REVISION OF *"FALCO" RAMENTA* WETMORE AND THE NEOGENE EVOLUTION OF THE FALCONIDAE

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ABSTRACT.—*"Falco" ramenta* Wetmore 1936 is redescribed and moved to a new genus as ***Pediohierax ramenta*** (Wetmore). In addition to the holotypical distal end of the tarsometatarsus, this species is now known from a complete tarsometatarsus, humerus, and coracoid from mid-Miocene (Late Hemingfordian and Early Barstovian) fossil localities in the Sheep Creek and Olcott formations, northwestern Nebraska. ***Pediohierax*** n. gen. is the primitive sister group of the Falconinae. The earliest fossil records now known of the Falconinae are a species of ?*Falco* from the late Miocene of Idaho and *Falco medius* from the late Miocene of the Ukrainian S.S.R. *Received 5 June 1986, accepted 4 November 1986.*

WETMORE (1936) described *"Falco" ramenta* based on the distal end of a single right tarsometatarsus from a mid-Miocene locality in Nebraska. The holotype of this species apparently was compared only with *Falco columbarius* and *F. sparverius,* and differed from the former in having the distal vascular foramen of the tarsometatarsus more elevated on the shaft in posterior view (Wetmore 1936). The incomplete, minimally diagnostic nature of the holotype has since caused the systematic position and validity of this species to be questioned (Jollie 1977).

I describe here new material from correlative mid-Miocene fossil localities in Nebraska of *"Falco" ramenta,* revise the systematic position of this species, document its stratigraphic range, and review all known Neogene records of the family Falconidae.

MATERIAL AND METHODS

Anatomical terminology follows Baumel et al. (1979). Measurements were taken with Kanon dial calipers, accurate to 0.05 mm and rounded to the nearest 0.1 mm. Fossil specimens examined are in the Frick collections at the American Museum of Natural History (F:AM), the Idaho Museum of Natural History (IMNH), and the National Museum of Natural History, Smithsonian Institution (USNM). Skeletons of Falconidae examined (subfamily names are used throughout in an informal sense to conveniently designate groups of related genera): Herpetotherinae (*Herpetotheres cachinnans,* 5); Micrasturinae (*Micrastur semitorquatus,* 5; *M. ruficollis,* 2); Polyborinae (*Daptrius ater,* 5; *D. americanus,* 3; *Milvago chimachima,* 7; *M. chimango,* 6; *Phalcoboenus australis,* 6; *Polyborus plancus cheriway,* 6; *Spiziapteryx circumcinctus,* 3); Falconinae (*Polihierax semitorquatus,* 7; *P. insignis,* 1; *Microhierax caerulescens,* 3; *Falco sparverius,* 2; *F. columbarius,* 26; *F. cherrug,* 2; *F. biarmicus,* 1; *F. subbuteo,* 2; *F. peregrinus,* 1; *F. berigora,* 1). Additionally, one skeleton each of *Buteo jamaicensis, Ictinia plumbea, Circus cyaneus,* and *Neophron percnopterus* were examined.

SYSTEMATICS

Family Falconidae Vigors 1824
Pediohierax n. gen.

Generic diagnosis.—As with the Falconinae, the head of the coracoid is rotated dorsally, causing the facies articularis clavicularis to be oriented more medially (especially in *Falco*). The foramen n. supracoracoidei on the procoracoid is intermediate in position between that of the Polyborinae and that of the Falconinae. The humerus of *Pediohierax* has a shallower fossa olecrani, a reduced process flexorius, and a brachial fossa that is oriented more nearly parallel to the shaft. It differs from all genera of Falconidae in having the margo caudalis more rounded. *Pediohierax* differs from the Falconinae in having a tarsometatarsus with a short hypotarsal ridge ending distally in a sharp point that extends less than one-quarter of the length of the tarsometatarsus.

Etymology.—From *pedion,* Greek, open country or plains, and *hierax,* Greek, m., hawk.

