



MORPHOLOGY, PHYLOGENETIC TAXONOMY, AND SYSTEMATICS OF ICHTHYORNIS AND APATORNIS (AVIALAE: ORNITHURAE)

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MORPHOLOGY, PHYLOGENETIC
TAXONOMY, AND SYSTEMATICS OF
ICHTHYORNIS AND *APATORNIS*
(AVIALAE: ORNITHURAE)

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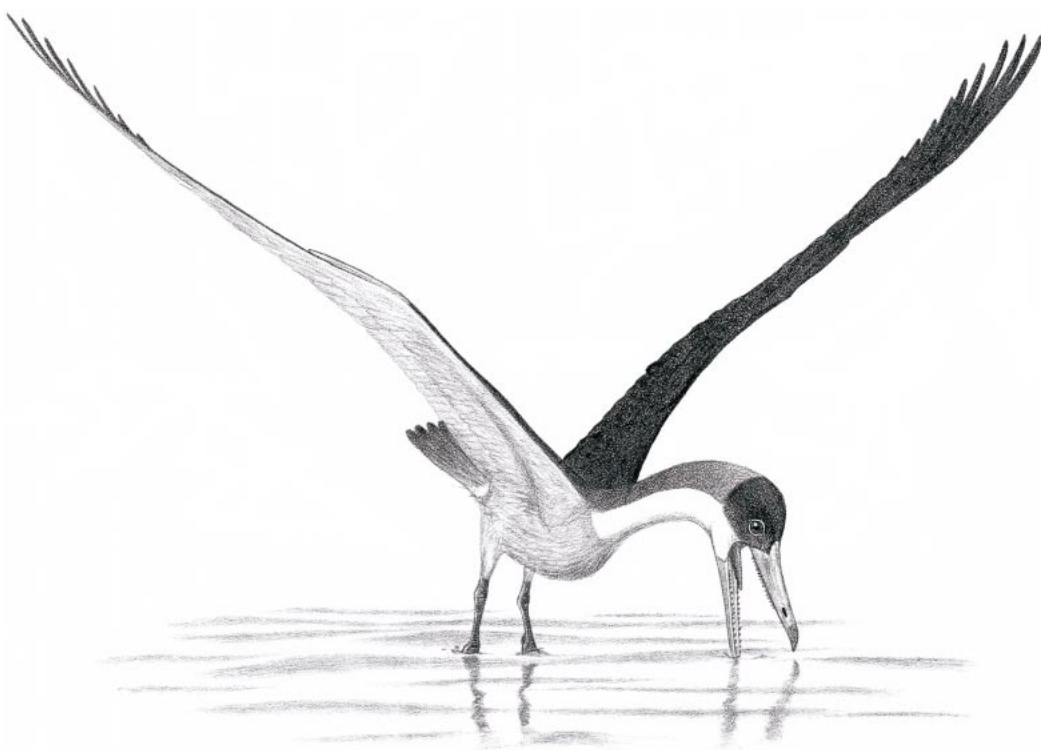
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A reconstruction of *Ichthyornis dispar* hover-feeding by Gregory Paul and based on the results of the present anatomical restudy.

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ABSTRACT

Charles Darwin commented that *Ichthyornis*, as one of the “toothed birds” from the Late Cretaceous of Kansas, offered some of “the best support to the theory of evolution” (in litt., C. Darwin to O.C. Marsh, August 31, 1880). *Ichthyornis* figures no less prominently today. It is one of the closest outgroups to crown clade Aves, and remains one of the only Mesozoic avialans known from more than a handful of specimens. As such, *Ichthyornis* is an essential taxon for analyses of deep divergences within Aves because of its influence in determining the morphologies ancestral to the crown clade.

Ichthyornis, however, has languished in need of new anatomical description and taxonomic revision. Many of the best *Ichthyornis* specimens were largely inaccessible, plastered into Yale Peabody Museum (YPM) exhibit mounts for nearly a century. The focus of this study was the entire YPM *Ichthyornis* collection, the largest at any institution.

The elements removed from the mounts were identified to the specimens with which they were originally associated. Detailed morphological study of the 81 YPM specimens yielded the following results: (1) there is evidence for only one species of *Ichthyornis*, rather than the eight previously proposed; (2) 78 specimens are part of this species, *Ichthyornis dispar*; (3) two previously identified species are not part of *Ichthyornis*; and (4) one new species is identified. This analysis also provided a case study in the application of phylogenetic nomenclature at the species level. The morphology of *Ichthyornis dispar* is described in detail from the holotype and referred specimens.

Phylogenetic analyses of 202 morphological characters, scored for 24 terminal taxa, evaluated the relationships among Mesozoic ornithurines including *Ichthyornis dispar* and the newly identified taxa. Analysis of 23 core taxa produced two most parsimonious trees (L: 384, CI: 0.66). Marsh’s “Ichthyornithiformes” is not monophyletic: Two previously named species of *Ichthyornis* as well as *Apatornis celer* are placed as more closely related to or as part of Aves. The results of the phylogenetic analyses have implications for previous hypotheses of the timing and pattern of the origin of Aves.

INTRODUCTION

Ichthyornis (sensu Marsh, 1872b) from the Late Cretaceous Niobrara Chalk of Kansas (Marsh, 1880) is among the most widely known Mesozoic avialans (Martin, 1983; Padian and Chiappe, 1998), not least because of its important and contentious role as early evidence in support of descent with modification. Indeed, Charles Darwin felt compelled to write that the description of “these old birds”, *Ichthyornis* and *Hesperornis*, in *Odontornithes: A Monograph on the Extinct Toothed Birds of North America* offered “the best support to the theory of evolution” since the publication of his *The Origin of Species* (in litt., C. Darwin to O.C. Marsh, August 31, 1880, in the Yale Peabody Museum [YPM] archives). One late 19th century student describes “parties of men and women . . . urging Professor Marsh to consider the advisability of concealing this specimen [of *Ichthyornis*] because it savored too much of evolution” (Barbour, 1902, in Martin, 1983).

However, even after evolution largely ceased to be scandalous, *Ichthyornis* re-

mained controversial. As late as the mid-1960s (e.g., Brodkorb, 1967) the association of teeth with the postcranium of *Ichthyornis* was argued to be the unnatural outcome of tinkering on the part of *Ichthyornis*’ original describer, O.C. Marsh. The combination of morphologies was more easily attributable to error or artifice than to nature. Marsh, however, has been roundly vindicated (Russell, 1967; Walker, 1967; Gingerich, 1972; Martin and Stewart, 1977).

More recently, however, hypotheses of *Ichthyornis*’ chimerical nature have resurfaced (Elzanowski, 1995; Clarke, 1999, 2000a). Clarke (1999, 2000a) commented that a collection of material mounted for exhibition, and which bore the catalogue number assigned to the *Ichthyornis victor* holotype, in fact contained none of the holotype. Instead, this material comprised the remains of more than a dozen different individuals (Clarke, 1999, 2000a).

This material was recently removed from the panel mount for the first time. Such removal allowed study of unprepared portions

of, for example, holotype and referred braincases and a referred sacrum. Significant portions of most included elements, inaccessible for more than a century because they were embedded in plaster and partially covered by paint, are now exposed.

The aim of the project undertaken with this YPM material as its focus is threefold: (1) undertake a redescription of the anatomy of *Ichthyornis* based on the extensive new information gained from reparation and, in the process of this study, (2) parse material with morphological differences when compared to the holotype for (3) evaluation in phylogenetic analyses.

A description of the morphologies of *Ichthyornis* may contribute to unraveling the phylogenetic relationships of extant birds. The abundance and quality of material from which *Ichthyornis* is known are only matched or exceeded by two other Mesozoic avialans, *Confuciusornis sanctus* (Chiappe et al., 1999) and *Hesperornis regalis* (Marsh, 1880). Because *Ichthyornis* has been placed as the nearest well-represented outgroup to Aves (Martin, 1983; Chiappe, 1995a; Norell and Clarke, 2001; although see Elzanowski, 1995), it must play an important role in assessing the ancestral states for the crown clade and, thus, is central to addressing the

currently poorly understood basal relationships within Aves.

The current work is organized in two parts: Part I, a description and taxonomic revision of *Ichthyornis*, and Part II, evaluation of the systematic position of *Ichthyornis dispar*, *Apatornis celer*, and newly named taxa. For the usage of taxonomic names in this document, please see the Methods section of the Taxonomic Revision (Part I).

