Journal of Vertebrate Paleontology 20(4):712–719, December 2000

AN AVIAN QUADRATE FROM THE LATE CRETACEOUS LANCE FORMATION OF WYOMING

ANDRZEJ ELZANOWSKI[1], GREGORY S. PAUL[2], and THOMAS A. STIDHAM[3]
[1]Institute of Zoology, University of Wrocław, Ul. Sienkiewicza 21, 50335 Wrocław, Poland;
[2]3109 N. Calvert St., Baltimore, Maryland 21218 U.S.A.;
[3]Department of Integrative Biology, University of California, Berkeley, California 94720 U.S.A.

ABSTRACT—Based on an extensive survey of quadrate morphology in extant and fossil birds, a complete quadrate from the Maastrichtian Lance Formation has been assigned to a new genus of most probably odontognathous birds. The quadrate shares with that of the Odontognathae a rare configuration of the mandibular condyles and primitive avian traits, and with the Hesperornithidae a unique pterygoid articulation and a poorly defined (if any) division of the head. However, the quadrate differs from that of the Hesperornithidae by a hinge-like temporal articulation, a small size of the orbital process, a well-marked attachment for the medial (deep) layers of the protractor pterygoidei et quadrati muscle, and several other details. These differences, as well as the relatively small size of about 1.5–2.0 kg, suggest a feeding specialization different from that of Hesperornithidae.

INTRODUCTION

The avian quadrate shows great taxonomic differences among the higher taxa of birds in the structure of its mandibular, temporal, pterygoid, and quadratojugal articulatory surfaces, as well as in the shape of orbital process and the presence and location of pneumatic foramina. Only two aspects of quadrate morphology have hitherto been studied in any detail. Lowe (1926) started the tradition of using the temporo-quadrate articulation for phylogenetic purposes. Witmer (1990) studied the pneumaticity of the quadrate in Mesozoic birds and noted a diversity in location of the pneumatopores among extant birds. The diversity of other aspects of the quadrate morphology in birds, including their mandibular joint, which counts among the most complex vertebrate articulations, has never been recorded and much less conceptualized. Thus, the detailed study of a fossil avian quadrate that is very different from all known quadrates of other birds necessitated an extensive survey of extant quadrate morphology as well as significant elaboration and revision of anatomical terminology (Table 1, Fig. 1) proposed by Baumel and Witmer (1993). We surveyed the quadrate specimens of all extant and some fossil genera of paleognaths, of all extant families of nonpasserine neognaths, and all available information on the quadrates of Mesozoic birds.

The right quadrate UCMP 73103, in the collection of the University of California Museum of Paleontology, was found in an outcrop of the Late Maastrichtian (Late Cretaceous) Lance Formation, which was deposited in a subtropical climate along the shoreline during the final retreat of the North American inland sea. Abundant plant and vertebrate fossils were found in exposures of the ancient, near-shore streambeds (Clemens, 1963). Several species of clearly neornithine birds were described from the Lance Formation (Brodkorb, 1963) including a probable galliform. The Lance Formation material is currently being revised and several new avian fossils have recently been discovered (Sylvia Hope, pers. comm.). Relevant to the present study are two tarsometatarsi, one in the collections of the University of California Museum of Paleontology (pers. obs.) and another in the collections of the University of Nebraska (Sylvia Hope, pers. comm.), that may belong to small hesperornithiforms.

Our survey demonstrated that the quadrate morphology is diagnostic for the genera of at least nonpasserine birds and that the quadrate UCMP 73103 is distinctly unique among all known quadrates of fossil and extant birds. In addition, a combination of its morphology, size, and both stratigraphic and geographic occurrence effectively precludes its assignment to any of a few fossil genera that are based on fragmentary material without the quadrate. We therefore assigned the quadrate UCMP 73103 to new genus, which is a real addition to the diversity of Mesozoic birds.

SYSTEMATIC PALEONTOLOGY

ODONTOGNATHAE Wetmore, 1930

Supplementary Diagnosis—Quadrate slender: the span of the mandibular condyles amounts to 50% or less of the bone height. Medial mandibular condyle continuous with the caudal condyle. Quadratojugal socket shallow.

?HESPERORNITHIFORMES Fürbringer, 1888

Supplementary Diagnosis—Head undivided or the division only barely indicated. Pterygoid condyle elongate, nearly continuous with the ventral margin of the orbital process and appressed on the medial mandibular condyle.

POTAMORNIS, gen. nov. incertae sedis

The quadrate UCMP 73103 shows a novel, unique combination of characters and clearly does not represent any of the established taxa of birds for which quadrates are known. *Baptornis* and *Zhyraornis* are two Late Cretaceous genera with possible odontognathous affinities (Unwin, 1993) and their quadrates are unknown, but none of them is comparable in size (see below) and none is known from the Maastrichtian. However, because it is conceivable that the new quadrate is derived from a representative of Baptornithidae or Zhyraornithidae, we refrain from erecting a new family.

Diagnosis—As for the species.

Etymology—Gk. *potamos* river, *ornis* bird.

POTAMORNIS SKUTCHI, sp. nov.
(Figs. 2, 3)

Holotype—Quadrate UCMP 73103.

Referred Specimens—Tentatively, tarsometatarsus UCMP 117605.

Locality and Horizon—UCMP locality V-5620 (Lull 2 quarry), near Buck Creek, a tributary of Lance Creek, Niobrara Co., Wyoming; Lance Formation, Late Maastrichtian (Late Cretaceous).

Diagnosis—Head of the quadrate strongly asymmetrical, with the beak-shaped medial part overhanging the otic process. A rostrally open pit near the medial apex of the head. Caudomedial depression shallow but distinct. Orbital process small. Lateral process with a quadratojugal buttress. Medial and lateral mandibular condyles meet at the angle of approximately 115° and both smoothly connect to the caudal condyle.

Etymology—In honor of Dr. Alexander F. Skutch, an eminent ornithologist, in recognition of his respect for birds' lives.

DESCRIPTION

The *Potamornis* quadrate is well preserved except for the broken tip of the orbital process (Figs. 2, 3). A salient preservation feature is the presence of hairline fractures that must reflect the underlying structure of bone tissue as they run remarkably parallel to the long axis of the bone and veer off to the orbital process to run parallel to its margins. The bone comes from a subadult individual as revealed by the combination of highly porous but otherwise well-shaped articular surfaces and largely smooth finish of the other surfaces (except for the hairline fractures). Basic anatomical terms used in the following description are summarized in Appendix 1.