Type species.—*Falco ramenta* Wetmore (1936: 75).

Pediohierax ramenta
(Wetmore 1936) n. comb.

Holotype.—Distal end of right tarsometatarsus, USNM 13898. Vertebrate Paleontology collections, National Museum of Natural History, Smithsonian Institution.

Newly referred material.—F:AM 8633, nearly complete right humerus, missing part of the deltoid crest and internal tuberosity, from Boulder Quarry; F:AM 10151, complete left tarsometatarsus, from Echo Quarry; F:AM 10214, complete left coracoid, from Thomson Quarry; F:AM 10068, humeral end left coracoid, from Observation Quarry. These specimens are from the Frick collections, Department of Vertebrate Paleontology, American Museum of Natural History.

Locality/horizon.—The holotype (USNM 13898) originated in "*Merychippus* Quarry," southwest corner of NW ¼, Sec. 14, T. 31, R. 47 Dawes Co., Nebraska. Wetmore (1936), citing correspondence from the collector Ted Galusha, reported that this quarry was probably equivalent to the Sheep Creek Beds, a suggestion followed without comment by Brodkorb (1964). Galusha (1975) later established that this locality is near Elias's (1942) type section for the "Sand Canyon Member of the Sheep Creek Formation" and is correlative to Observation Quarry, Sand Canyon Beds.

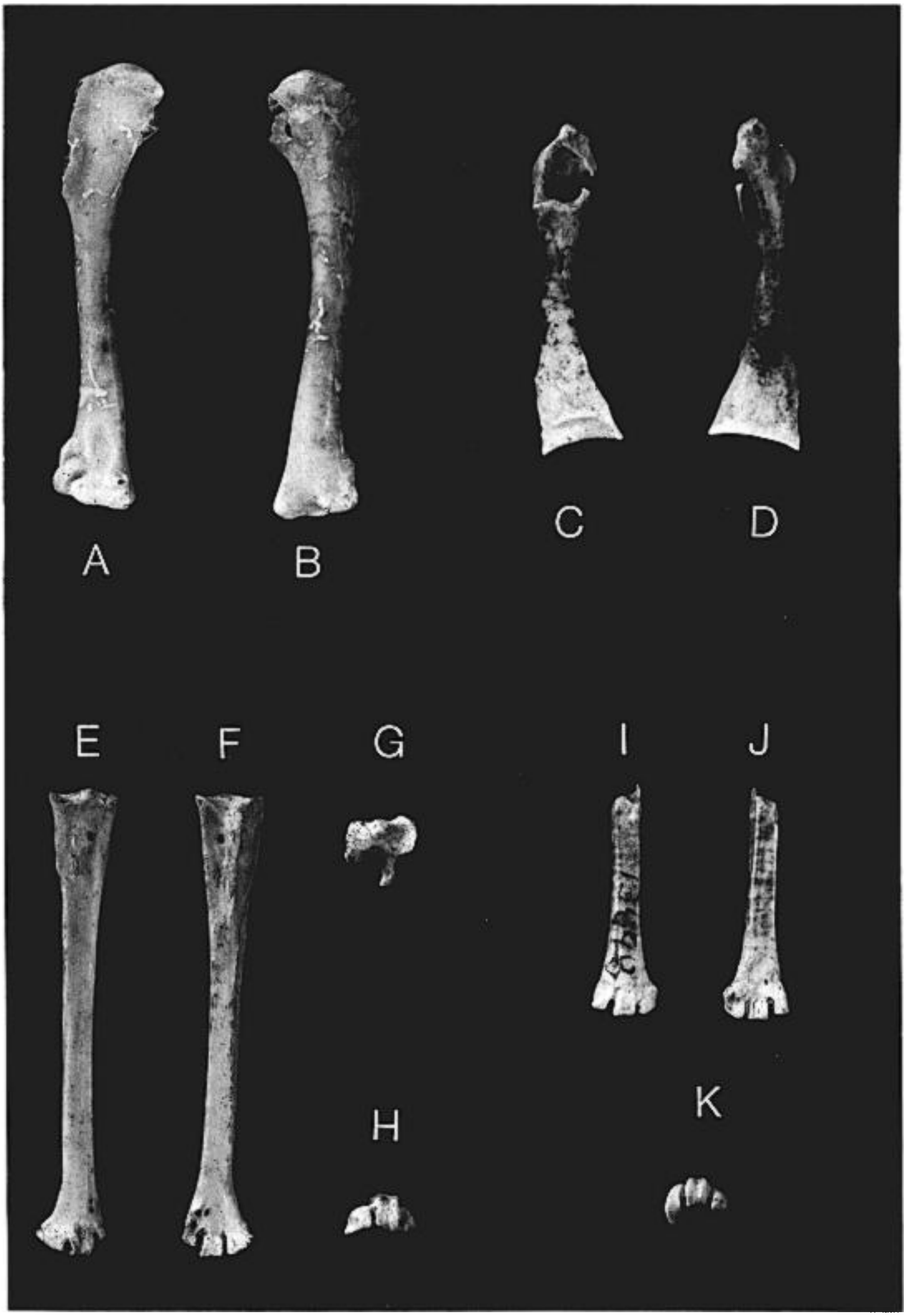
Excluding the material from Observation Quarry, each referred specimen is from a separate quarry locality in the Sheep Creek or Olcott formations, Sioux Co., Nebraska. The Olcott Formation [= Lower Snake Creek Beds of Matthew (1924)] directly overlies (unconformably) the Sheep Creek Formation. Skinner et al. (1977) discussed the following quarries in detail and placed them in the following stratigraphic sequence. Thomson Quarry, Late Hemingfordian, is from the base of the middle part of Sheep Creek Formation. Observation Quarry, early Early Barstovian, is from the Sand Canyon Beds, Dawes Co., Nebraska. Observation Quarry is located 48–64 km from the other localities included here and cannot be correlated lithically to the Olcott Formation (Skinner et al. 1977), but the undescribed vertebrate fauna from this quarry may be intermediate between the faunas of the Sheep Creek Formation and the Olcott Formation (Tedford et al. in press). Boulder Quarry, Early Barstovian, is from the type section of the Olcott Formation, representing the lower stratigraphic levels of this formation. Echo Quarry, Early Barstovian, is from an undetermined stratigraphic position within the Olcott Formation, but the mammalian fossils from it agree with those from other quarries in this formation.