INSTITUTIONAL ABBREVIATIONS

AMNH American Museum of Natural History; **BMNH** British Museum of Natural History; **ET** East Texas State University (now the ETSU collection of the TMM); **GMV** National Geological Museum of China; **IGM** Institute of Geology, Ulan Baatar; **IVPP** Institute of Vertebrate Paleontology and Paleoanthropology; **KUVP** Kansas University Museum of Natural History; **LH** Las Hoyas Collection, Universidad Autonoma de Madrid; **MDM** Mordon and District Museum; **MLP** Museo de La Plata; **SMF** Forschungsinstitut Senckenberg; **SMM** Sternberg Memorial Museum; **SMNH** Royal Saskatchewan Museum; **TMM** Texas Memorial Museum; **UCMP** University of California Museum of Paleontology; **USNM** United States National Museum; **YPM** Yale Peabody Museum of Natural History.

PART I: TAXONOMIC REVISION AND ANATOMICAL DESCRIPTION OF *ICHTHYORNIS* MARSH 1872b AND *APATORNIS* 1873b

Part I is organized into three subsections. First, a context for the current work is given in which the history of the material identified as *Ichthyornis* and *Apatornis* prior to this analysis is described in detail. Second, as part of the taxonomic revision, the name “*Ichthyornis*” is defined as it will be used throughout the rest of this document. *Ichthyornis* is diagnosed, and the specimens considered referable to it are identified. The taxonomic revision also includes, where possible, diagnoses of all other recognized taxa and definitions of all taxon names according to the principles of a system of phylogenetic nomenclature. Several new clade names and one species name are defined. The taxonomic revision also addresses the question of how

many species are recognized as part of *Ichthyornis*: Only one is recognized. Further, descriptions are provided of all holotype specimens, even those of previously recognized species, as most of these specimens have received only passing comments. Finally, an anatomical description of *Ichthyornis* (as defined here) is undertaken based upon material identified in the taxonomic revision as part of that taxon.

HISTORICAL BACKGROUND AND SCOPE

While *Ichthyornis* (sensu Marsh, 1872b) has featured in every investigation of the affinities of birds since its discovery in the late 19th century, it has remained “notoriously

poorly understood” (Olson, 1985: 91). Ironically, perhaps *because* of the apparent thoroughness of Marsh’s (1880) monograph, *Odontornithes*, and its 48 excellent lithographic plates, study of *Ichthyornis* has languished. This monographic treatment seems to have been taken as definitive (Martin, 1983). More recently it has often been remarked that *Ichthyornis* has been in critical need of detailed anatomical description (Martin, 1983; Padian and Chiappe, 1998) and taxonomic revision (Olson, 1985; Elzanowski, 1995; Padian and Chiappe, 1998). Elzanowski (1995: 44) commented, “hardly any other material of fossil birds is in greater need of revision.”

Other early controversy over *Odontornithes* concerned its authorship rather than its contents. S. W. Williston (1887) suggested in Oscar Harger’s obituary, that Harger, an assistant to Marsh, might have been the actual author of nearly all the volume. Although Williston said he had no personal knowledge of this point, his statement quickly became the centerpiece of competing paleontologist Edward Drinker Cope’s public campaign to discredit his Marsh in the *New York Herald* (Shor, 1974). Marsh responded by specifying Harger’s contributions to the volume but disputing his primary authorship of the text; he indicated Harger supervised the preparation of the illustrations and contributed observations and measurements for the volume as well as taking notes on the structure of vertebrae (letter to the *Herald* Jan. 19, 1890; reproduced in Shor, 1974: 170–171). A testimonial by Marsh’s other assistant, G. B. Grinnell, was also published in the *Herald* (reproduced in Shor, 1974: 171), indicating that Marsh dictated to Grinnell the description and conclusions in *Odontornithes*. There is no clear resolution to this “Bone Wars” era controversy and it is not clear what implications this would have for the interpretation of the contents of the volume. However, it seems indisputable that Harger, Grinnell, and Williston with many other YPM collectors contributed importantly to the monumental *Odontornithes*.

After the early evolution-related debates around the time of its discovery, *Ichthyornis* next experienced a brief period of heightened interest in the mid-20th century when the as-

sociation of the toothed jaws and postcranium in specimens of *Ichthyornis* and *Hesperornis* were called into question (Martin, 1983). Beginning with Gregory’s (1951, 1952) proposal that the teeth and jaws of the “toothed birds” belonged instead to small mosasaurs, through Swinton (1958) and Brodkorb (1967, 1971), the hypothesized “Fable of the Toothed Birds” (Brodkorb, 1971) gained momentum. Renewed interest in *Ichthyornis* brought new research and the effective demonstration that the jaws and the “bird” were one (Russell, 1967; Walker, 1967; Gingerich, 1972; Martin and Stewart, 1977).

However, hypotheses of *Ichthyornis*’ chimerical nature have resurfaced more recently (Elzanowski, 1995; Clarke, 1999, 2000a). Now it is the identification of various postcranial elements as *Ichthyornis*, rather than the jaws, that has been questioned. For example, Elzanowski (1995: 44) considered that “Marsh’s assignments of those bones that are not well represented in the holotype of *Ichthyornis dispar*, such as the scapulae, are likely to be wrong. . .”. Clarke (1999, 2000a) commented that a collection of material mounted for exhibition that bore the number of the holotype of *Ichthyornis victor* actually contained none of the holotype and was itself a chimera.

A number of factors have contributed to the confusion concerning the association of the elements on which Marsh based his description of *Ichthyornis*. First, in *Odontornithes* the figures and reconstruction of *Ichthyornis victor* are repeatedly described as based on “portions of several skeletons” including the holotype (Marsh, 1880: pl. XXXIV, figure caption). However, only a partial coracoid from the holotype is possibly figured in the monograph (Clarke, 2000a; see Anatomical Description). The rest of the material figured in *Odontornithes* includes elements from more than a dozen individuals (Clarke, 2000a) of varying sizes. As is discussed below, some of these elements are so heavily reconstructed that they display morphologies not represented in the actual material. An enlargement of the figure of the *Ichthyornis dispar* skull was used in the *Ichthyornis victor* reconstruction but indicated

as drawn from *Ichthyornis victor* material (Marsh, 1880: pl. XXXIV).

Further, many of the figured elements were later mounted for exhibit in two plaster slabs or “panel mounts” by Marsh’s preparator Hugh Gibb. Gibb began work at the Yale Peabody Museum in 1882 and worked there until his death in the 1920s (M. A. Turner, personal commun.). The *Ichthyornis dispar* (fig. 1) and “*Ichthyornis victor*” (fig. 2) panel mounts were probably made around the turn of the century when many of the YPM specimens were mounted for exhibition in the museum’s Great Hall (M. A. Turner, personal commun.).

While the panel mount for *Ichthyornis dispar* included only holotype material, that for *Ichthyornis victor*, the species to which most of the Niobrara material has been referred, included no part of the holotype. A copy of Gibb’s notes (fig. 3) on the preparation of the “*Ichthyornis victor*” mount (fig. 2) from the YPM Vertebrate Paleontology archives indicates (though not without some ambiguity or errors; see Anatomical Description) what specimens were incorporated. The “*Ichthyornis victor*” mount included material referred to *Apatornis celer* (YPM VP-Catalogue; Elzanowski, 1995), which Marsh (1873b, 1880) considered most closely related to *Ichthyornis*. The contents of the mount have been largely inaccessible, half covered in plaster and paint and exposed from a single view only. Additionally, the basicranial fragment in the “*Ichthyornis victor*” mount was embedded upside down and was not figured or described. Finally, a dentary referred by Marsh (1880) to another species of *Ichthyornis* was included in the “*Ichthyornis victor*” mount as a maxilla.

Compounding the difficulty of discerning the association of material, at some time before 1937, the specimen number of the *Ichthyornis victor* holotype (YPM 1452) was mistakenly reassigned to the panel mount (Clarke, 2000a). In 1997, the YPM catalog noted that the holotype was composed of “major portions of skeleton” as well as listing the three elements that actually comprise it (table 1).

These were the conditions under which the *Ichthyornis* material could be studied until 1997 when Jacques Gauthier authorized the

dismantling of the mounts. At the same time, reparation of all of the material in the “*Ichthyornis dispar*” and “*Ichthyornis victor*” panel mounts was undertaken.

Eighty-one specimens comprise the material at the YPM that is the subject of this analysis (tables 1 and 2). This material includes the largest collection of *Ichthyornis* specimens at any institution, as well as four specimens recognized as a result of the phylogenetic analyses (Part II) as not part of *Ichthyornis*. It is also taxonomically important, including all but one of the holotypes of previously named species of *Ichthyornis*, as well as the holotype and a referred specimen of *Apatornis celer*.

