high relief has exposed all of the major skeletal elements except the skull and most of the vertebral column, which probably became disarticulated before the specimen was finally buried although they may lie buried in the slab. The bones, lying more or less in a single plane, are well preserved, although many of the larger ones are moderately to severely crushed. Judging by the fairly close association on the slab of most of the toe bones and the proximity to each other of the limb bones of right and left sides, it seems that the skeleton was partly articulated when buried and that much of the bird was decomposed. Some shifting of individual bones occurred as sediments accumulated over the fossil. At burial it seems that the bird was on its right side, with the wings still articulated and held over the back. The left leg was directed forward and ventrally, and the right leg was forward under the spinal column. Subsequently, the bones of the right wing distal to the elbow became disarticulated and moved behind the sternum. The corresponding bones in the left wing lie in front of the keel of the sternum. The leg bones remained approximately in place except that the toes of the right foot now lie above the supposed original position of the pelvis. The head of the left femur is still closely adjacent to the left acetabulum. Most of the keel of the sternum is well preserved, but the sternal plate is badly crushed. The pelvis is badly crushed and is rotated (in relation to the sternum) so that its left side is up and its long axis is almost at right angles to the long axis of the sternum. (See Figure 1 and Plate 10.)

General proportions and conformation of the individual bones indicate clearly that the Oligocene bird is galliform. Characteristic gallinaceous features are especially evident in the sternum, coracoid,

Procrax brevipes. Photograph of type, SDSM No. 511, × ½.