The otic process has a medial slant (from the parasagittal plane) of ca. 25° (measured with the medial and lateral mandibular condyles approximately at the same level and the quadratojugal socket directed laterally), which indicates that the temporo-quadrate articulation was oblique (in the transverse plane) and centered medially to the quadrato-mandibular articulation (Figs. 2A, D, 3A, B). The head fans out (transversely) to a width of 5.9 mm; it is 2.0 mm deep (rostrocaudally), deeper than the adjacent shaft of the otic process, and projects for 0.2 mm beyond the shaft rostrally (but not caudally). In dorsal view, the head shows a slight waist at the proximal third of its long diameter (Fig. 2G), which may or may not indicate its former division into the otic and squamosal capitula. Another possible vestige of this division is a shallow pit that opens rostrally and separates the minor, most medial part of the head from the rest. A similar pit marks the boundary between the otic and squamosal capitula in the partly (and sometimes completely as in *Francolinus*) fused head in the Phasianidae. However, the waist and the pit do not coincide and thus only one of them may indicate the former division. The otic process is strongly asymmetric mediolaterally. Whereas the squamosal end of the head is almost flush with the shaft, the otic end projects far beyond the shaft, overhanging it like the beak overhangs the neck; this rostrate appearance is strengthened by a consistently concave medial profile of the head. Just ventral to the otic, beak-shaped part of the head, there are two shallow depressions, rostromedial and caudomedial.

The lateral crest (crista lateralis), extending from the head to the quadratojugal cotyla is fairly prominent (Figs. 2C, 3D). The medial crest (crista medialis) is rounded and marked only dorsally and ventrally as it is interrupted in the middle by the medial impression, which is slightly bipartite (divided by a weak ridge) (Figs. 2B, E, 3C). The medial impression, located on the medial side of the otic process, at its transition to the body of the quadrate, in all probability marks the attachment of the medial (deep) layers of the protractor pterygoidei et quadrati muscle, which in many other birds attach to the medial crest (Fuchs, 1954; Elzanowski, 1987; Weber, 1996). There is no trace of the tympanic crest.

The orbital process is small (Figs. 2, 3) by comparison to most of the neornithine birds (Fig. 1), which suggests less attachment area and leverage for the lateral (superficial) layer of the protractor pterygoidei et quadrati as well as for the entire quadratomandibularis (=pseudotemporalis profundus) muscle. The functional significance of weakening the lateral layer of the protractor pterygoidei et quadrati and strengthening its medial layer (as indicated by the medial impression) remains to be determined. The orbital process tapers very rapidly toward its rostral end: by geometric extrapolation, the broken tip extended beyond the preserved part for about one millimeter. The ventral margin is straight. The process is convex laterally and concave medially. The medial concavity, which deepens ventrally into the basiorbital fossa, accommodates the insertion of the lateral (superficial) layers of the protractor pterygoidei et quadrati muscle. The base of the orbital process is connected to the quadratojugal socket by a rounded but distinct rib, the orbito-

TABLE 1. Terminology of the avian quadrate.

- Crista medialis(1)
- Foramen pneumaticum mediale(2)
- Crista lateralis

- Processus orbitalis
  - Crista orbitalis(3)
  - Facies pterygoidea (pterygoid facet)
  - Depressio protractoris

- Processus oticus
  - Caput quadrati(4)
    - Capitulum oticum
    - Capitulum squamosum
    - Vallecula intercapitularis (Incisura intercapitularis)(5)
  - Crista tympanica(6)
  - Foramen pneumaticum postcapitulare(7)

- Corpus quadrati
  - Fossa basiorbitalis(8)
  - Foramen pneumaticum basiorbitale

- Pars mandibularis
  - Processus medialis
    - Condylus medialis
    - Condylus pterygoideus
  - Processus lateralis
    - Condylus lateralis
    - Cotyla quadratojugalis (quadratojugal socket)
    - Depressio praecondylaris
  - Vallecula intercondylaris (Sulcus intercondylaris)(9)
  - Condylus caudalis(10)

---

(1) A ridge for the attachment of the protractor quadrati and pterygoidei muscle (Fuchs, 1954; Elzanowski, 1987).

(2) Its dorsoventral position varies between the otic process and quadrate body.

(3) Weber (1996) called it Crista lateralis, but this is an obvious term of choice for the lateral ridge extending over most of the bone length between the head and the quadratojugal cotyla (Fig. 1A, C). We therefore propose a new term, Crista orbitalis.

(4) In many birds it is undivided or incompletely divided, hence a need of this term.

(5) It encloses a well-defined space, its rostrocaudal depth being frequently comparable to its mediocaudal dimension, which makes the term incisura inadequate.

(6) An oblique ridge for the attachment of the tympanic membrane, descending toward the medial crest from the area of the squamosal capitulum. The tympanic crest is absent in some birds, indicating an unexplored diversity of the attachments of the tympanic membrane.

(7) One or more pneumatic foramina behind and below the head are present in some paleognaths (Tinamidae, *Rhea, Lithornis plebius* and probably *Paracathartes*), *Turnix*, some gruiforms (*Psophia, Cariama, Balearica*), *Ciconia*, and *Opisthocomus*.

(8) Fossa corporis quadrati (Fuchs, 1954), medially at the base of the orbital process.

(9) Commonly a rounded depression, it seldom if ever takes the form of a groove (sulcus).

(10) In the majority of birds continuous with the lateral condyle, only in a few taxa continuous with the medial condyle.

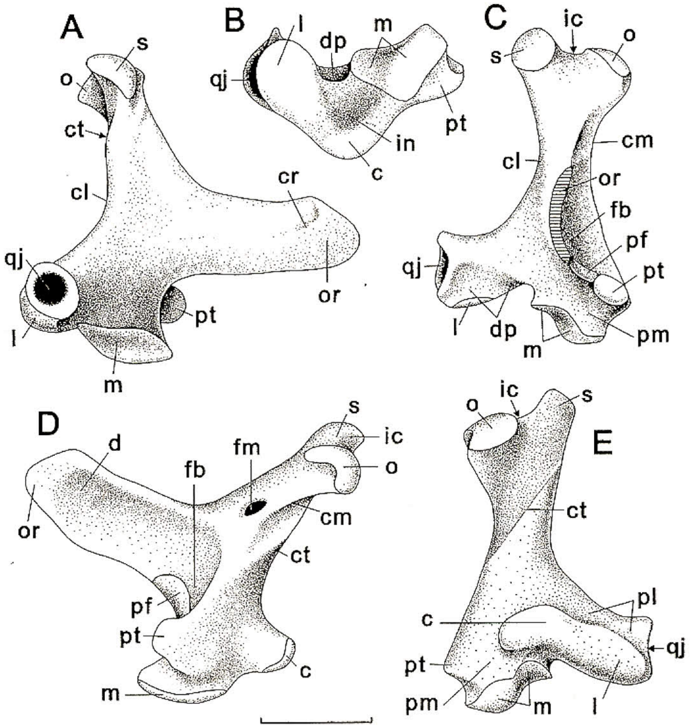

FIGURE 1. Right quadrate of *Fulica atra* in **A**, lateral, **B**, ventral, **C**, rostral, **D**, medial, and **E**, caudal views. Abbreviations: **c**, condylus caudalis; **cl**, crista lateralis; **cm**, crista medialis; **cr**, crista orbitalis; **ct**, crista tympanica; **d**, depressio protractoris; **dp**, depressio praecondylaris; **fb**, fossa basiorbitalis; **fm**, foramen pneumaticum mediale; **ic**, vallecula intercapitularis; **in**, vallecula intercondylaris; **m**, condylus medialis; **l**, condylus lateralis; **or**, processus orbitalis; **pl**, processus lateralis; **pm**, processus medialis; **pf**, facies pterygoidea; **pt**, condylus pterygoideus; **qj**, cotyla quadratojugalis. Scale bar equals 3 mm.