Marsh named seven species of *Ichthyornis* (sensu Marsh, 1872b). The first named, and name bearer of the taxon name “*Ichthyornis*”, is *Ichthyornis dispar* (Marsh, 1872b). The jaws found with the partial skeleton that comprises the holotype of *Ichthyornis dispar* were considered to belong to a new reptile, *Colonosaurus mudgei* (Marsh, 1872c). Upon additional preparation of the specimen and exposure of the skull and additional parts of the jaws, Marsh (1873b) recognized their association with the rest of the holotype of *Ichthyornis dispar* (Marsh, 1873b). The species *Graculavus anceps* (Marsh, 1872a) was named several months before this publication (May [Marsh, 1872a] vs. October [Marsh, 1872b]) but this species was only later referred to *Ichthyornis* (Marsh, 1880). *Graculavus anceps* is not the name bearer of the taxon name “*Graculavus*”, and thus its name was changed to *Ichthyornis anceps* (Marsh, 1880). *Graculavus agilis* (Marsh, 1873c) was named shortly after *Ichthyornis dispar* (Marsh, 1872b) and was subsequently referred to *Ichthyornis* (Marsh, 1880). *Ichthyornis victor*, the taxon to which Marsh would eventually refer the majority of specimens (Marsh, 1880), was named next (Marsh, 1876). *Graculavus lentus* (Marsh, 1877b) became *Ichthyornis lentus* in 1880 when Marsh also named two additional species, *Ichthyornis validus* and *Ichthyornis tener* (Marsh, 1880). The YPM collection includes the holotypes of these seven taxa, 71 additional YPM specimens referred to *Ichthyornis* by Marsh (1880) and subsequent authors (i.e., Gingerich, 1972; Lucas and Sullivan, 1982),

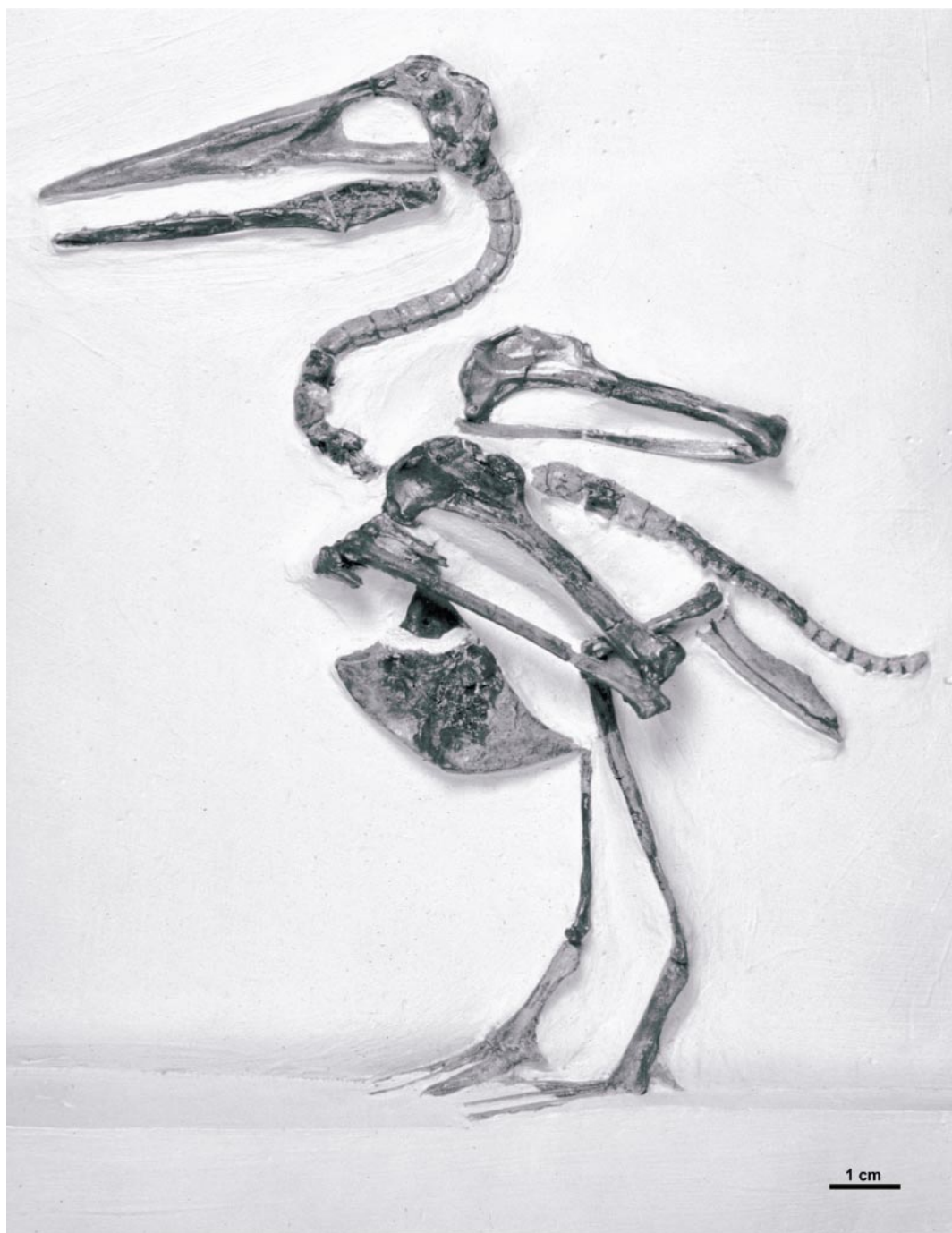


Fig. 1. The *Ichthyornis dispar* panel mount in 1997, which contained the only holotype of that taxon, YPM 1450.



Fig. 2. The “*Ichthyornis victor*” panel mount in 1997, which contained none of the *Ichthyornis victor* holotype.

TABLE 1
YPM Specimens Referred to *Ichthyornis dispar*
 Holotype specimens of Marsh (1880) species are in bold.

Specimen number	Taxonomic assignment in Marsh (1880)	Reference ^a	Elements represented ^b	Basis for referral to <i>Ichthyornis</i> ^c
YPM 1208	<i>Ichthyornis anceps</i>		carpometacarpus	8
YPM 1209	<i>Ichthyornis agilis</i>		carpometacarpus	YPM 1775
YPM 1446	<i>Ichthyornis validus</i>	page 147	coracoid	YPM 1452
YPM 1447	<i>Ichthyornis victor</i>	page 151	humerus*	5
YPM 1450	<i>Ichthyornis dispar</i>	holotype	cranium, mandible, cervical vertebrae, thoracic vertebrae, sacral vertebrae, sternum, ribs, coracoid, humerus, ulna, radius, carpometacarpus, femur, tibiotarsus, fragments	specifier for the name " <i>Ichthyornis</i> "; 2, 5, 6, 7, 8
YPM 1452	<i>Ichthyornis victor</i>		coracoid, scapula, humerus (ulna also supposed to be present, but not found)	4, 5
YPM 1453	<i>Ichthyornis agilis</i>	page 153	ulna*	6
YPM 1454	?	?	ulna	YPM 1450
YPM 1456	<i>Ichthyornis victor</i>	page 176	tarsometatarsus	YPM 1739
YPM 1457	<i>Ichthyornis victor</i>	page 151	humerus, radius, ulna	YPM 1540
YPM 1458	<i>Ichthyornis victor</i>	page 146	coracoid, scapula (fragment from 1459 part of 1458 coracoid)	4
YPM 1459	?	?	cranial fragments (see above and Anatomical Description; coracoid fragment numbered as part of this specimen found a year later than cranial material)	YPM 1450
YPM 1460	?	?	ulna	6
YPM 1461	<i>Ichthyornis victor</i>	page 148	sternum*, ribs, coracoid, humerus	YPM 1450
YPM 1462	?	?	ulna	6
YPM 1463	<i>Ichthyornis victor</i>	page 158	manual phalanx II: 1	YPM 1755
YPM 1464	<i>Ichthyornis victor</i>	page 175	tarsometatarsus	YPM 1739
YPM 1718	<i>Ichthyornis dispar</i>	pages 143, 145	coracoid, scapula	4
YPM 1719	?	?	coracoid	YPM 1450
YPM 1720	?	?	humerus	5
YPM 1721	?	?	humerus	5
YPM 1722	?	?	humerus	5
YPM 1723	<i>Ichthyornis dispar</i>	page 173	tibiotarsus	YPM 1450
YPM 1724	<i>Ichthyornis victor</i>	page 156	carpometacarpus*	8
YPM 1725	?	?	humerus	5
YPM 1726	<i>Ichthyornis victor</i>	page 159	manual phalanx II: 1*	9
YPM 1727	<i>Ichthyornis victor</i>	page 146	coracoid, scapula	4
YPM 1728	?	?	cranial material*	YPM 1450
YPM 1729	?	?	humerus	5
YPM 1730	<i>Ichthyornis dispar</i>	page 155	humerus, carpometacarpus	5, 8
YPM 1731	?	?	ulna	YPM 1450