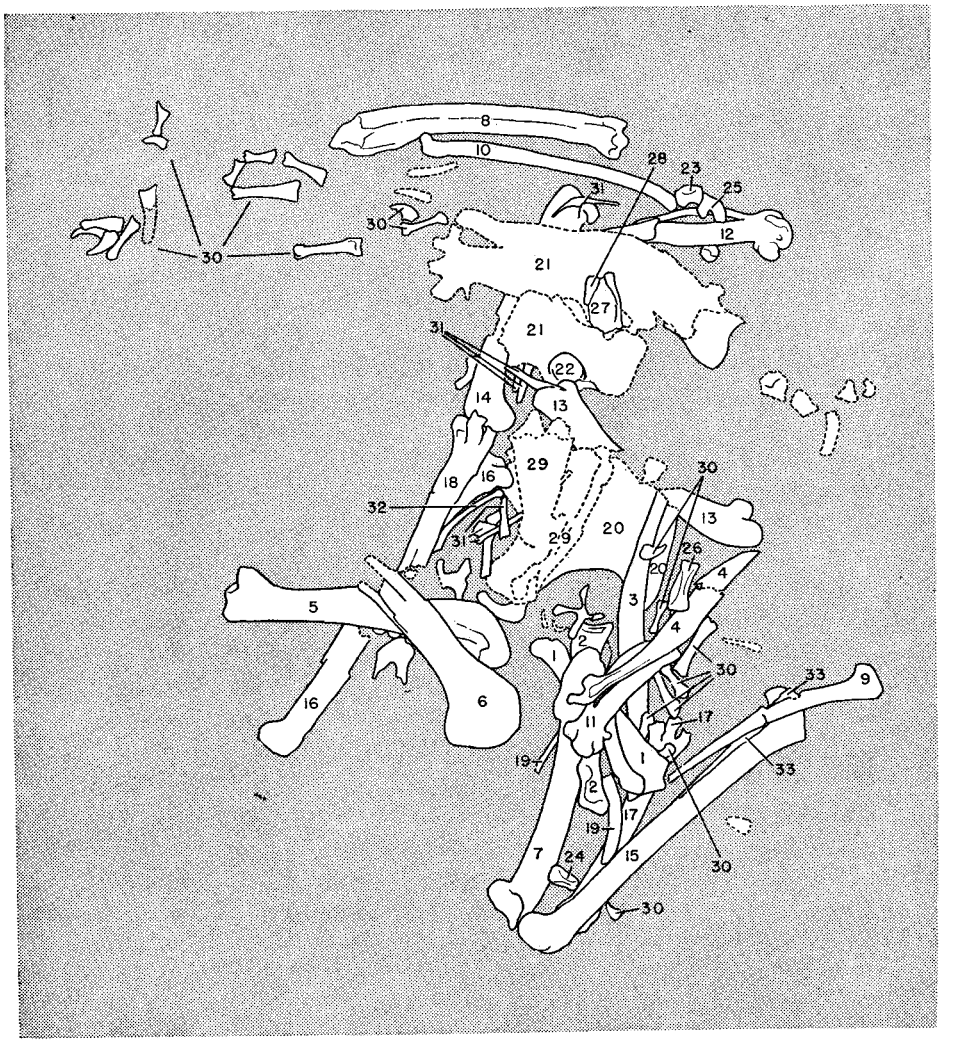

FIGURE 1. **Procrax brevipes.** Diagrammatic drawing, identifying various elements of the skeleton, × ½. 1, left coracoid; 2, right coracoid; 3, left scapula; 4, right scapula; 5, left humerus; 6, right humerus; 7, left ulna; 8, right ulna; 9, left radius; 10, right radius; 11, left carpometacarpus; 12, right carpometacarpus; 13, left femur; 14, right femur; 15, left tibiotarsus; 16, right tibiotarsus; 17, left tarsometatarsus; 18, right tarsometatarsus; 19, clavicles; 20, keel of sternum; 21, crushed pelvis; 22, acetabulum; 23, right scapholunar; 24, left scapholunar; 25, right cuneiform; 26, left proximal phalanx, digit II of manus; 27, right proximal phalanx, digit II of manus; 28, digit III of manus; 29, crushed sternal plate; 30, pedal claws and phalanges; 31, ribs; 32, right fibula; 33, left fibula.

humerus, radius, ulna, carpometacarpus, and tarsometatarsus. Cracid features of the fossil are numerous, the most diagnostic being (1) absence of the strongly developed intermetacarpal tuberosity on metacarpal II (present in all Superfamily Phasianoidea except Numididae), (2) absence of the prominent notch on the posterior palmar surface of the carpal trochlea found in the Phasianoidea, (3) small pollical facet on metacarpal I, (4) flaring of the internal condyle into the shaft of the tibiotarsus, (5) less prominent internal condyle of humerus and absence of prominent groove on distal end of humerus between internal condyle and entepicondyle, (6) prominent depression at anterior end of articular groove on medial surface of metatarsal trochlea for digit III, (7) and general conformation of coracoid, which is less ruggedly built in cracids than in New World members of the Phasianoidea.

Although many details of the Oligocene fossil have been obscured by crushing of the bones, the proportions of the bird and those details not lost through crushing show that the fossil represents a new genus and species.

Procrax new genus

Type.—*Procrax brevipes* new species.

Diagnosis.—Agrees with modern Cracidae as described above. Differs from *Mitu, Crax, Penelope, Ortalis,* and *Penelopina* in having relatively shorter legs (Tables 1 and 2) and smaller feet and claws. In relative length of wing and leg, *Procrax* most resembles *Pipile* among modern genera, but differs from *Pipile* in: smaller size; proportionately shorter and thicker claws on feet; a deeper, more sharply outlined groove at the dorsal border of the sternal facet of the coracoid; and a more pointed (less rounded) carinal apex and anterior ventral carinal margin. Distinguished from *Boreortalis* Brodkorb (1954: 180–182) from the Miocene of Florida and *Palaeonossax* Wetmore (1956: 234–235) from the Oligocene of South Dakota on the basis of larger size and the presumed relationship of *Boreortalis* and *Palaeonossax* to *Ortalis* among modern cracids. *Procrax* shows no close relationship to *Ortalis*. *Boreortalis* and *Palaeonossax* were diagnosed on the basis of characteristics not discernible in *Procrax*.