A black vitric tuff (Sheep Creek Ash No. 3 of Skinner et al. 1977; KA 891 of Evernden et al. 1964) occurs approximately 28 stratigraphic meters above the Thomson Quarry and has yielded a zircon fission track date of 17.5 ± 0.5 and 16.5 ± 0.6 MYBP (million years before present) (Tedford et al. in press). These fission track dates approximate the geologic age of *Pediohierax ramenta*.

Diagnosis.—As for the genus.

Description.—The skeletal elements of *Pediohierax ramenta* are smaller than in any member of the Polyborinae and are comparable in size to small males of *Falco sparverius* and *F. columbarius.* Because of the great size variation between the sexes in this family, and because each specimen is from a separate locality representing a slightly different interval of geologic time, little can be said concerning the limb proportions of *Pediohierax*.

Measurements.—Coracoid (F:AM 10214, F:AM 10068): length from head through internal distal angle (25.4, —); length from head through scapular facet (7.7, 8.0); least depth of head (2.5, 2.4); width of midshaft (3.3, —); depth of midshaft (2.4, —); length from internal distal angle to procoracoid process (19.2, —). Humerus (F:AM 8633): greatest length from the head of the humerus through the midpoint of the lateral (ventral) condyle (35.3); transverse width of midshaft (3.3); depth of midshaft (2.8); depth of head, measured parallel to the axis of the head (7.5); transverse width of distal end from the ventral to the dorsal epicondyle (7.1); depth of distal end from cranial face of external (dorsal) condyle through ridge slightly mediad from external tricipital groove, measured at right angles to the long axis of the shaft (4.0); depth from the tuberculum supracondylare ventrale through the processus flexoris, measured at right angles to the long axis of the shaft (3.2). Tarsometatarsus (F:AM 10151, USNM 13898): length from intercondylar eminence through trochlea for digit III (37.0, —); transverse width of midshaft (2.5, 2.3); depth of midshaft (2.2, 2.0); intercondylar eminence to middle of tubercle for m. tibialis cranialis (6.3, —); greatest transverse width proximal articular surface, measured across dorsal surface (5.7, —); greatest depth medial cotyla (3.2, —); greatest depth lateral cotyla (3.6, —); depth of proximal end,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measured from dorsal edge of the proximal articular surface through the hypotarsal crest (5.7, —); greatest transverse width of distal end (*5.8, *5.1) (* = specimen broken, actual measurement would be greater).

Genus *Falco* Linnaeus 1758
?*Falco* sp.

Material.—Nearly complete left coracoid, IMNH 27937, Vertebrate Paleontology collections, Idaho Museum of Natural History. Collected 22 June 1968 by John A. White.

Locality.—IMNH Vertebrate Paleontology locality 67001, Owyhee Co., Idaho (NW ¼, Sec. 19, T. 16S, R. 5W, Star Valley Quadrangle, U.S. Geological Survey 7.5-min series topographical map, 1973). Early Hemphillian Land Mammal Age (late Miocene), approximately 8 MYBP (Becker 1980). Sediments are probably correlative to the Big Island Formation (Coats 1985).

Description.—Coracoid is referable to the Falconinae in having the foramen n. supracoracoidei placed along medial margin of procoracoid. Similar in size to *Falco columbarius* (*F. sparverius*, *F. tinnunculus*, and *F. rufigularius* are smaller; all other New World species are larger), but distinguished from these species by the greater length of glenoid facet, smaller length of coracoid, and presence of a strong crest on the ventral, sternal end of the coracoid.

Measurements.—Data are IMNH 27937; mean ± SD, observed range of *Falco columbarius* (n = 26: 4 males, 11 females, 11 unknown sex). Asterisks indicate specimen broken, measurement estimated. Length from the processus acrocoracoideus through the midpoint of the sternal end (*26.6; 28.57 ± 1.58, 26.1–31.3). Length from the midpoint of the sternal facet to the triosseal canal (21.4; 21.86 ± 2.20, 19.9–27.6). Length from the external end of the sternal facet through the internal distal angle (*10.6; 10.50 ± 0.66, 9.6–11.9). Length of the glenoid facet from the most cranial portion of the glenoid through the most caudal point of the scapular facet (6.6; 5.89 ± 0.42, 5.1–7.0).

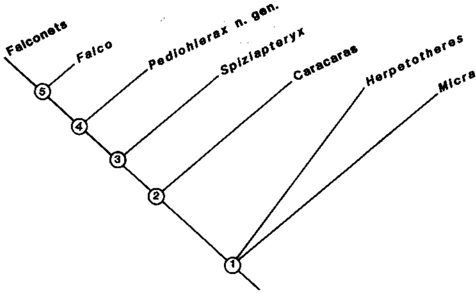

Fig. 2. Proposed phylogeny of the major groups of the Falconidae based on osteological characters and using the Accipitridae as an outgroup. Shared derived characters for each node are defined in the text.

Discussion

A phylogeny, based on shared derived osteological characters (Fig. 2), is essentially the same as those proposed by Ridgway (1875, 1876) and Jollie (1977) except that *Spiziapteryx* is not allied with the falconets, following Olson (1976a). Characters that define the family Falconidae (Fig. 2, node 1) are given by Ridgway (1875, 1876) and Jollie (1976, 1977). Osteological characters include the presence of a long supraciliary process of the lacrimal, presumably from a single ossification center, and the procoracoid process of the coracoid being produced forward to contact the furculum.