TABLE 1
Continued

Specimen number	Taxonomic assignment	Reference ^a	Elements represented ^b	Basis for referral to <i>Ichthyornis</i> ^c
YPM 1732	<i>Ichthyornis victor</i>	page 165	thoracic* and caudal* vertebrae, sacrum*, femur*, tibiotarsus*, pedal phalanx*	3
YPM 1733	<i>Ichthyornis victor</i>	many pages	cervical vertebrae*, coracoid, scapula, humerus, radius, sacrum, part of ilium?	2, 4
YPM 1735	?	?	mandible	YPM 1450
YPM 1736	?	?	carpometacarpus	8
YPM 1737	?	?	humerus	5
YPM 1738	<i>Ichthyornis tener</i>	page 151, figured: fig. 8, pl. XXX	humerus	YPM 1450
YPM 1739	<i>Ichthyornis victor</i>	page 175	tarsometatarsus*	J. Lamb, personal commun.
YPM 1740	<i>Ichthyornis validus</i>		ulna (Brodkorb, 1967, also listed a radius but there is no evidence of a radius in the catalog or with the specimen)	6
YPM 1741	<i>Ichthyornis victor</i>	pages 146, 152	coracoid, scapula, humerus, radius*	7
YPM 1742	<i>Ichthyornis victor</i>	page 150	humerus	5
YPM 1743	<i>Ichthyornis victor</i>	page 146	coracoid	YPM 1450
YPM 1744	?	?	ulna	6
YPM 1745	<i>Ichthyornis victor</i>	page 146	coracoid	YPM 1450
YPM 1746	?	?	coracoid	YPM 1450
YPM 1747	?	?	humerus	5
YPM 1748	?	?	humerus	YPM 1450
YPM 1749	<i>Ichthyornis anceps</i>	page 124	mandible, humerus	5
YPM 1750	?	?	humerus	YPM 1450
YPM 1751	?	?	carpometacarpus	8
YPM 1752	?	?	carpometacarpus	8
YPM 1753	?	?	scapula	4
YPM 1754	?	?	tibiotarsus	YPM 1450
YPM 1755	?	?	furcula, humerus, ulna, radius, carpo-metacarpus, manual phalanx II:1	5, 6, 8
YPM 1756	?	?	humerus	5
YPM 1757	?	?	coracoid, humerus, ulna	5
YPM 1758	?	?	ulna, radius	6, 7
YPM 1759	?	?	manual phalanges II:1, I:1? (box top label indicates part of YPM 1758)	YPM 1755
YPM 1761	?	?	mandibular fragment	YPM 1450
YPM 1762	?	?	humerus	YPM 1450
YPM 1763	?	?	coracoid, scapula, humerus, radius?	4
YPM 1764	<i>Ichthyornis dispar</i>	Olson, 1975	humerus, ulna	5
YPM 1765			coracoid	YPM 1450
YPM 1766	<i>Ichthyornis tener</i>	page 198	coracoid	YPM 1450
YPM 1767	?	?	coracoid	YPM 1450
YPM 1768	?	?	coracoid	YPM 1452
YPM 1769	?	?	carpometacarpus	YPM 1775
YPM 1770	?	?	radius	7

TABLE 1
Continued

Specimen number	Taxonomic assignment	Reference ^a	Elements represented ^b	Basis for referral to <i>Ichthyornis</i> ^c
YPM 1771	?	?	tarsometatarsus	YPM 1739
YPM 1772	?	?	scapula	4
YPM 1773	?	?	coracoid, scapula, radius, humerus, carpometacarpus, endocast?	4, 8
YPM 1774	?	?	coracoid	YPM 1450
YPM 1775	<i>Ichthyornis victor</i>	page 159	mandible, quadrate, thoracic vertebrae, pygostyle?, humerus, ulna, radius, carpometacarpus, manual phalanges II:1 and III:1, femur, tibiotarsus	1, 2, 5, 6, 7, 8
YPM 1776	?	?	coracoid	YPM 1452
YPM 6264	<i>Ichthyornis</i> sp.	Gingerich, 1972	posterior mandibular fragment	YPM 1450
YPM 9148	<i>Ichthyornis</i> sp.	Lucas and Sullivan, 1982	humerus	YPM 1450
YPM 9685	?	?	humerus	YPM 1450
YPM 56577	new specimen	found in collection by L. Murray	coracoid, scapula	4

^aPage number in Marsh (1880) of referral to *Ichthyornis* species or other citation for referral.

^bElements marked with an asterisk (*) were included in the "*Ichthyornis victor*" mount.

^cNumbers 1–9 refer to the numbered apomorphies of *Ichthyornis dispar* listed in the Diagnosis. YPM specimen numbers indicate specimen with apomorphies compared as basis for referral.

and one additional specimen recently discovered in unsorted Smoky Hill Chalk material by L. Murray (YPM 56577) and here referred to *Ichthyornis dispar*. All of these specimens are listed in tables 1 and 2.

All 79 specimens were collected from the Smoky Hill Member of the Niobrara Formation of Kansas (Marsh, 1880), with the exception of a humerus (YPM 9148) from the Juan Lopez Member of the Mancos Shale of New Mexico (Lucas and Sullivan, 1982) and a tarsometatarsus (i.e., the holotype of *Ichthyornis lentus*, YPM 1796) from the Austin Chalk of Texas (Marsh, 1880). The eighth and last species of *Ichthyornis* named is "*Ichthyornis antecessor*" from the Mooreville Chalk of Alabama and is housed at the United States National Museum (USNM; Olson, 1975). It was originally referred to the "genus" *Plegadornis* (Wetmore, 1962) but eventually referred to *Ichthyornis* by Olson (1975).

Several additional taxa from Central Asia have been named as "ichthyornithids" (Nessov, 1984, 1986, 1990; Nessov and Borkin,

1983; e.g., *Zhyraornis kashkarovi*, *Zhyraornis logunovi*, *Ichthyornis malshevskiyi*, *Ichthyornis minusculus*). However, these taxa are known from isolated sacral and thoracic vertebrae (Nessov, 1986, 1990) and were not evaluated here. These taxa were said to be enantiornithines by Kurochkin (1995, 2000), and one, *Ichthyornis malshevskiyi*, was also identified as an enantiornithine by Chiappe and Walker (2002). While the support for these specimens being Enantiornithes appears generally weak, neither is there any evidence indicating relationship to *Ichthyornis*. These taxa should be further evaluated.

Dyke et al. (2002) recently suggested affinities of a new fragmentary avialan specimen from the Maastrichtian of the Netherlands with *Ichthyornis*. If the description given is faithful to the specimen, it is not referable to *Ichthyornis dispar*, otherwise indicated as closely related to it, or confirmably supported as part of Ornithurae. For example, the specimen is described as including a "proximal tarsal" (Dyke et al., 2002: 411) but the proximal tarsals fuse indistin-

TABLE 2
YPM Specimens Not Part of *Ichthyornis*, but Previously Referred to
Ichthyornis or Identified as Part of “*Ichthyornithes*” (Marsh, 1873b)
Holotype specimens of Marsh (1880) are in bold.

Specimen number	Taxonomic assignment in Marsh (1880)	Reference in Marsh (1880) ^a	Elements represented ^b	Notes
YPM 1451	<i>Apatornis celer</i>	page 192	sacrum	valid species; converted clade and species name
YPM 1734	<i>Apatornis celer</i>	many references	scapula,* coracoid,* furcula, sternum, radius, carpometacarpus, ulnare, radiale, manual phalanges, II:I and II:II,* rib, femur, tibiotarsus*	designated the type of a new species: <i>laceornis marshi</i>
YPM 1760	<i>Ichthyornis tener</i>	page 198	sacrum	removed from <i>Ichthyornis</i> ; part of a new clade: <i>Guildavis</i>
YPM 1796	<i>Ichthyornis lentus</i>	page 198	tarsometatarsus	removed from <i>Ichthyornis</i> ; part of a new clade: <i>Austinornis</i>

^aPage number in Marsh (1880) of referral to *Ichthyornis* species or other citation for referral.
^bElements marked with an asterisk (*) were included in the “*Ichthyornis victor*” mount.

guishably to the tibia in *Ichthyornis* and, indeed, all adult ornithurines and in taxa more basally divergent within Avialae (e.g., Chiappe, 2001; Clarke and Norell, 2002). Further, the new specimen is described as having a “deep” brachial depression, but in *Ichthyornis* this muscular impression is an extremely faint scar and not a depression (see Anatomical Description). The specimen is described as having a well-developed sulcus for the transverse ligament and this feature is developed as a discrete pit and not as a sulcus in *Ichthyornis* (see Anatomical Description).