Measurements.—Depth of carina, from carinal apex to ventral lip of right coracoidal sulcus, 35.4 mm.; depth of carina, from carinal apex to anterodorsal margin of manubrium (estimated), 45; greatest width of anterior end of pelvis (estimated), 36. Length of coracoid, 53.2; of scapula, 75; of humerus, 79; of radius, 71.8; of ulna, 80.7; of carpometacarpus (estimated), 44; of proximal phalanx of digit II

TABLE 1

MEASUREMENTS IN MILLIMETERS OF CRACIDS AND *Opisthocomus*

Species (number of specimens in parens.)	1 *Carina depth*[1]	2 *Carina depth*[2]	3 *Width anterior end of pelvis*	4 *Coracoid*	5 *Scapula*	6 *Humerus*	7 *Radius*	8 *Ulna*	9 *Carpometacarpus*	10 *Proximal phalanx of digit II (manus)*	11 *Femur*	12 *Tibiotarsus*	13 *Tarsometatarsus*	14 *Wing (6+8+9+10)*	15 *Leg (11+12+13)*
Opisthocomus hoazin (3)	—	—	25.4	48.6	62.6	69.2	64.6	71.3	38.8	16.8	66.0	89.1	53.8	196	209
Gallinuloides wyomingensis (1)	24.2	(est.) 27.8	—	29.0	42.2	46.8	46.9	49.2	25.8	10.7	40.8	57.6	33.8	133	132
Procrax brevipes (1)	35.4	(est.) 45	(est.) 36	53.2	75	79	71.8	80.7	(est.) 44	15.9	72.3	101.0	65.9	220	239
Penelope purpurascens (3)	37.4	52.8	46	68.5	89.6	103.7	97.6	106.9	56.1	19.5	108.6	149.3	89.2	286	347
P. marail (1)	34	45	42.5	62	74.3	85.5	80.0	88.3	46.0	16.6	95	136	82	236	313
P. obscura (2)	33	45	37.8	56.0	77.3	83.7	75.8	82.5	43.6	14.9	96.1	134	81.3	225	311
P. superciliaris (1)	27	37	(est.) 35	49.6	64.1	69.6	62.4	68.2	36.9	13.0	78.8	114	75.0	188	268
P. argyrotis (1)	23	32	27.8	41.7	58.0	66.2	62.0	67.5	34.8	12.1	68.0	—	55.6	181	—
Ortalis motmot (1)	21.4	28.3	24.0	38.4	50.0	56.7	48.4	52.8	28.7	10.3	64.7	92.8	57.5	149	215
O. wagleri (1)	30.0	39.6	33.0	49.0	66.0	73.2	64.4	68.6	37.5	13.0	78.6	111.0	71.6	193	262
O. vetula (3)	24.7	32.6	25.3	41.3	56.7	61.2	52.7	56.2	30.5	10.8	68.5	103.4	65.7	159	237
O. garrula (1)	23.7	32.0	26.3	46.4	60.5	65.5	58.8	62.9	32.8	12.2	69.6	103.7	68.8	174	243
O. canicollis (2)	28.4	37.7	25.9	45.6	60.9	67.0	59.7	64.5	33.4	12.2	69.2	101.8	63.4	177	234
Penelopina nigra (1)	29.8	39.3	32.3	47.2	63.0	64.6	58.7	63.3	37.4	12.5	82.0	119.0	75.7	178	276
Pipile cumanensis (2)	35.7	47.5	38.0	58.6	78.4	89.1	89.0	96.6	48.2	17.4	79.5	112	68.0	251	260
Mitu mitu (2)	62	77.0	53.2	78.5	99.3	112.5	107.5	120	61.2	21.0	110	166.5	114.1	315	391
Crax alberti (1)	(est.) 62	(est.) 75	51	77	(est.) 110	111.7	110	117	58	18.7	109	166	112	305	387
C. fasciolata (1)	62	76.5	44.9	72.7	98.4	108.4	101.5	110.0	56.5	18.8	106	157	102.8	294	366
C. rubra (5)	67.7	86.5	49.0	83.3	108.5	122.3	119.3	131.3	63.5	21.4	120.8	180.3	118.1	339	419

[1] From carinal apex to ventral lip of right coracoidal sulcus.

[2] From carinal apex to anterodorsal margin of manubrium.