cotylar crest (Figs. 2C, E, F, 3D). The orbitocotylar crest and the base of the orbital process enclose dorsally an extensive suborbital depression.

The pterygoid condyle is triangular, has a prominent caudal apex at its mid-height but does not project rostrally (Figs. 2B, 3C). It is slightly heterocoelous, that is, slightly concave along the long diameter and convex transversely. Dorsally it is nearly continuous with the ventral edge of the orbital process. There is no indication of an additional articulation surface further distally on the orbital process. Ventrally, the pterygoid condyle extends onto the medial side of the medial mandibular condyle.

The lateral process is very short and the mandibular articulation narrow (Table 2, Figs. 2A, D, 3A, B). The medial and lateral mandibular condyles meet rostrally at an angle of approximately 115°. The medial condyle is narrower and more than one millimeter longer than the lateral condyle. The intercondylar valley is shallow. The caudal condyle, which points caudodorsally, is a caudo-dorso-lateral extension of the medial condyle but also intergrades smoothly with the lateral condyle (Fig. 2H).

The quadratojugal socket is relatively shallow (by comparison to the extant neognaths), somewhat triangular, and opens with a slight ventral slant (its dorsal rim projecting slightly more than the ventral margin) (Figs. 2C, F, H, 3D). The rostral section of its rim projects far beyond the lateral condyle as a quadratojugal buttress, which is separated by notches from both the caudodorsal and ventral parts of the rim, the latter being confluent with the lateral condyle. The buttress is itself shored up by a precondylar crest on the rostral surface of the quadrate. Enclosed between the precondylar crest and the lateral condyle is a triangular precondylar depression.

If present, the pneumatic foramina are small and poorly distinguishable, which makes the pneumaticity of the *Potamornis* quadrate very uncertain. The bone seems to be porous in the postcapitular area, but this may be related to its juvenile age rather than pneumaticity. A tiny foramen, 0.1 mm in diameter, seems to be present in the basiorbital fossa.

COMPARISONS

The survey of quadrate morphology in extant and fossil nonpasserines revealed the odontognathous affinities of *Potamornis*. Consequently, we drew the most detailed comparisons to the Hesperornithidae (Marsh, 1880; Bühler et al., 1988) using the casts of their quadrates, to *Ichthyornis* using the illustrations of Yale Peabody Museum quadrate specimen YPM1775 (Marsh, 1880; Witmer, 1990; the original was unavailable for study) and evidence from the mandibles (Fig. 4; see also Gingerich, 1972); and an important Mesozoic avian quadrate described by Martin and Tate (1976) as belonging to *Baptornis advenus*. For the outgroup comparisons we used the scanty information on the quadrates of *Archaeopteryx* (Elzanowski and Wellnhofer, 1996) and *Gobipteryx* (Elzanowski, 1974).

The quadrate described by Martin and Tate (1976) as belonging to the American Museum of Natural History specimen AMNH5101 of *Baptornis advenus* seems to be derived from a different bird. The published photograph shows the above specimen number, but neither the quadrate nor any record of its loan could be located at the American Museum of Natural History and neither a quadrate nor any other cranial fragment has ever been catalogued with the specimen number AMNH5101. Therefore, the quadrate must have been referred to the postcranial bones and the basis of this referral remains unknown. In addition, this assignment is called into question by size comparisons (Table 2). Based on the postcranial skeleton, Martin and Tate (1976) estimated *Baptornis advenus* to be the size of Yellow-billed loon (*Gavia adamsii*) (body mass 5,500 g). However, if the magnification provided for their figure 1 is approximately correct, then the quadrate derives from a bird smaller than the Red-throated loon (*Gavia stellata*) (body mass 1,551 g). We conclude that the assignment of the quadrate to specimen AMNH5101, and thus to *Baptornis advenus,* is most probably incorrect. We will, therefore, refer to this specimen as the "*Baptornis*" quadrate.

Proportions

In *Potamornis* the quadrate is more slender and its mandibular articulation narrower relative to the height than in all the paleognaths and and the overwhelming majority of neognaths except the Galliformes and Anhimidae, but it is wider than in *Gobipteryx, Hesperornis* (Table 2), and *Ichthyornis* (in which the condylar width is 43% of the height). In *Archaeopteryx* and *Gobipteryx* the height of the quadrate amounts to one fourth of the total skull length, which is much more than in any extant bird. Because the bone is certainly relatively longer (taller) than the quadrate of any extant bird, the dorsal and ventral widths are presumably better indicators of the body mass. In these two dimensions *Potamornis* comes close to *Phalacrocorax auritus floridanus* (body mass 1,540–1,808 g). It is clearly larger than *Zhyraornis kashkarovi* (Nesov, 1984), which has the dorsal vertebra 6.9 mm long, and smaller than *Baptornis advenus* (Martin and Tate, 1976).

Because the quadrate is relatively shorter in the theropods than it is in the basal birds, it appears that the origin of birds entailed an elongation of this bone. There is a possible link between the elongation of the quadrate and the origins of rostral kinesis (prokinesis or rhynchokinesis), because a longer quad-