Two other characters listed as supporting affinities of the Maastricht specimen with *Ichthyornis*, so far as their meaning was understood, are not present in any holotype or referred *Ichthyornis* material, or optimized as synapomorphies of that taxon: i.e., “medial deflection of the distal end of the humerus” and “hooked dorsal and ventral humeral condyle” (Dyke et al., 2002: 411). The described presence of a brachial scar and globose head of the humerus (the two characters supporting its placement as part of Ornithurae; Dyke et al., 2002) could not be discerned in the photograph of the extensively crushed, poorly preserve proximal and distal ends of the humerus (Dyke et al., 2002: fig. 1a). The

specimen is considered Avialae incertae sedis and to merit restudy. It is not treated here.

Also from the Niobrara Formation of Kansas, “*Apatornis celer*” was named by Marsh (1873b). Originally referred to *Ichthyornis* (Marsh, 1873a), the species originally “*Ichthyornis celer*” was removed to become the type species of “*Apatornis*” (Marsh, 1873b). Marsh (1873b, 1880), however, continued to consider *Apatornis celer* to be most closely related to *Ichthyornis* (placed in the now [Marsh, 1873b] monotypic “*Ichthyornidae*” [Marsh, 1873a]).

Marsh (1873b) named his “sub-class” of “toothed birds” “*Odontornithes*”, for *Ichthyornis* and *Apatornis* (although the latter is not known from any cranial material); he also placed both taxa in the “order” *Ichthyornithes* (Marsh, 1873b, 1873c). These two taxa remained classified together within the “toothed birds” after a second “order” of “*Odontornithes*”, *Odontolcae* (Marsh, 1875), was created when *Hesperornis regalis* was recognized to be toothed. Shortly thereafter, Marsh changed “*Ichthyornithes*” (Marsh, 1873b) to “*Odontotormae*” (Marsh, 1876), believing the former name to be preoccupied, but not citing *by what* it was supposed to be preoccupied (Marsh, 1876). Recent attempts to discover a prior use of the

name have not yielded positive results (J. Gauthier, personal commun.).

Fürbringer (1888) corrected Marsh's "Ichthyornidae" to "Ichthyornithidae", and included only *Ichthyornis* in this taxon and coined "Apatornithidae" for *Apatornis celer* (Brodkorb, 1967). "Ichthyornithes" was used for Marsh's (1873b) original contents (i.e., *Apatornis* and *Ichthyornis*) that were now in the Apatornithidae and Ichthyornithidae (Fürbringer, 1888). Fürbringer (1888) also coined an additional name, "Ichthyornithiformes", for a more inclusive taxon than "Ichthyornithes" but with the same contents. Brodkorb (1967) used "Ichthyornithiformes" for both *Ichthyornis* and *Apatornis* (included in the Ichthyornithidae and Apatornithidae, respectively) and listed "Odontornithes", "Ichthyornithes", and "Odontornithes" as invalidly formed synonymous names for this taxon (Brodkorb, 1967).

Both the *Apatornis celer* holotype specimen and the only specimen referred to this species (Marsh, 1880; table 2) are housed at the YPM. As will be discussed, it was this referred specimen (and not the holotype) that was the basis for nearly all that Marsh (1880) and subsequent authors (e.g., Howard, 1955; Olson, 1985; Martin, 1987) have said about that taxon.

One specimen from the Late Cretaceous of Wyoming (Lance Formation) was placed in the taxon *Apatornis* by Brodkorb (1963, 1967) but later removed from this taxon (Brodkorb, 1970). It had been originally recognized as the holotype specimen of *Cimolopteryx retusus* (Marsh, 1892) and Brodkorb (1970) returned it to *Cimolopteryx*. The proximal coracoid that is the holotype and only known specimen of *Cimolopteryx retusus* does not overlap the sacrum that is the holotype specimen of *Apatornis celer*. The two characters cited by Brodkorb (1963) to support referral of this species to *Apatornis*, a recurved glenoid facet and a cup-shaped scapular cotyla, cannot be assessed in the holotype of *Apatornis celer* as the two specimens have no overlapping parts. They must have been assessed in the one referred *Apatornis celer* specimen.

No characters to support the species' return to *Cimolopteryx* or to support this genus' placement within crown clade Charad-

riiformes were supplied (Brodkorb, 1970). *Cimolopteryx retusus* lacks a recurved acrocoracoid process and a procoracoid process (as noted by Brodkorb, 1970), which may suggest it is an outgroup of Hesperornithes + Aves. A depression in the medial surface of the coracoid resembles that in *Apsaravis ukhaana* (Clarke and Norell, 2002). However, these morphologies have also argued to indicate that the taxon is a crown clade galliform (Hope, 2002). Wherever this fragmentary specimen is finally placed, it cannot be assessed to be part of *Apatornis*, as it cannot be compared to the holotype specimen of this taxon. Only the holotype and the sole specimen referred to the species *Apatornis celer* will be treated here.

The current study includes additional material from the Smoky Hill Member of Niobrara Formation of Kansas in the collections of the Natural History Museum in London and the Sternberg Memorial Museum in Fort Hays, Kansas. Several elements referred to *Ichthyornis* from three Canadian localities are also commented upon, but they were studied from their description in the literature: the Campanian Vermilion River Formation, Manitoba (Martin and Stewart, 1982); the Turonian Kaskapau Formation, Alberta (Fox, 1984); and the Cenomanian Belle Fourche Formation, Saskatchewan (Tokaryk et al., 1997). Several additional elements are discussed from the Pflugerville and Gober Formations of Texas (Parris and Echols, 1992) and from the Chico Formation of California (Hilton et al., 1999). These were also studied from the literature. Small bones tentatively referred to *Ichthyornis* from the Late Cretaceous of Antarctica but unfigured (Zinsmeister, 1985) were not studied, and evaluation of these will be the subject of future work. Finally, extensive but undescribed material (Niobrara Formation and Mooreville Chalk Formation) referred to *Ichthyornis* (e.g., at the University of Kansas and Red Mountain Museum) was not evaluated for this project. All of this material, as well as the aforementioned Central Asian taxa, should be the object of much-needed future study. Such study, however, must take as a base the redescription, taxonomic revision, and identification of potential apomorphies of *Ichthyornis* provided here.

TAXONOMIC METHODS

In this section, taxonomic methods are detailed including the approach taken to the application of a system of phylogenetic taxonomy at the species level. This discussion is followed by a revision of *Ichthyornis*. To summarize the result of this revision, all material referred to *Ichthyornis* is currently considered to be part of a single species. The variation in size and morphology among *Ichthyornis* specimens is detailed, and possible evidence for additional species is discussed. It is concluded that explanations of the limited variation exhibited among the referred YPM material as (1) anagenetic change within a single lineage, (2) different stages in ontogeny, and (3) sexual dimorphism cannot be rejected at this time. However, some evidence suggests that, with the collection of further specimens or histological data, more than one species could be determined to be present. Two previously named species are removed from *Ichthyornis* and a newly identified species and *Apatornis celer* are addressed next.

All named taxa used in this document are clade or species names applied according to the principles of a system of phylogenetic taxonomy (de Queiroz and Gauthier, 1990). The clade names used have been or are defined as node-based, stem-based, or apomorphy-based names (de Queiroz and Gauthier, 1990). A “specifier” (sensu Cantino and de Queiroz, 2000) is a taxon and/or specimen used in the definition of a clade name and to which that name is formally tied. Several clade names are defined for the first time in a phylogenetic context. The definitions of these names and those of the converted clade names attempt to follow the published draft of the PhyloCode (Cantino and de Queiroz, 2000). One recommendation of the PhyloCode was not followed here (Recommendation 6.1A): that all scientific names be italicized. Only least-inclusive clade names (i.e., clades with their current contents limited to species, not other named clades and/or names in the process of being converted to clade names) and species names were italicized in this document. During the current transitional period, prior to full PhyloCode implementation, maintaining as many of the stylistic

conventions of name appearance is desirable. Furthermore, Recommendation 6.1B (Cantino and de Queiroz, 2000) that [L] and [P] be used to specify if a name is governed by the PhyloCode was not used here as the code has not yet been implemented and, thus, cannot formally govern any names.