TABLE 2

LIMB PROPORTIONS IN CRACIDS AND *Opisthocomus*

Species (no. of specimens in parens.)	*Wing / Leg*	*Coracoid / Wing*	*Coracoid / Leg*	*Coracoid / Femur*	*Femur / Tibiotarsus*	*Femur / Tarsometatarsus*	*Tibiotarsus / Tarsometatarsus*	*Humerus / Carpometacarpus*
Opisthocomus hoazin (3)	.94	.25	.23	.74	.46	1.2	1.7	1.8
Gallinuloides wyomingensis (1)	1.01	.22	.22	.71	.45	1.2	1.7	1.8
Procrax brevipes (1)	.92	.24	.22	.74	.43	1.1	1.5	1.8
Penelope purpurascens (3)	.82	.24	.20	.63	.46	1.2	1.7	1.9
P. marail (1)	.75	.26	.20	.65	.44	1.2	1.7	1.9
P. obscura (2)	.72	.25	.18	.58	.45	1.2	1.6	1.9
P. superciliaris (1)	.70	.26	.19	.63	.42	1.1	1.5	1.9
P. argyrotis (1)	—	.23	—	.61	—	—	—	1.9
Ortalis motmot (1)	.69	.26	.18	.59	.43	1.1	1.6	2.0
O. wagleri (1)	.74	.25	.19	.62	.43	1.1	1.6	1.9
O. vetula (3)	.67	.26	.17	.60	.41	1.0	1.6	2.0
O. garrula (1)	.72	.27	.19	.67	.40	1.0	1.5	2.0
O. canicollis (2)	.76	.26	.20	.66	.42	1.1	1.6	2.0
Penelopina nigra (1)	.65	.27	.17	.58	.42	1.1	1.6	1.7
Pipile cumanensis (2)	.97	.23	.23	.74	.44	1.2	1.6	1.9
Mitu mitu (2)	.81	.26	.20	.71	.39	.96	1.5	1.8
Crax alberti (1)	.79	.25	.20	.71	.39	.97	1.5	1.9
C. fasciolata (1)	.80	.25	.20	.69	.41	1.0	1.5	1.9
C. rubra (5)	.81	.25	.20	.69	.40	1.0	1.5	1.9

of manus, 15.9; of femur, 72.3; of tibiotarsus, 101.0; of tarsometatarsus, 65.9. Length of toes, estimated by comparison of disarticulated phalanges with toes of *Penelopina nigra* (Fraser), I, 26; II, 39; III, 55; IV, 40. The longest ungual phalanx of the five (length: 10 mm., 8.8, 7.7, 7.7, 6.6) preserved in *Procrax* is approximately equal in length to the shortest ungual phalanx (10.8 mm. on toe IV) of a male *Ortalis canicollis* (Wagler). Three of the five fossil claws are markedly shorter than any in *O. canicollis*, even though the fossil represents a bird larger than the modern *Ortalis canicollis*.

Procrax brevipes new species

Figure 1 and Plate 10

Type.—Skeleton, lacking skull and cervical vertebrae, otherwise nearly complete, in limestone matrix, most bones more or less crushed, preservation otherwise good, No. 511, South Dakota School of Mines and Technology. From fresh-water limestone at the top of the Chadron formation, lower Oligocene, NE ¼ Sec. 4, T1S, R17E, Pennington County, South Dakota. Collected by H. H. Krumvieda.

Diagnosis.—Same as generic diagnosis. In size, larger than male *Ortalis canicollis* (Wagler), smaller than female *Penelope obscura* Temminck, slightly larger than *Opisthocomus hoazin* (P. L. S. Müller).

Procrax brevipes represents the earliest species yet ascribed to the Cracidae. Five other fossil members of the family are known from North America. They are *Ortalis phengites* Wetmore (1923) from the lower Pliocene of Nebraska, *Ortalis tantala* Wetmore (1933) from the lower Miocene of Nebraska, *Ortalis pollicaris* Miller (1944) from the Flint Hill fauna, middle Miocene of South Dakota, *Boreortalis laesslei* Brodkorb (1954) from the lower Miocene of Florida, and *Palaeonossax senectus* Wetmore (1956) from the upper Oligocene of South Dakota. The family, now of Neotropical distribution, seems to have originated in North America and undergone a substantial adaptive radiation there before its retreat southward, which may have been hastened or brought about by competition with contemporaneous species of the Tetraonidae and, perhaps, Odontophorinae.