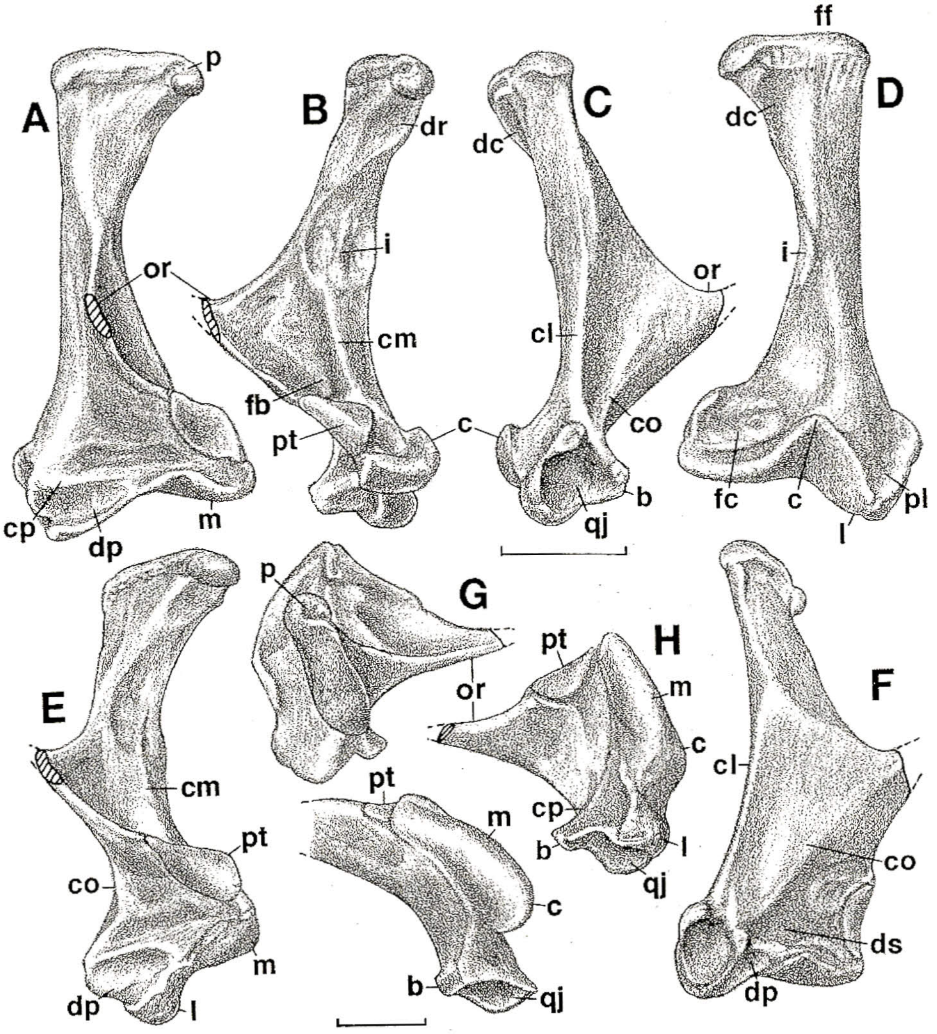

FIGURE 2. Right quadrate of *Potamornis skutchi,* gen. et sp. nov. (holotype; UCMP 73103) in **A**, rostral, **B**, medial, **C**, lateral, **D**, caudal, **E**, rostro-ventro-medial, **F**, rostro-ventro-lateral, **G**, dorsal, and **H**, ventral views. Quadrate of, **I**, *Hesperornis regalis* (KUVP 71012) in ventral view. Abbreviations as in Fig. 1 except **b**, quadratojugal buttress; **co**, crista orbitocotylaris; **cp**, crista praecondylaris; **dc**, depressio caudomedialis; **dr**, depressio rostromedialis; **ds**, depressio suborbitalis; **fc**, fossa supracondylaris; **ff**, minuscule foramina; **i**, impressio medialis (probably for the pars profunda musculi protractoris pterygoidei et quadrati); **p**, a pit in the head. Scale bars equal 5 mm.

rate provides a better leverage for moving the upper jaw, and the skull of *Archaeopteryx* suggests the avian type of kinesis (Elzanowski and Wellnhofer, 1996). Whatever its functional interpretation, a slender quadrate is a primitive avian trait. The quadrate is shortened in all modern birds, both the paleognaths and neognaths including the Galloanseres, which show secondarily slender proportions of the quadrate. Because the *Potamornis* quadrate shows no other similarity to that of Galloanseres, its slenderness is probably primitive (Table 2).

Head

It is still uncertain whether the quadrate head (caput quadrati) of the first birds articulated with the braincase as well as the squamosal and, even if it did, whether it was divided. The most ancient bird with an unquestionably avian, double temporo-quadrate articulation is *Enaliornis,* in which the otic and squamosal surfaces are separated by the dorsal pneumatic recess (Elzanowski and Galton, 1991). The heads of the known quadrates of *Archaeopteryx* (Elzanowski and Wellnhofer, 1996:fig. 3, not slightly schematized fig. 2), *Gobipteryx* (Elzanowski, 1974), and *Patagopteryx* (Chiappe, 1996; Sylvia Hope, pers. comm.) are damaged. However, as far as preserved, the conformation in the seventh specimen of *Archaeopteryx* does not seem compatible with the presence of a broad head with two widely separated, approximately equivalent capitula seen in extant birds, but it could be compatible with the configuration found in the oviraptorids, in which the apex of the otic process is formed by the prominent lateral (squamosal) capitulum and the medial capitulum is attached just below, on the medial slope of the lateral capitulum (Maryańska and Osmólska, 1997). The oviraptorids show many other avian similarities and their close avian relationships have been suggested (Elzanowski, 1999).

The head is divided in the majority of modern birds (Fig. 1) but is single or poorly divided in *Potamornis, Ichthyornis, Hesperornis,* paleognaths, and a number of neognaths including *Fregata, Pelecanus, Anhinga,* Spheniscidae, Threskiornithidae (including Plataleinae), *Psophia,* Cariamidae, Phasianidae, Pteroclididae, *Opisthocomus,* Cuculiformes, and *Nyctibius.* In some of these, especially *Opisthocomus* and some Cuculiformes, the two articular surfaces are better defined than in others, and there seems to be a morphological continuum between a perfectly single head and the presence of two distinct capitula. The lack