Micrastur and *Herpetotheres* each have a unique, highly derived tarsometatarsus (Jollie 1977). In addition, these genera share with the Accipitridae the primitive conditions of unfused dorsal vertebrae (Storer 1982) and lack a lateral opening of the extensor canal on the distal end of the tibiotarsus (a very small opening may be present in some individuals of *Micrastur*). These conditions suggest that *Micrastur* and *Herpetotheres* have long been separate from the other members of the Falconidae and probably from each other.

The Falconinae and the Polyborinae (Fig. 2, node 2) are united by the presence of the derived notarium and the lateral opening of the

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Fig. 1. Bones of *Pediohierax ramenta*. (A, B) Referred right humerus, F:AM 8633: (A) caudal (anconal) view, (B) cranial (palmer) view. (C, D) Referred left coracoid, F:AM 10214: (C) dorsal view, (D) ventral view. (E–H) Referred left tarsometatarsus, F:AM 10151: (E) anterior (dorsal) view, (F) posterior (plantar) view, (G) proximal end view, (H) distal end view. (I–K) Holotype, USNM 13898, distal end of right tarsometatarsus: (I) anterior (dorsal) view, (J) posterior (plantar) view, (K) distal end view. All photographs are 2× natural size.

extensor canal of the tibiotarsus. Both have a tarsometatarsus that is square in cross section, but the tarsometatarsus differs markedly in hypotarsal structure. The falconine hypotarsus has a very long ridge extending down from the hypotarsus to blend gradually with the shaft. The Polyborinae have a shortened hypotarsal ridge that ends distally in a sharp point, and that usually extends less than one-quarter of the length of the tarsometatarsus. The polyborine tarsometatarsus is probably the closest to the primitive condition for this family (Jollie 1976, 1977). Therefore, the characters of the tarsometatarsus shared between *Pediohierax* and the Polyborinae are primitive and cannot be used to support a close systematic relationship.

Spiziapteryx was associated traditionally with the falconets *Polihierax* and *Microhierax* (Suschkin 1905, Peters 1931, Brown and Amadon 1968). Olson (1976a) found characters that distinguish *Spiziapteryx* from the falconets and suggested that *Spiziapteryx* should be placed closer to the caracaras. *Spiziapteryx* has a primitive polyborine tarsometatarsus and shares with the caracaras the reduction in interorbital ossification (Olson 1976a), possibly developed in parallel. It also has a number of unique (autapomorphic) characteristics that include a strongly curved humerus and a relatively elongated coracoid. *Spiziapteryx* shares with the Falconinae (Fig. 2, node 3) the presence of a prominent "tooth" on the maxillary tomium. Although some indications of this tooth can be seen on the tomium of some genera of caracaras (*Milvago* and *Phalcoboenus*), it cannot be detected on the underlying bone (Ridgway 1876).

Caracaras are a distinctive neotropical group of falconids (Ridgway 1876, Brown and Amadon 1968, Vuilleumier 1970, Olson 1976b, Jollie 1977). All caracaras have the interorbital septum poorly ossified, possibly developed in parallel with *Spiziapteryx*, an elongated shape of the skull, and a reduced supraciliary process of the lacrimal bone (Olson 1976a). The exact systematic relationship of *Spiziapteryx* to the caracaras is still uncertain. *Spiziapteryx* may be the sister group to the caracaras, or it may be the sister group to the Falconinae + *Pediohierax* as indicated in Fig. 2.

Pediohierax is allied with the Falconinae by the characters of the coracoid (Fig. 2, node 4). The humeral end of the coracoid is rotated dorsally. The foramen n. supracoracoidei is intermediate between the primitive condition of the Polyborinae (foramen n. supracoracoidei set well within the procoracoid process away from the medial margin) and the derived condition of the Falconinae (incisura n. supracoracoidei located in the medial margin of the procoracoid process as either an open notch or closed by a tendinous thread that may or may not be ossified; Olson 1976a).