Ortalis tantala is small, approximately half the size of the modern Chachalaca, *O. vetula* (Wagler). *O. phengites* is somewhat smaller than *vetula*. *Palaeonossax* is approximately the size of *vetula*. *O. pollicaris* is larger than *vetula*, about equalling the modern *O. wagleri* G. R. Gray. *Boreortalis* is still larger, falling between *O. vetula* and *Penelopina* in size. *Procrax* is the largest of the fossil cracids, almost as large as a small guan (*Penelope*). Each of the fossil species except

Procrax is known only from a single bone, permitting no deductions regarding adaptations or behavior of the species in question. *Procrax*, although lacking the extremely important skull, is sufficiently complete to permit some speculation regarding its habits. *Procrax* was a medium-sized cracid probably somewhat superior in flying ability to modern members of the family, but with shorter legs, somewhat shorter toes, and shorter, thicker claws. Judging from these physical characteristics, it seems that *Procrax*, although capable of rapid locomotion on the ground and through trees, probably fed largely in trees and did not scratch for its food. Most modern cracids feed extensively in trees, but many also scratch in ground litter for some of their food.

The relationship to the Cracidae of *Gallinuloides wyomingensis* Eastman (1900), sole representative of the galliform Family Gallinuloididae deserves comment here.

Gallinuloides, from the middle Eocene of Wyoming, was thought by Eastman to be intermediate between true gallinaceous birds and the Family Rallidae. Lucas (1900) studied *Gallinuloides*, known from a complete, fairly well-preserved skeleton, in detail and summarized his findings (p. 84) as follows:

"*Galline Characters.*—Pedate end of internal xiphoid process, arrangement of the costal facets, and shape of the distal end of coracoid.

"*Cracine Characters.*—Blunt, upright, subtriangular costal process, shallow inner sternal notch, small prepubis, proportions of pelvis, elongate tarsus with all the toes on the same level.

"*Peculiar Characters.*—Absence of recurved mandibular process; short, stout, U-shaped furcula with large hypocleideum and articular facet for coracoid."

Lucas concluded that *Gallinuloides* represented a distinct galliform family closest to the Cracidae, the supposed resemblances to rallids being superficial. We have restudied the relationships of *Gallinuloides*, using the excellent plate and figures in Lucas (1900) and a cast of the type courteously furnished by authorities of the Museum of Comparative Zoölogy, Harvard University. We see no basis for maintaining a separate family for this genus. Herewith is a discussion of the "peculiar characters" listed by Lucas. (1) "Short, stout, U-shaped furcula with large hypocleideum"—in size and thickness the clavicles of *Gallinuloides* agree with modern cracids of comparable size and, on a relative basis, with *Procrax;* the hypocleidium of *Gallinuloides* is only slightly larger proportionately and of the same general shape as in the modern cracid genera *Ortalis* and *Pipile*, and