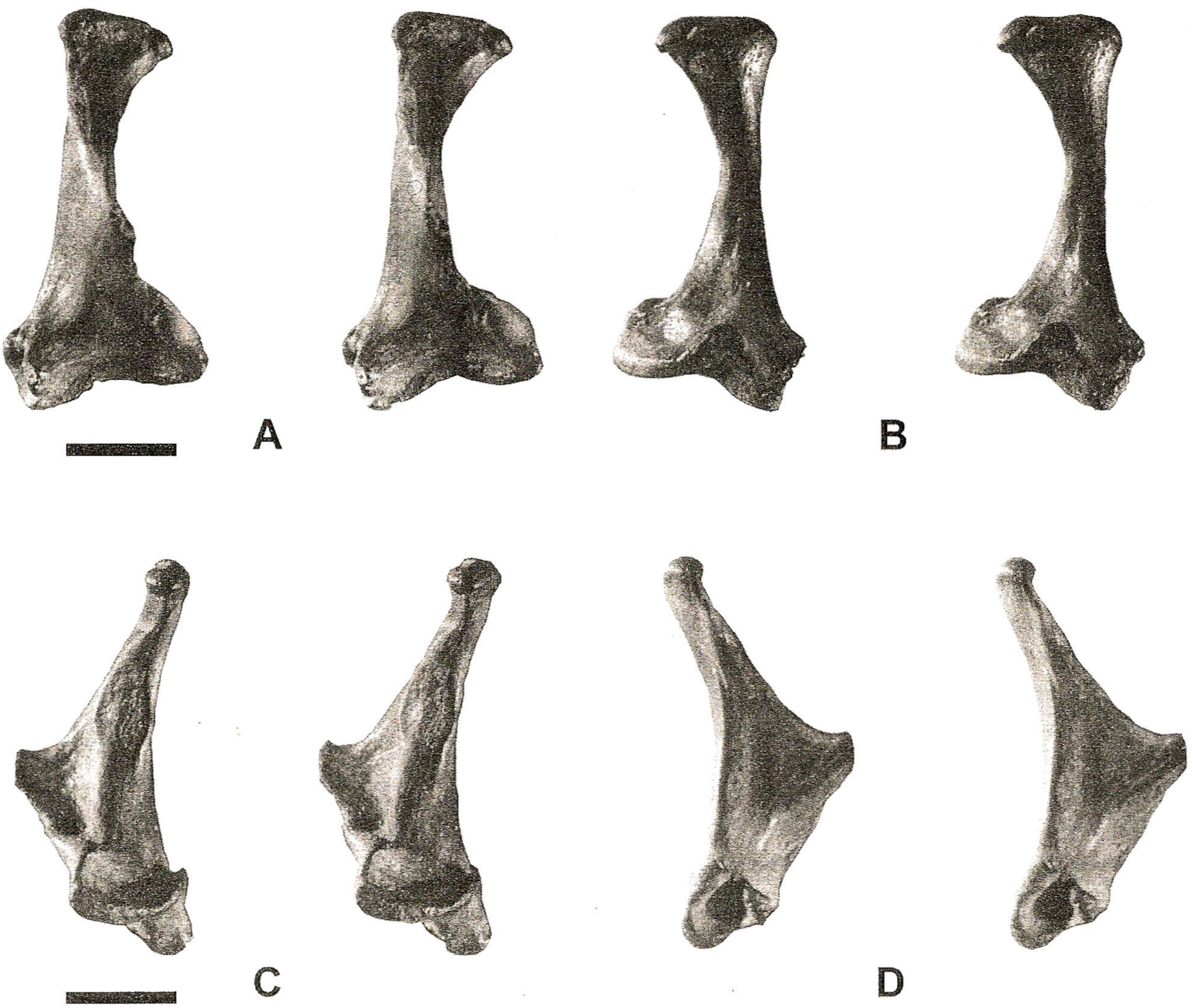

FIGURE 3. *Potamornis skutchi,* gen. et sp. nov. Stereopairs of the holotype right quadrate UCMP 73103 in **A**, rostral, **B**, caudal, **C**, medial, and **D**, lateral views. Scale bars equal 5 mm.

TABLE 2. Dimensions (in mm) and ratios of the quadrate in Mesozoic and selected modern birds.

	Height(1)	Condylar width(2)	Capital width(3)	Ratio
Gobipteryx minuta	11.0	5.0	—	1:0.45:—
Hesperornis regalis	30.0	12.5	9.0	1:0.42:0.30
Ortalis canicollis	9.4	3.9	2.2	1:0.41:0.23
Chauna torquata	18.0	8.5	4.9	1:0.47:0.27
"*Baptornis*"	—	6.5[4]	—	—
Potamornis skutchi	18.0	9.0	6.0	1:0.50:0.33
Phaethon lepturus	13.0	7.5	6.3	1:0.58:0.48
Gavia stellata	12.85	7.6	5.5	1:0.59:0.43
Podiceps cristatus	9.5	5.7	3.7	1:0.60:0.39
Pygoscelis papua	18.0	11.0	6.8	1:0.60:0.38
Spheniscus magellanicus	16.5	11.2	6.0	1:0.68:0.36
Sula nebouxi	19.6	13.5	10.0	1:0.69:0.51
Phalacrocorax auritus	15.0	10.7	5.5	1:0.71:0.37

(1) Perpendicular to the line connecting the two mandibular condyles.
(2) Between the ventral rim of the quadratojugal socket and the most medial point of the medial mandibular (but not pterygoid) condyle, along a straight line connecting the centers of the two condyles.
(3) The transverse diameter of the head.
(4) Based on Martin and Tate (1976:fig. 1).

of a distinct division in such unrelated and highly derived taxa as *Nyctibius, Opisthocomus,* Phasianidae, and Spheniscidae suggests that this condition evolved more than once and is secondary in some neognaths. The nearly single club-shaped head in the phasianids results from the transverse, lateral superposition of the capitula, which is the very opposite of the hinge-like structure in *Potamornis,* the paleognaths, and the remaining neornaths. However, the above distribution leaves it unresolved whether the undivided head is primitive or derived among the neornithines. The ambiguous phylogenetic status of the undivided head and a continuous variation between the lack and presence of division makes the differentiation of the quadrate head of little use for the reconstruction of remote relationships.

A single, rostrocaudally flattened (hinge-like) and asymmetrical head with the medial, prootic part forming a beak-like process in *Potamornis* is shared with most of the paleognaths (including the lithornithids) and a few neognaths including *Psophia,* Cariamidae (the beak-like overhang is more pronounced in *Cariama cristata* than it is in a single examined specimen of *Chunga burmeisteri*), *Nyctibius,* and, to a lesser degree, with *Opisthocomus. Apteryx* and *Pelecanus* have a single hinge-like head with the beak-shaped overhang on both sides whereby the otic process is subsymmetrical. Whether one-sided or subsymmetrical, the rostrate morphology occurs predominantly in taxa with an undivided (or poorly divided) quadrate head. A distinct division coexists with a strong asymmetry of the quadrate head only in the Strigiformes. However, in many birds (for example in the Threskiornithidae) the head is poorly divided without any tendency to form beak-shaped projections. The undivided quadrate head of Hesperornithidae is thick rostrocaudally, and, in contrast with *Potamornis,* its prootic part only slightly overhangs the neck of the otic process.

Medial Impression

The attachment area for the medial (deep) layers of the protractor pterygoidei et quadrati muscle is marked only in some birds, including many diving birds, but greatly varies in form. No extant bird has the medial impression as strongly marked as does *Potamornis.* The closest approach is the flattened area in some Procellariidae and Spheniscidae (e.g., *Pygoscelis,* much less in *Spheniscus*), which is slightly concave in rostral or caudal view. In *Gavia* and *Phaethon* there is a vertical, elongate depression in front of and along the medial crest. In *Phalacrocorax* and *Anhinga* there is a flat platform instead of an impression.