While a preliminary code of phylogenetic nomenclature governing clade names exists (i.e., the PhyloCode; Cantino and de Queiroz, 2000), a code governing species names has not yet been developed. The new and converted clade names in this document follow all articles and most recommendations of the PhyloCode (exceptions noted in the text; see Introduction). Species are considered entities of a different sort from clades (consistent with Note 3.1.1 of the PhyloCode; Cantino and de Queiroz, 2000). A clade is considered a monophyletic group of species (de Queiroz and Donoghue, 1990) but species are not considered to have monophyly as one of their necessary properties (per the concept of de Queiroz, 1998, 1999, used here).

CLADE NAMES

The converted clade names defined in this document include “*Ichthyornis*”, “*Ichthyornithes*”, “*Hesperornithes*”, and “*Hesperornithidae*”. “*Ichthyornis*” and “*Ichthyornithes*” are defined in the Taxonomic Revision of Part I. “*Hesperornithes*” and “*Hesperornithidae*” are defined here because these names are used throughout this document but have not been previously defined phylogenetically.

The name “*Hesperornithes*” (Fürbringer, 1888) is the first applied to the contents of a lineage including, but not limited to, *Hesperornis regalis* (Gauthier and de Queiroz, 2001). It is here converted as a stem-based clade name (de Queiroz and Gauthier, 1992) for all taxa and/or specimens more closely related to *Hesperornis regalis* than to Aves. The species that is the specifier for this stem-based name is *Hesperornis regalis* (holotype: YPM 1200). “*Hesperornithiformes*” (Sharpe, 1899; Brodkorb, 1967) is a later name, although more commonly used. “*Hesperornithes*” was simply modified to have an ordinal suffix (Gauthier and de Queiroz, 2001).

As discussed in Clarke (2002), the other

available name, and the first named supra-specific taxon to include *Hesperornis regalis*, is “Hesperornithidae” (Marsh, 1872a). Two new species, *Lestornis crassipes* and *Hesperornis gracilis*, were later named and included in Hesperornithidae (Marsh, 1876). However, *Baptornis advenus* (Marsh, 1877a), described a year later, was not. “Hesperornithidae” is defined here as a stem-based name (de Queiroz and Gauthier, 1992) for all taxa more closely related to *Hesperornis regalis* (Marsh, 1872a) than to *Baptornis advenus* (Marsh, 1877a). The usage of “Hesperornithidae” in Martin (1984) is approximated by the definition of the name here (i.e., it was taken refer to the contents, *Parahesperornis alexi* and *Hesperornis regalis*, but not to *Baptornis advenus*).

The name “Pangalliformes” is additionally proposed as a name for the galliform stem clade in Part I (Taxonomic Revision). This name for this clade should ideally be part of a consensus decision concerning the form of clade names in Aves. It is proposed here for increased precision, as one of the fossils addressed in this document would be Pangalliformes incertae sedis but there is no evidence that it is part of the galliform crown clade (Galliformes; see Results in Part II).

Other previously phylogenetically defined taxon names are repeatedly used throughout the current document. To briefly summarize the usage of these names: “Dinosauria” is used as a node-based name for the clade comprised of the most recent common ancestor of Owen’s (1842) specifiers for his “Dinosauria” (*Megalosaurus* and *Iguanodon*) and all of its descendants; “Theropoda” (Gauthier, 1986) refers to Aves and all saurishian dinosaurs more closely related to Aves than Sauropodomorpha; “Avialae” is used sensu Gauthier (1986) as a node-based name for the most recent common ancestor of *Archaeopteryx* + Aves and all of its descendants.

“Ornithurae” (Haeckel, 1866) is used as an apomorphy-based name (de Queiroz and Gauthier, 1992) sensu Gauthier and de Queiroz (2001: 27) for the “clade stemming from the first panavian with a ‘bird tail,’ namely, a tail that is shorter than the femur (subequal to or shorter than the tibiotarsus) with a pygostyle of avian aspect . . . that is homolo-

gous (synapomorphic) with that of Aves (*Vultur gryphus*; Linnaeus, 1758).” This usage differs from that of previous authors who have applied this name to a variety of more or less inclusive clades (see discussion in Gauthier and de Queiroz, 2001). The currently known content of this Ornithurae is the clade comprised of the last common ancestor of *Apsaravis ukhaana* and Aves and all of its descendants. As noted above, “Ornithurae” is an apomorphy-based name and, therefore, not defined with reference to *Apsaravis ukhaana*.

“Aves” (Linnaeus, 1758) is used for the last common ancestor of all living birds and all of its descendants as defined in Gauthier (1986) using the internal referents Ratitae, Neognathae, and Tinami. This usage is consistent with that of Gauthier and de Queiroz (2001), although the specifiers used to bracket the avian crown clade are species taxa (i.e., *Struthio camelus* Linnaeus, 1758, *Tetrao [Tinamus] major* Gmelin, 1789, and *Vultur gryphus* Linnaeus, 1758). “Neoaves” (Sibley et al., 1988) is used following Gauthier and de Queiroz (2001) as a node-based name for the last common ancestor of all extant neognaths more closely related to *Passer domesticus* than to Galloanserae.

SPECIES NAMES AND DEFINITIONS

Forms for the definitions of species names, unlike the forms for clade definitions (i.e., node-, stem-, and apomorphy-based and “modified” variants thereof) have not yet been specified under the PhyloCode. Nor have there been any published recommendations for the form of these definitions, although there has been ongoing debate over the form of species names (e.g., Graybeal, 1995; Schander and Thollessen, 1995; Cantino, 1998; Cantino et al., 1999; Artois, 2001) and if species should be used as taxa at all (Pleijel and Rouse, 2000a, 2000b). The approach to the form of such definitions outlined below is intended as a starting place for a future dialogue, but such an approach will not be sufficient for all cases, and further work on these issues is underway (de Queiroz, in prep.).

The approach to the form of species names taken here is based upon one version of

“Group III” definitions, “Option M”, of Cantino et al. (1999) in which species names are uninomials (e.g., “*dispar*”) but a clade address is cited as a “taxonomic address” to indicate additional information about the phylogenetic relationships of the species discussed. Thus, “*Ichthyornis dispar*”, although identical in appearance to a Linnaean binomial, is not a combination of taxonomic units of different ranks (i.e., genus and species) but the combination of the name of the least inclusive named clade (e.g., *Ichthyornis*) of which the species (e.g., with the uninomial name “*dispar*”) is a part.

The phylogenetic definitions of species names take the form: “the species containing specimen X” in which the word “species” refers to species under the general lineage concept as articulated by de Queiroz (1998, 1999). For example, the definition of the species name “*dispar*” is “the species that includes YPM 1450”. The general lineage concept considers species as separately evolving segments of population-level lineages (de Queiroz, 1998, 1999), which may or may not be monophyletic. Monophyly, for example, may be a property used operationally in the recognition of a species, but it is not considered a necessary property of a species (de Queiroz, 1999). Further, not all segments of population-level lineages are species, but only those demarcated by two defining events (although there is little agreement on what should constitute these defining events; de Queiroz, 1998, 1999).

As summarized by Cantino et al. (1999), although the criteria used to recognize species remain contentious, it is commonly agreed that species are fundamental units of organizing knowledge of biodiversity (Baum, 1998), and, as such, worth naming (though see Pleijel and Rouse, 2000a, 2000b). It is here assumed for the taxa addressed that an individual is part of only one species, however problematic it may be to determine what other specimens are part of this species. The criteria by which specimens are identified as part of a species (e.g., by autapomorphy; potentially interbreeding) is left to individual authors, as in the case of the multiple criteria for the recognition of species under the general lineage concept (de Queiroz, 1998, 1999).

I used a combination of autapomorphy and morphological correspondence to refer individuals to a particular species. Specimens were identified as correspondent if they agreed in all the enumerated details of their morphology (details discussed at length in the Anatomical Description) with specimens referred on the basis of autapomorphy (see further elaboration below with reference to *Ichthyornis dispar*). Unfortunately, it seems unrealistic to expect that every bone or portion of the skeleton will have autapomorphies of a species. If, for example, a species is diagnosed by a single autapomorphy of the skull, no other portions of isolated postcranial elements can or will preserve diagnostic characters.