as in *Numida* (the hypocleidium is covered by other bones in *Procrax*); the supposed U-shape of the furcula of *Gallinuloides* is almost certainly the result of distortion through flattening. Our cast of the type shows clearly by the position of the hypocleidium that the furcula was originally oriented in a plane approximately 35° from that in which it now lies. The furcula of a chachalaca such as *Ortalis canicollis* can be superimposed over that of *Gallinuloides* in a manner that convinces us that the original shape of this bone in the fossil differed little, if at all, from that of the modern species. (2) Furcula with "articular facet for coracoid"—Lucas (1900: 81) stated that the presence of this facet ("acrocoracoid process") served to separate *Gallinuloides* "from all existing Galliformes." Actually, a distinct facet on the clavicles for articulation with the coracoid is a distinctive feature of cracids of the Subfamily Penelopinae, although this facet is weakly developed or lacking in the Subfamily Cracinae and in the Phasianoidea. The furcular facets in *Gallinuloides* and in modern cracids seem essentially identical. (3) "The mandible is stout and imperforate, and while it has a blunt angular projection, the recurved process so characteristic of the Galliformes is lacking. This is the most notable departure from the galliform structure found in the skeleton" (Lucas, 1900: 80). This projection, the postarticular process, is not so uniform in the Galliformes as might be supposed. Although it is well developed in the Phasianoidea, it is reduced to a small, sharp point in the Opisthocomidae, and varies in the Cracidae from small and straight in *Pipile* to well-developed in *Penelope* and *Crax*. Furthermore, the process can readily be broken off, as shown by its frequent accidental absence in modern cracid skeletons in museum collections. Re-examination of the original specimen of *Gallinuloides* might establish whether the process has been lost through accident or is actually small and blunt. In either event, this does not seem to be a valid basis for establishment of a separate family.

An additional point mentioned by Lucas (1900: 83) is that in *Gallinuloides* "the tarsus is longer in proportion to the tibia than in any other species examined." This is an error. The tarsometatarsus of *Gallinuloides* measures 33.8 mm., not 45 as stated by Lucas. The ratio of tibiotarsus to tarsometatarsus is not 1.27 as Lucas said, but 1.7, which agrees closely with the corresponding ratio in *Procrax* (1.5) and in modern cracids (1.5–1.7). The notches on the posterior border of the sternum in *Gallinuloides* agree with those of the Cracidae and differ from those of the Phasianoidea in that the internal notch is shallower than the external notch. The hind toe of *Gallinuloides* is inserted at the same level as the anterior toes; this also serves to distinguish the Cracoidea from the Phasianoidea.

Procrax seems to be intermediate between *Gallinuloides* and modern cracids. Although *Procrax* is larger than *Gallinuloides*, the two agree in proportionate length of limb bones (Table 2), in each having a rather deeply keeled sternum with the carinal apex fairly pointed and produced well forward and the anterior ventral carinal margin little rounded, and in having, for cracids, short legs, short toes, and short, thick claws. We think relationships among *Gallinuloides*, *Procrax*, and other cracids can be shown best by placing *Gallinuloides* and *Procrax* in a separate subfamily, Gallinuloidinae, in the Cracidae. Uniting the Gallinuloididae with the Cracidae extends the geologic range of the Cracidae to middle Eocene. The groups should stand as follows:

Order Galliformes
  Suborder Galli
    Superfamily Cracoidea
      Family Cracidae
        Subfamily Gallinuloidinae (*Gallinuloides*, *Procrax*)
        " Penelopinae
        " Cracinae
        " Oreophasinae

Miller (1953: 485–488), discussing a Miocene opisthocomid, *Hoazinoides*, showed that the fossil hoatzin resembled *Ortalis* in shape of brain case. He thought that this should be interpreted as indicating relationship between the two groups, but admitted the possibility that the similarities might have developed independently.

Opisthocomus, *Procrax*, and *Gallinuloides* have closely similar limb proportions (Table 2). There are, of course, many peculiar features of the skeleton of *Opisthocomus* which are not shared by the cracids. Even so, the bones of the appendicular skeleton of *Opisthocomus* look essentially galliform. Characters shared by *Opisthocomus* and the cracids but lacking in the Phasianoidea include absence of the intermetacarpal tuberosity on metacarpal II, absence of the prominent notch on the posterior palmar surface of the carpal trochlea, small pollical facet on metacarpal I, less prominent internal condyle of humerus and absence of prominent groove on distal end of humerus between internal condyle and entepicondyle, internal notch on posterior border of sternum shallower than external notch, hallux inserted on same level as anterior toes, and prominent depression at anterior end of articular groove on medial surface of metatarsal