Orbital Process

A small size of the orbital process makes the *Potamornis* quadrate look very different from that of the hesperornithids. The orbital process is reduced in an extinct paleognathous genus *Paracathartes* (Houde, 1988); in three families of pelecaniform flying divers, Sulidae, Phalacrocoracidae, and Anhingidae, which are closely related (Siegel-Causey, 1997); and in three other neognathous lineages: Caprimulgiformes, Tytonidae, and Psittaciformes. This set is obviously polyphyletic and demonstrates that the process was independently reduced in at least five lineages of birds (in addition to *Potamornis*).

Pterygoid Articulation

The pterygoquadrate articulation of birds is a propulsion joint adapted for transferring the rostrocaudal components of forces between the quadrate and the pterygoid, which is necessary for the cranial kinesis of birds. The avian type of the pterygoquadrate articulation seems to be present in *Archaeopteryx* (Elzanowski and Wellnhofer, 1996).

The quadrates of *Ichthyornis,* "*Baptornis*" (Martin and Tate, 1976:fig. 1c, the pterygoid condyle seems to be broken off), *Apteryx,* and the overwhelming majority of the neognaths including *Phaethon* bear a peg-like, rostrally projecting pterygoid condyle, separate from the medial mandibular condyle (Fig. 1). Among extant birds, the pterygoid condyle is more or less superimposed on the medial mandibular condyle only in the paleognaths except *Apteryx,* the majority of pelecaniforms, the questionable ciconiiforms (*Balaeniceps, Scopus*), and in some caprimulgiforms (*Steatornis, Aegotheles*). This distribution suggests the plesiomorphic presence of the peg-like condyle in the Euornithes and the synapomorphic superposition of the pterygoid condyle on the medial mandibular condyle in *Potamornis* and Hesperornithidae.

The pterygoid articulation of the hesperornithiform quadrate, which is very similar in *Potamornis* and the Hesperornithidae, is unique in its geometric simplicity conveyed by its near-continuity with the orbital process and its superposition on the medial mandibular condyle. In contrast with the hesperornithiforms, in all these birds that have the pterygoid condyle superimposed on the medial condyle there is a deep embayment that widely separates the pterygoid condyle from the orbital process. However, in the majority of extant birds the pterygoid articulates with the orbital process in addition to the pterygoid condyle and in many of them the condylar surface is more or less continuous with that on the orbital process, a condition that may be plesiomorphic for all the Euornithes or at least extant birds.

Mandibular Articulation

The mandibular articulation of birds shows a great diversity at the ordinal and higher taxonomic levels but proves remarkably constant within families (with the notable exception of the Rallidae, which show an unusual variability in their cranial kinesis and jaw morphology).

Archaeopteryx and *Gobipteryx* have two simple, relatively small (to the size of the bone) condyles, medial and lateral, broadly separated from each other. By contrast, in the quadrate of the odontognaths, paleognaths and most neognaths the mandibular articulation is expanded caudally and thus more or less triangular or triradiate in ventral view; the caudal expansion is usually identified as the caudal condyle although it is often perfectly continuous with the lateral or medial condyle and greatly varies in shape (which is not condyloid in some birds, such as the Pteroclidae). Among extant birds, only the quadrates of Columbidae (see Lowe, 1926:pl. II/5) and Galloanseres including the Gastornithiformes (Andors, 1992) and *Aptornis* (Weber and Hesse, 1995) lack any indication of the caudal condyle.

In *Patagopteryx* (Chiappe, 1996; Sylvia Hope, pers. comm.) and the majority of neornithines, the medial condyle is more prominent and remains a separate ventral tubercle, whereas the lateral condyle extends mediocaudally and projects caudally (or caudodorsally) as the caudal condyle. This configuration is characteristic of the Palaeognathae (except Rheidae), *Turnix, Psophia,* Cariamidae, Gruidae, *Phaeton,* Procellariidae, Cathartidae, *Scopus,* Spheniscidae, *Podiceps,* Phasianidae, Anhimidae, Anatidae, Threskiornithidae, and some Rallidae (*Porphyrio*). The continuity between the lateral and caudal condyles disappears and the caudal condyle projects as a separate tubercle (whereby the quadrate becomes tritubercular) in the Diomedeidae, Phalacrocoracidae, Anhingidae, Sulidae, Laridae, Phoenicopteridae, Ardeidae, and some Rallidae including *Fulica* (Fig. 1). The two variants clearly have a common origin as attested by their interdigitating taxonomic distribution and the presence of intermediate configurations in *Balaeniceps,* Ciconiidae, and *Heliornis.* The Rheidae and *Pelecanus* have syncondylar quadrates without separate condyles, a configuration that is clearly derived as attested by its isolated occurrence and the presence of an intermediate between the tritubercular and syncondylar configurations in *Fregata.*

Only *Ichthyornis* (Fig. 4), Hesperornithidae, *Gavia, Opisthocomus,* and, with reservations, Psittacidae have the medial rather than the lateral condyle extending caudally (laterocaudally) into the caudal condyle. This rare configuration is present but less pronounced in *Potamornis* and "*Baptornis.*" The latter differs from *Potamornis* in having the medial condyle much thicker and the intercondylar incisure much deeper (i.e., the condyles meet at a more acute angle in the transverse plane). Hesperornithidae differ from *Potamornis* and, contrary to Martin and Tate (1976), from "*Baptornis,*" in the orientation of the medial condyle and the depth of the intercondylar incisure. The medial condyle is subparallel to the orbital process (closest to the sagittal plane) in Hesperornithidae, intermediate in *Potamornis,* and most transverse in "*Baptornis.*" The intercondylar valley is deepest in *Hesperornis,* intermediate in "*Baptornis,*" and shallowest in *Potamornis.*

Quadratojugal Articulation

The quadratojugal buttress with a precondylar ridge similar to that in *Potamornis* is present in "*Baptornis*" (Martin and Tate, 1976:fig. 1D), and *Parahesperornis alexi* (Ginger-