The number of characters that are unambiguously optimized as autapomorphies of a taxon is contingent not only upon the amount of missing data for the taxon of interest, but the amount of missing data for the taxa supported as its nearest outgroups (and/or sister taxon). Missing data for the taxon of interest and/or for these other sampled and closely related taxa results in characters being ambiguously optimized across several internal nodes. Missing taxa, or low taxon sampling, would be an extreme case of missing data affecting the optimization of characters as diagnostic autapomorphies. In this light, the autapomorphy-based species concept is clearly seen as relational; knowledge of the morphology and relationships of other species being required for the recognition = diagnosis of the species of interest.

Indeed, that phylogenetic and phenetic species concepts (summarized in de Queiroz, 1998) imply a “relational view” of species (de Queiroz, 1999) generally has already been discussed. While there is nothing necessarily bad in relational definitions, I believe that strict adherence to the application of relational definitions is untenable, at least in the case of fossil taxa. What I used here is operationally a “relaxed” apomorphy criterion for species recognition, but a nonrelational species definition (general lineage species concept; de Queiroz, 1999).

A relational view of the nature of the species is implicit when one of the identified necessary properties of species (e.g., including similarity, apomorphy, and diagnosability)

ty; de Queiroz, 1999) require reference to other species (de Queiroz, 1999), just as a “sibling” is someone defined in relation to or requiring the existence of another (cf. Mayr, 1963). Under the general lineage concept, these properties are recognized as contingent (rather than necessary) properties of species that may be used as criteria for the recognition of a separately evolving population level lineage (de Queiroz, 1998, 1999).

The binomial form of species names and the manner of definition of new species in this document ensures that they are also valid under the International Code of Zoological Nomenclature (ICZN; International Commission of Zoological Nomenclature, 1999) although this required several additional clades to be named that currently have the same known contents. However, even the number of these additional names is no more than required under the ICZN. Although the binomials used in this document are explicitly defined as clade + species name couplets, there is no exclusion in the ICZN that these clades cannot be considered genera by those that use the ICZN or that the taxon must be called a “genus” for a name to be valid genus name under the ICZN, if the other provisions of this code are met (including typification; International Commission of Zoological Nomenclature, 1999: Article 61.1). In addition to facilitating the translation between the two systems of nomenclature during the current transitional period, the closer structure of the names themselves allows a refocusing on other positive differences such as the increased explicitness in alpha taxonomy under a system of phylogenetic taxonomy. However, it is also clear that there are important elements of good alpha taxonomic practice consistent with the principles of both systems of nomenclature (e.g., aspects of typification) that allow the names defined here to also meet ICZN criteria.

SYSTEMATIC PALEONTOLOGY

AVIALAE GAUTHIER, 1986

ORNITHURAE HAECKEL, 1866

ICHTHYORNITHES MARSH, 1873b
(CONVERTED CLADE NAME)

DEFINITION: “Ichthyornithes” (Marsh, 1873b) is converted and defined as a stem-

based name (de Queiroz and Gauthier, 1992) for all taxa/specimens more closely related to YPM 1450 (holotype of *Ichthyornis dispar* Marsh, 1872b) than to Aves (internal specifiers of Gauthier and de Queiroz, 2001; see Introduction). Although the current contents of Ichthyornithes are the same *Ichthyornis*, and indeed, *dispar*, it was considered advisable to convert this name given the material with suggested affinities to *Ichthyornis* yet to be reevaluated (e.g., Nesso and Borkin, 1983; Nesso, 1984, 1986, 1990; Dyke et al., 2002).

“Ichthyornithes” (Marsh, 1873b) and “Ichthyornithiformes” (Fürbringer, 1888) were applied to *Apatornis* + *Ichthyornis*, which are not found to be most closely related to each other in the current analyses (Results, Part II). One earlier name (“Ichthyornidae”; Marsh, 1873a) was not used in Marsh’s later papers (e.g., 1880), nor by subsequent authors. It was corrected to “Ichthyornithidae” by Fürbringer (1888). “Ichthyornithes” is elected as the name for conversion (contra Clarke, 2002) because it is least likely to be confused for a Linnean ranked taxon and to keep available for conversion, as necessary, names previously applied to less inclusive taxa if additional taxa are discovered to be more closely related to *Ichthyornis* than to Aves.

Ichthyornis Marsh, 1872b
(converted clade name)

DEFINITION: “*Ichthyornis*” is defined as a modified apomorphy-based name for the clade stemming from an ancestor that possessed all of the morphologies described by apomorphies 2, 5, 6, 7, 8 (in the *Ichthyornis dispar* Diagnosis) homologous (sensu Patterson, 1982) with those in YPM 1450 (holotype of *Ichthyornis dispar* Marsh, 1872b) and more closely related to YPM 1450 than to Aves (internal specifiers of Gauthier and de Queiroz, 2001; see Introduction). YPM 1450 is the holotype of “*Ichthyornis dispar*”, which is the valid type species of the genus name “*Ichthyornis*” as specified by Marsh (1872b) and under the ICZN (International Commission on Zoological Nomenclature, 1999).

While nine characters are currently found

to be autapomorphies of *Ichthyornis dispar*, only those characters preserved in YPM 1450 are used in the definition of the name. Thus, even if some or all of the other characters used in the diagnosis of *dispar* (e.g., 1, 3, 4, 9) are found to be absent in the species of which YPM 1450 is a part and instead diagnostic of another species of *Ichthyornis*, the name “*Ichthyornis*” will still apply to a clade including YPM 1450.

Further, if some of the characters used in the definition of the name “*Ichthyornis*” are discovered to be plesiomorphies of a more inclusive clade of which Aves is a part, the definition would remain valid and apply to the portion of the stemclade intended by the definition (i.e., a subclade of the YPM 1450 stem clade). The name “*Ichthyornis*” could not refer to a clade including Aves, as mentioned, because the modifier of this apomorphy-based name used specifies only that specimens more closely related to YPM 1450 than to Aves may be part of a clade named “*Ichthyornis*”.

However, if all five of the autapomorphies used in the definition were optimized as plesiomorphies of a more inclusive clade of which Aves was a part, “*Ichthyornis*” would apply to the total *dispar* stem clade and become a heterodefinitional synonym of “*Ichthyornithes*” (defined earlier in the document and presumably to be converted before it; Cantino and de Queiroz, 2000: Article 14). The definition would remain valid as the characters currently found to be autapomorphies would remain homologous as plesiomorphies of a more inclusive clade. The name “*Ichthyornis*”, in this instance (i.e., as a heterodefinitional synonym), would not be reavailable for redefinition. In the unlikely event that all five characters are so optimized, it is mandated here as one additional formal modifier of the definition that the given definition be invalidated if the intent of the definition (i.e., to name a subclade of the total stem) is violated. Such an occurrence is considered highly unlikely, however.

SPECIFIER: The internal specifier of the name “*Ichthyornis*” is YPM 1450, the holotype of *Ichthyornis dispar* (described in Marsh, 1872a, 1872b, indicated by description and specimen number as “YPM 1450” by Marsh, 1880). Following Article 11.8 of

the current draft of the PhyloCode (Cantino and de Queiroz, 2000), the internal specifier of the clade name “*Ichthyornis*” as converted from a genus name should use the type of the genus as the internal specifier. As noted below, although the species name “*anceps*” was coined before “*dispar*” for a specimen now supported as part of *Ichthyornis* (Marsh, 1872a vs. Marsh, 1872b), it was not one of the original nominal species of the genus *Ichthyornis* and cannot, according to the ICZN (International Commission on Zoological Nomenclature, 1999: Article 67.2) be the type of the genus *Ichthyornis*. Thus, given this provision of the ICZN as well as Article 11.8 of the PhyloCode, the appropriate internal specifier for the converted clade name “*Ichthyornis*” is the first named nominal species (and type) of the genus *Ichthyornis*, which is *dispar*.

dispar Marsh, 1872b
(converted species name)

DEFINITION: The species epithet of “*Ichthyornis dispar*” (Marsh, 1872b) is converted here. The name “*dispar*” is defined as the species that includes YPM 1450. With its clade address, the name appears as “*Ichthyornis dispar*”. The species names “*Ichthyornis anceps*” Marsh, 1872a (Marsh, 1880), “*Ichthyornis agilis*” Marsh, 1873c (Marsh, 1880), “*Ichthyornis victor*” Marsh, 1876, “*Ichthyornis validus*” Marsh, 1880, and “*Ichthyornis antecessor*” Wetmore, 1962 (Olson, 1975) are not converted to clade and species names and are considered currently junior synonyms of “*Ichthyornis dispar*”.

The name of the originally designated type species of the genus *Ichthyornis* (Marsh, 1872b) is converted here as the name for the one currently recognized species of *Ichthyornis* (see further discussion below). This species, *Ichthyornis dispar*, is the valid type species of the genus *Ichthyornis* according to the ICZN (International Commission of Zoological Nomenclature, 1999: Article 67.2), as well as the appropriate internal specifier of the converted clade name “*Ichthyornis*” according to the current draft of the PhyloCode (Cantino and de Queiroz, 2000: Article 11.8).