trochlea for digit III. Also, some cracids, for example, *Pipile*, agree with *Opisthocomus* in the small size of the postarticular process on the lower jaw. The well-known peculiarities of the pectoral girdle and skull of *Opisthocomus* as well as other distinctive characteristics certainly warrant family and probably subordinal status for the bird. The hoatzin-cracid resemblances described by Miller (1953) and by us above, however, constitute evidence that both groups of birds were derived from the same primitive galliform stock. The fact that *Procrax* and *Gallinuloides* are closer than modern cracids to *Opisthocomus* only in proportions, as far as we can tell, suggests that the common ancestral stock was cracid-like and that the peculiarities of *Opisthocomus* are secondary specializations rather than primitive characters. The shape of the cranium of *Gallinuloides* is somewhat intermediate between that of modern cracids and *Opisthocomus*, but the significance of this is impossible to determine because details of the structure of the skull in *Gallinuloides* have been lost.

The primitive characters of cracids and *Opisthocomus* are shared, at least to some extent, by the families Megapodiidae and Numididae. Detailed study of these families might show that the current classification which distributes these geographically peripheral, probably primitive groups among the two suborders and two superfamilies of the Galliformes is in error. Especially suggestive in this connection is *Filholornis* Milne-Edwards, from the late Eocene of Europe, which "seems also to be related to the cracids, and at the same time to suggest a link with the hoatzin" (Howard, 1950: 13).

Specimens examined.—*Gallinuloides wyomingensis*, 1 (cast); *Procrax brevipes*, 1; *Mitu mitu*, 2; *Crax alberti*, 1; *C. fasciolata*, 2; *C. rubra*, 5; *Penelope purpurascens*, 3; *P. marail*, 1; *P. obscura*, 2; *P. superciliaris*, 1; *P. argyrotis*, 1; *Ortalis motmot*, 1; *O. wagleri*, 1; *O. vetula*, 4; *O. garrula*, 1; *O. canicollis*, 2; *Penelopina nigra*, 1; *Pipile cumanensis*, 2; also *Megapodius*, various *Phasianoidea*, and *Opisthocomus hoazin*, 3.

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SUMMARY

Procrax brevipes is described as a new genus and species of the Cracidae from the lower Oligocene of South Dakota. Comparison of *Procrax* to modern cracids and to *Gallinuloides wyomingensis* Eastman from the middle Eocene of Wyoming indicates that *Gallinuloides* is a cracid, closely enough related to *Procrax* to justify placing the two genera in a separate subfamily, the Gallinuloidinae. *Opisthocomus* is compared with cracids (fossil and Recent). Both groups probably were derived from primitive cracid-like ancestors. Brief mention is made of the similarities of hoatzins and cracids to mound-builders and guinea fowl and the possible relationship of these groups.

LITERATURE CITED

BRODKORB, P. 1954. A chachalaca from the Miocene of Florida. Wilson Bull., **66**: 180–183.

EASTMAN, C. R. 1900. New fossil bird and fish remains from the middle Eocene of Wyoming. Geol. Mag., New Series, Decade 4, Vol., **7**: 54–58.

HOWARD, H. 1950. Fossil evidence of avian evolution. Ibis, **92**: 1–21.

LUCAS, F. A. 1900. Characters and relations of Gallinuloides, a fossil gallinaceous bird from the Green River shales of Wyoming. Bull. Mus. Comp. Zoöl., **36**: 79–84 + 1 plate.

MILLER, A. H. 1944. An avifauna from the lower Miocene of South Dakota. Univ. Calif. Publ., Bull. Dept. Geol. Sci., **27**: 85–100.

MILLER, A. H. 1953. A fossil hoatzin from the Miocene of Colombia. **Auk, 70**: 484–489.

WETMORE, A. 1923. Avian fossils from the Miocene and Pliocene of Nebraska. Bull. Amer. Mus. Nat. Hist., **48**: 483–507.

WETMORE, A. 1933. A fossil gallinaceous bird from the lower Miocene of Nebraska. Condor, **35**: 64–65.

WETMORE, A. 1956. A fossil guan from the Oligocene of South Dakota. Condor, **58**: 234–235.

Museum of Natural History, University of Kansas, Lawrence, Kansas; Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, April 1, 1956.