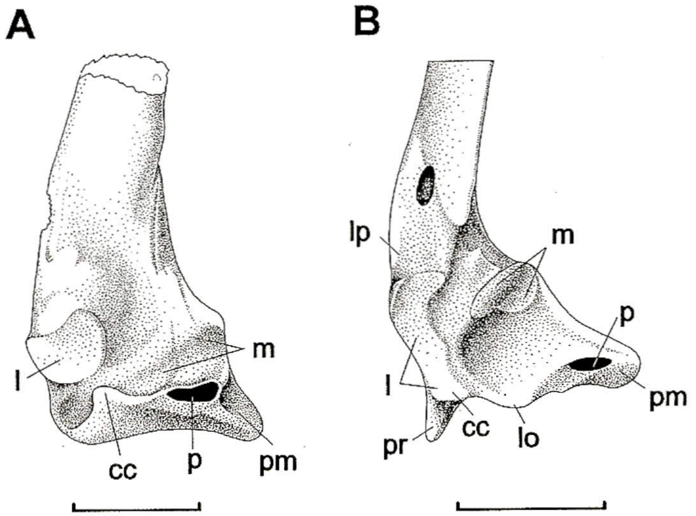

FIGURE 4. Left mandible, caudal ends in dorsal view. **A**, *Ichthyornis* sp. YPM 1761. **B**, *Fulica atra.* Abbreviations (new terms are asterisked): **cc**, contracondylus caudalis* (which articulates with the caudal condyle of the quadrate); **l**, lateral cotyla; **lo**, tuberculum ligamenti occipitomandibularis*; **lp**, tuberculum ligamenti postorbitalis*; **m**, medial cotyla; **p**, pneumatic foramen; **pm**, processus medialis; **pr**, processus retroarticularis. Note that the contracondylus is an extension of the elongate *medial* cotyla in *Ichthyornis* but of the *lateral* cotyla in modern birds. Scale bars equal 5 mm.

ich, 1976), but the buttress is absent and only the crest is present in *Hesperornis regalis* (Bühler et al., 1988:fig. 3C). Among the paleognaths the buttress is present in the Tinamidae, *Rhea, Apteryx,* and Lithornithidae (Houde, 1988:fig. 8), but poorly developed in *Struthio* and absent in the Casuariiformes. Among the neognaths it has been found in the Procellariidae, Ciconiidae, some Gruidae (*Grus*), *Opisthocomus,* Cuculiformes (where it is the largest), and some Caprimulgiformes (*Nyctibius* and, a smaller one, in *Caprimulgus*), as well as in many Passeriformes. Once claimed to be a paleognathine character (Houde, 1988), the quadratojugal buttress is neither limited to nor present in all of the paleognaths. Its distribution and variation within the paleognaths and Hesperornithidae demonstrate that this character is of little value for the reconstruction of distant relationships. The buttress intergrades with the flattening and expansion of the rostral and rostroventral rim of the quadratojugal socket that provides an additional surface for the quadratojugal articulation in the Galliformes and some other neognaths.

As in *Potamornis,* the quadratojugal socket is shallow in *Patagopteryx* (Chiappe, 1966:fig. 14), *Ichthyornis,* "*Baptornis,*" Hesperornithidae, the paleognaths including Tinamidae, and *Lithornis plebius* (but deeper in *Paracathartes*), and in some neognaths including *Turnix, Heliornis, Scopus, Pelecanus, Pygoscelis, Opisthocomus,* Cuculiformes, Strigiformes, Caprimulgidae, and *Nyctibius.* Although the socket is deep in the majority of neognaths (Fig. 1) and intermediate in a few remaining taxa, this distribution suggests that a shallow socket is primitive for the Euornithes and possibly for the neognaths, although in some neognaths (especially in the caprimulgiforms) it is probably secondary.

Pneumaticity

The quadrate is pneumatic in some theropods, including the oviraptorids (Maryańska and Osmólska, 1997), tyrannosaurids, ornithomimids and troodontids (Witmer, 1997), but it remains unknown whether it was pneumatic in *Archaeopteryx* and *Gobipteryx.* The quadrate is pneumatic in the majority of other birds except *Apteryx, Paracathartes,* and many diving birds including Hesperornithidae (Witmer, 1990), *Podiceps, Gavia,* and Spheniscidae. Contrary to Martin and Tate (1976), there is no way of knowing that the quadrate of "*Baptornis*" was apneumatic, because only its mandibular end is preserved and, as in *Parahesperornis* but not *Hesperornis,* the articular bone was pneumatic (Witmer, 1990).

DISCUSSION AND CONCLUSIONS

The relationships of Hesperornithiformes remain unknown. Wetmore (1930) united the Hesperornithidae and Ichthyornithidae in the Odontognathae but did not justify this decision and the hesperornithiforms and ichthyornithids succeed one another (although in a variable order) as separate branches in nearly all reconstructions of avian phylogeny (see Padian and Chiappe, 1998). This is not surprising since, out of the paucity of data on the skull of *Ichthyornis,* the relationships of the odontognaths are reconstructed almost exclusively with the postcranial characters. However, the postcranial skeleton of the hesperornithids is highly transformed and unlikely to have preserved any synapomorphies with their flighted relatives.

Comparisons of the jaw bones raise a possibility that the Odontognathae are monophyletic (Elzanowski, 1999). A closer relationship between these two taxa is suggested by the lack of mandibular symphysis, with the tips of the mandibular rami possibly separated by a predentary bone; the presence and detailed similarities of the intraramal joint (Gingerich, 1972); and the lingual alveolar margin, which evidently replaced the interdental plates, being flush with the buccal margin. The similarity of the mandibular articulation in the hesperornithids and *Ichthyornis* (Fig. 4), which apparently correlates with the remarkably straight quadrate, lends additional support to the monophyly of the Odontognathae.

Based exclusively on the similar locomotor specialization, Martin (1983) expanded the Hesperornithiformes to include all of the known Mesozoic foot-propelled diving birds, but the phylogenetic basis of this classification is highly questionable, especially in the case of *Baptornis* (Elzanowski, 1995). The "*Baptornis*" quadrate is probably odontognathous but does not reveal a single hesperornithiform trait.

The combination of a simple but rare configuration of mandibular condyles with slender proportions and a shallow quadratojugal socket identifies *Potamornis* as a representative of the Odontognathae, and the combination of the shape and location of the pterygoid condyle, an undivided or poorly divided head, and the reduction of pneumaticity suggests its hesperornithiform affinities. The latter are consistent with the presence in the same formation of two apparently hesperornithiform tarsometatarsi that derive from birds of the size of *Potamornis.* However, the *Potamornis* quadrate differs substantially from the hesperornithid quadrate in the rostrate, hinge-like shape of the head, a shallow intercondylar valley and a smooth transition between the lateral and the medial-plus-caudal condyles, presence of a distinct caudal apex of the pterygoid condyle, shorter lateral process, the reduction of the orbital process and its angle relative to the mandibular articulation, the presence of a distinct medial impression, and a few other superficial details. These differences make it compelling to classify *Potamornis* into a family separate from the Hesperornithidae and place a caveat on its classification into the Hesperornithiformes. The monophyly of the Odontognathae predicts the existence of a variety of small to medium-sized water birds that fill the morphological gap between *Ichthyornis* and Hesperornithidae. *Zhyraornis,* placed in a separate family of the Ichthyornithiformes (Nesov, 1984), and an undescribed bird species that yielded the "*Bap-*

tornis" quadrate are likely examples of the emerging diversity of the odontognaths.