The coracoid of both *Pediohierax* and *Falco* has the facies articularis clavicularis excavated in medial view. This apparently derived character may indicate that *Falco* and *Pediohierax* are more closely related to each other than are *Falco* and the falconets, in which case the falconine tarsometatarsus would have developed independently in the falconets and in *Falco.*

Characters of the humerus provide little systematic evidence, because of the difficulty in determining their polarities. The humerus of *Pediohierax* is similar to that of both the Polyborinae and the Falconinae (excluding *Spiziapteryx,* which has a slender, strongly curved humerus). The similar orientation of the brachial fossa between the Falconinae and *Pediohierax* may provide additional support for a close systematic relationship, but other characters of the humerus (a shallow fossa olecrania and a less-developed process flexorius) are probably primitive as the conditions seen in *Pediohierax* are similar to those of the caracaras.

The reduction of palatines to noncancellous cups or shelves and the placement of the coracoid fenestra on the internal margin of the procoracoid process (Olson 1976a) unite the falconets with *Falco* (Fig. 2, node 5). These two groups also share a falconine tarsometatarsus.

The Falconidae have a long, disjunct fossil history. The earliest reported occurrence is pre-Neogene in the Eo-Oligocene Phosphorites du Quercy, France (Mourer-Chauviré 1982). Umanskaja (1981) described *Falco medius* based on a left carpometacarpus from alluvial sands of Maeotian age (late Miocene) from Cherevichnyi in the Odessa district, Ukrainian S.S.R. This small species is closely related to *Falco tinnunculus, F. vespertinus,* and *F. naumanni* (Umanskaja 1981: 19). The geologic age of this species is comparable to that of ?*Falco* from Idaho, discussed above. The only other proposed falconid from the Neogene of Europe is *Falco pisianus* Portis (1887), which was moved to the Columbidae (Olson 1985).

One Neogene fossil species is known from Asia. Kurochkin (1985) recently revised *Sushkinia pliocaena* Tugarinov (1935) from the early Pliocene "Gusinyi perelet" locality of Pavlodar (lower levels) on the banks of the Irtysh River in eastern Kazakh S.S.R. The descriptions and photographs of the coracoid and tarsometatarsus of *Sushkinia* given by Kurochkin (1985) show clearly that *Sushkinia* is closely related to, if not actually congeneric with, the genus *Falco.*

The earliest record of falconids from South America is *Badiostes patagonicus,* originally described by Ameghino (1894) as an owl from the Santa Cruz Formation (Santacrucian, early Miocene) of Patagonia, Argentina. Based on the published illustrations of this species, Wetmore (1922) moved this species to the Falconidae, a decision supported by Lambrecht (1933), Brodkorb (1964), and Olson (1985). Olson (1985) refined the systematic placement of this species because Ameghino's illustrations of hypotarsal structure were sufficient to include it in the Polyborinae on the structure of the hypotarsus. Ameghino (1894) reported the transverse width of the proximal articular end of the tarsometatarsus as 10 mm, nearly twice that of the comparable measurement of *Pediohierax ramenta,* thus removing the possibility that these two species are conspecific. Because the polyborine tarsometatarsus is probably primitive, however, the generic relationships of *Badiostes* require further evaluation when the holotype of this genus is restudied. Tonni (1980) also reported an indeterminate genus and species of Falconidae from an unnamed formation in Neuquén province, Argentina, of Friasian age (late Miocene).

The only other North American Neogene falconid is an indeterminate species of *Falco* from the Fox Canyon local fauna, Kansas, of early Blancan (Pliocene) age (Feduccia and Ford 1970). This small falcon was larger than *F. sparverius,* and approximately the size of *F. columbarius.*

The earliest record of the true falcons in Europe, Asia, and North America are all small merlin-size species either referable to the genus *Falco* or very closely related to it. Based on the present fossil record, the Polyborinae may have originated in South America, but the genus *Falco* has had a long holarctic history with much of the evolution in this genus taking place outside of South America.

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