The Hesperornithidae are obviously derived from flying birds, and thus, contrary to the sweeping generalizations about the flightlessness of all hesperornithiform birds (Martin, 1983), some of their small relatives must have been capable of flight, as were *Ichthyornis* and probably *Enaliornis* (Elzanowski and Galton, 1991). Unfortunately, nothing can be determined about the flight ability of *Potamornis,* because its estimated body mass (1.5–2.0 kg) falls in the broad overlap between flying and flightless birds.

The reduction of pneumaticity suggests diving habits of *Potamornis* and the presence of hesperornithiform tarsometatarsi of appropriate size in the Lance Formation provides circumstantial evidence of its foot-propelled diving. However, the feeding behavior and ecology of *Potamornis* may have been very different from that of Hesperornithidae. Among extant birds, the most extensive medial impression is known in the flying or wing-propelled marine birds and the reduction of the orbital process is known only in some pelecaniform divers. It is possible that the relatively small *Potamornis* was adapted to the coastal environment of the Lance Formation and the large Hesperornithidae to the open sea environment of the Niobrara Formation.

ACKNOWLEDGMENTS

We thank Larry Witmer (Ohio University, Athens), Erich Weber (University of Tübingen), and Kevin Padian (University of California, Berkeley) for excellent reviews; Sylvia Hope (California Academy of Sciences) for discussion and unpublished information, John H. Ostrom (Yale Peabody Museum) for his permission (to A. E.) to study the mandible of *Ichthyornis*; Victor Krantz (Smithsonian Institution) for taking the photographs; Jan Kusznierz (University of Wrocław) for help in processing illustrations; and Helen James and Richard L. Zusi (both Smithsonian Institution) for multifarious support.

LITERATURE CITED

Andors, A. V. 1992. Reappraisal of the Eocene groundbird *Diatryma* (Aves: Anserimorphae). Science Series Natural History Museum of Los Angeles County 36:109–125.

Baumel, J. J., and L. M. Witmer. 1993. Osteologia; pp. 45–132 *in* J. J. Baumel (ed.), Handbook of Avian Anatomy (Nomina Anatomica Avium, 2nd ed.). Nuttall Ornithological Club, Cambridge, Massachusetts.

Bühler, P., L. D. Martin, and L. M. Witmer. 1988. Cranial kinesis in the Late Cretaceous birds *Hesperornis* and *Parahesperornis.* The Auk 105:111–122.

Brodkorb, P. 1963. Birds from the Upper Cretaceous of Wyoming. International Ornithological Congress, Proceedings 13:55–70.

Chiappe, L. M. 1996. Late Cretaceous birds of southern South America: anatomy and systematics of Enantironithes and *Patagopteryx deferrariisi.* Münchner Geowissenschaftliche Abhandlungen A30:203–244.

Clemens, W. A. 1963. Fossil mammals of the type Lance Formation, Wyoming, Part I. Introduction and Multituberculata. University of California Publications in Geological Sciences 48:1–105.

Elzanowski, A. 1974. Preliminary note on a palaeognathous bird from the Upper Cretaceous of Mongolia. Palaeontologia Polonica 30: 103–109.

——— 1987. Cranial and eyelid muscles and ligaments of the tinamous (Aves, Tinamiformes). Zoologische Jahrbücher, Abteilung Anatomie 116:63–118.

——— 1995. Cretaceous birds and avian phylogeny. Courier Forschungsinstitut Senckenberg 181:41–59.

——— 1999. A comparison of the jaw skeleton in theropods and birds, with a description of the palate in the Oviraptoridae. Smithsonian Contributions to Paleobiology 89:311–323.

———, and P. M. Galton. 1991. Braincase of the Early Cretaceous bird *Enaliornis.* Journal of Vertebrate Paleontology 11:90–107.

———, and P. Wellnhofer. 1996. The cranial morphology of *Archaeopteryx*: evidence from the seventh skeleton. Journal of Vertebrate Paleontology 16:81–94.

Fuchs, A. 1954. On the correlation between the skull structure and the muscles in the male *Phasianus colchicus* L. IV. The attachment of the musculus protractor quadrati et pterygoidei and of the musculus depressor mandibulae. Koninklige Nederlandse Akademie van Wetenschappen, Proceedings, C, 57:666–672.

Gingerich, P. D. 1972. A new partial mandible of *Ichthyornis.* The Condor 74:471–473.

——— 1976. Evolutionary significance of the Mesozoic toothed birds. Smithsonian Contributions to Paleobiology 27:23–33.

Houde, P. W. 1988. Paleognathous birds from the Early Tertiary of the Northern Hemisphere. Publication of the Nuttall Ornithological Club 22:1–148.

Lowe, P. R. 1926. More notes on the quadrate as a factor in avian classification. The Ibis 1926:152–188.

Marsh, O. C. 1880. Odontornithes: A monograph on the extinct toothed birds of North America. Memoirs of the Peabody Museum of Yale College 1:1–201.

Martin, L. D. 1983. The origin and early radiation of birds; pp. 291–353 *in* A. H. Brush and A. Clark (eds.), Perspectives in Ornithology. Cambridge (UK), Cambridge University Press.

———, and J. Tate. 1976. The skeleton of *Baptornis advenus* (Aves: Hesperornithiformes). Smithsonian Contributions to Paleobiology 27:35–66.

Maryańska, T., and H. Ormólska. 1997. The quadrate of oviraptorid dinosaurs. Acta Palaeontologica Polonica 42:377–387.

Nesov, L. A. 1984. Pterozavry i ptitsy pozdnego mela Sredney Azii [Pterosaurs and birds of the Late Cretaceous of Central Asia]. Paleontologicheskiy Zhurnal 1984:47–57.

Padian, K., and L. M. Chiappe. 1998. The origin and early evolution of birds. Biological Reviews 73:1–42.

Siegel-Causey, D. 1997. Phylogeny of the Pelecaniformes: molecular systematics of a privative group; pp. 159–171 *in* D. P. Mindell (ed.), Avian Molecular Evolution and Systematics. Academic Press, San Diego.

Unwin, D. M. 1993. Aves; pp. 717–737 *in* M. J. Benton (ed.), The Fossil Record 2. Chapman and Hall, London.

Weber, E. 1996. Das Skelet-Muskel-System des Kieferapparates von *Aepypodius arfakianus* (Salvadori, 1877) (Aves, Megapodiidae). Courier Forschungsinstitut Senckenberg 189:1–132.

Wetmore, A. 1930. A systematic classification for the birds of the world. Proceedings of the United States National Museum 76:1–8.

Witmer, L. M. 1990. The craniofacial air sac system of Mesozoic birds (Aves). Zoological Journal of the Linnean Society 100:327–378.

——— 1997. Craniofacial air sinus systems; pp. 151–159 *in* P. J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego.

Received 21 May 1999; accepted 26 May 2000.