If a large species of *Ichthyornis* were to be recognized with a diagnostic feature being

size, and since "*Ichthyornis anceps*" Marsh, 1872a (Marsh, 1880) appears to be a valid name, then "*Ichthyornis anceps*" Marsh, 1872a, and not the more commonly discussed "*Ichthyornis victor*" Marsh, 1876 could have priority as a name for a single, larger taxon. The holotype of *Ichthyornis anceps* (Marsh, 1872a) is from an individual the same size as that represented in the holotype of *Ichthyornis victor* (see section on *Ichthyornis anceps*, below).

HOLOTYPE SPECIMEN: YPM 1450 consists of portions of the skull, mandible, cervical, thoracic and sacral vertebrae, sternum, ribs, coracoid, humerus, ulna, radius, carpometacarpus, femur, tibiotarsus, and several vials of unidentifiable fragments (table 1). The holotype is described and figured in the Anatomical Description.

LOCALITY AND HORIZON: Marsh (1880: 197) identified YPM 1450 as collected by B. F. Mudge in 1872 "near the Solomon River". Brodkorb (1967) specified that locality as the Smoky Hill Chalk Member, Niobrara Formation, near the Solomon River in Section 1, Township 6, Range 19, in Rooks County. Although the source of this additional information was not cited (Brodkorb, 1967: 177), Bardack (1965) appears to be the source followed. Bardack (1965) himself did not discuss how this more exact information on the locality was obtained. Stewart (1988) identified the locality of the holotype of *Ichthyornis dispar* as being from the combined zones of *Cladoceramus undulatopectatus* and *Platyceramus platinus* that was taken to be most likely early Santonian in age (Stewart, 1990).

REFERRED MATERIAL: The 77 YPM specimens referred to *Ichthyornis dispar* (table 1) fall into two kinds: those which are referred based on the presence of one of the nine preserved autapomorphies used in the diagnosis of *Ichthyornis dispar*, and those referred based on correspondence of their morphologies with those of specimens referred on the basis of autapomorphy. The latter type of referral is an obviously weaker form of inference. Table 1 lists YPM specimens referred to *Ichthyornis dispar*, and the basis for their referral. For those specimens referred based on the preserved presence of one of the identified autapomorphic characters, numbers are

given that correspond to the nine characters used in the Diagnosis (table 1). For those specimens that are referred on the basis of correspondence in every detailed aspect of their morphology, the specimen number of one specimen is given to which the element can be compared and which itself preserves one or more of the nine autapomorphies (table 1). Those specimens that are referred to *Ichthyornis* in this analysis, but differ in any attribute from the condition seen in the reference specimen listed for them in table 1, are discussed in the Taxonomic Revision below and are listed in table 4.

One partial postcranium from the BMNH (BMNH A905) and one partial skeleton from the SMM (SMM 2503) are referred to *Ichthyornis dispar* on the basis of apomorphy; in the case of BMNH A905, the specimen preserves characters 4 and 5 from the diagnosis below and in the case of SMM 2503, characters 2, 4, 5, 8, and 9. SMM 2503 must be the same as a specimen as that cited as SMM "13520" in Martin and Stewart (1977); the specimen, recently studied at the SMM (SMM 2503), was listed as collected in 1970 by J. D. Stewart and is a partial skeleton of a large *Ichthyornis* individual (matching the collection date, collector, and description of SMM "13520" in Martin and Stewart, 1977: 1331). These specimens are discussed because they preserve elements or morphologies not represented in the YPM material. One further specimen (SMM 2139) is discussed because it is the oldest *Ichthyornis* specimen from Kansas (Martin and Stewart, 1982). SMM 2139 is a proximal carpometacarpus that can be referred only by morphological correspondence to *Ichthyornis*.

Several other elements previously referred to *Ichthyornis* are reviewed here as evaluated from their description and figures from the literature. This preliminary review is undertaken because the age range assessed for *Ichthyornis* is based on the referral of elements from as early as the Cenomanian, older than the Coniacian-Campanian YPM Smoky Hill Chalk Member material. A nearly complete referred humerus from the early Turonian (Kaskapau Formation) of Alberta (Fox, 1984) may be referable to *Ichthyornis dispar* as it corresponds in all of its few figured

morphologies with that taxon. However, the basis for this evaluation is weak: The diagnostic feature of the humerus of *Ichthyornis dispar* (see Diagnosis, character 5) is not visible or described.

Five partial coracoids and a radius from the late Cenomanian Belle Fourche Formation of Saskatchewan (Tokaryk et al., 1997) were referred to *Ichthyornis*, with the referral of the coracoid based on the position of the scapular cotyla relative to the glenoid facet (Tokaryk et al., 1997). In YPM specimens referred to *Ichthyornis dispar* by apomorphies this morphology is also seen (see Anatomical Description). However, this morphology is not found to be an apomorphy of *Ichthyornis*. Further study of the material is necessary to evaluate this referral. Several additional elements from the Campanian (Pflugerville Formation) and Coniacian (Gober Formation) of Texas (Parris and Echols, 1992) were referred to *Ichthyornis dispar* and *Ichthyornis antecessor*. Those referred to *Ichthyornis antecessor* are treated in the Taxonomic Revision. No morphologies were listed as the basis for the one complete humerus and one partial forelimb referred to *Ichthyornis dispar*. Again, no identified apomorphies of *Ichthyornis* are described or figured. A partial humerus from the Campanian Chico Formation of California (Hilton et al., 1999) was referred to *Ichthyornis*, but no characters were cited for the basis of the referral. It corresponds in the few figured morphologies to those of *Ichthyornis dispar* in the short flexor process and the pronounced pits on the dorsal supracondylar process. However, none of these mentioned characters are apomorphies of *Ichthyornis*. A thoracic vertebra from the Campanian (Vermilion River Formation) of Manitoba (Martin and Stewart, 1982) appears to have a centrally located parapophysis (L. Chiappe, personal commun.), a character synapomorphic of Enantiornithes, and is removed from *Ichthyornis*.

Diagnosis of *Ichthyornis dispar*

Nine autapomorphies are considered to currently diagnose *Ichthyornis dispar*. They are illustrated in figure 4. Marsh (1872b) commented on only a single character in his

original note recognizing and naming *Ichthyornis dispar*, the “type species” of the name “*Ichthyornis*”. He noted that *Ichthyornis dispar* differed “widely from all known birds, in having *biconcave* vertebrae” (emphasis original, Marsh, 1872b: 344) and considered that the “rest of the skeleton presents no marked deviation from the ordinary avian type” (Marsh, 1872b: 344). He recognized the cervical, thoracic, and caudal vertebrae to be “biconcave” (i.e., amphicoelous). However, in 1880 he considered this morphology unique to his “Odontotormae” (which also included *Apatornis*) and to “separate them widely from all birds recent and extinct, and point back unmistakably to a very low ancestry, even below the reptiles” (Marsh, 1880: 119). Thus, apparently, while considering this character diagnostic originally of *Ichthyornis* and later of “Odontotormae”, he also considered it essentially plesiomorphic and even listed it as one of a list of characters that would be expected in the “ancestral type of the class of Birds” (Marsh, 1880: 188). As discussed below, the morphology of the vertebral centrum articular surfaces (although of only the cervical vertebrae and not best described as a “biconcave” articulation) are currently found to diagnose *Ichthyornis*.

Subsequent to Marsh’s work, essentially the only proposed apomorphic “character” of *Ichthyornis* was from the humerus. Harrison (1973: 123; followed by Martin, 1983, and Olson, 1985) proposed “the humerus of *Ichthyornis* as a taxonomically isolating character” considering a dorsally projecting deltopectoral crest (appendix 1, character 112) and the lack of a bicipital crest to be autapomorphic of *Ichthyornis*. Harrison (1973) considered *Archaeopteryx* to lack a dorsally projecting deltopectoral crest and to share a anteriorly projecting crest condition similar to that of extant birds. However, a dorsally projecting (appendix 1, character 112) deltopectoral crest is developed in other basal avialans (e.g., *Confuciusornis sanctus*, *Cathayornis yandica*, *Concornis lacustris*, *Neuquenornis volans*, *Gobipteryx minuta*, and *Apsaravis ukhaana*) and is optimized as plesiomorphically present in *Ichthyornis*. A weakly developed bicipital crest is also plesiomorphic for Avialae. Furthermore, what

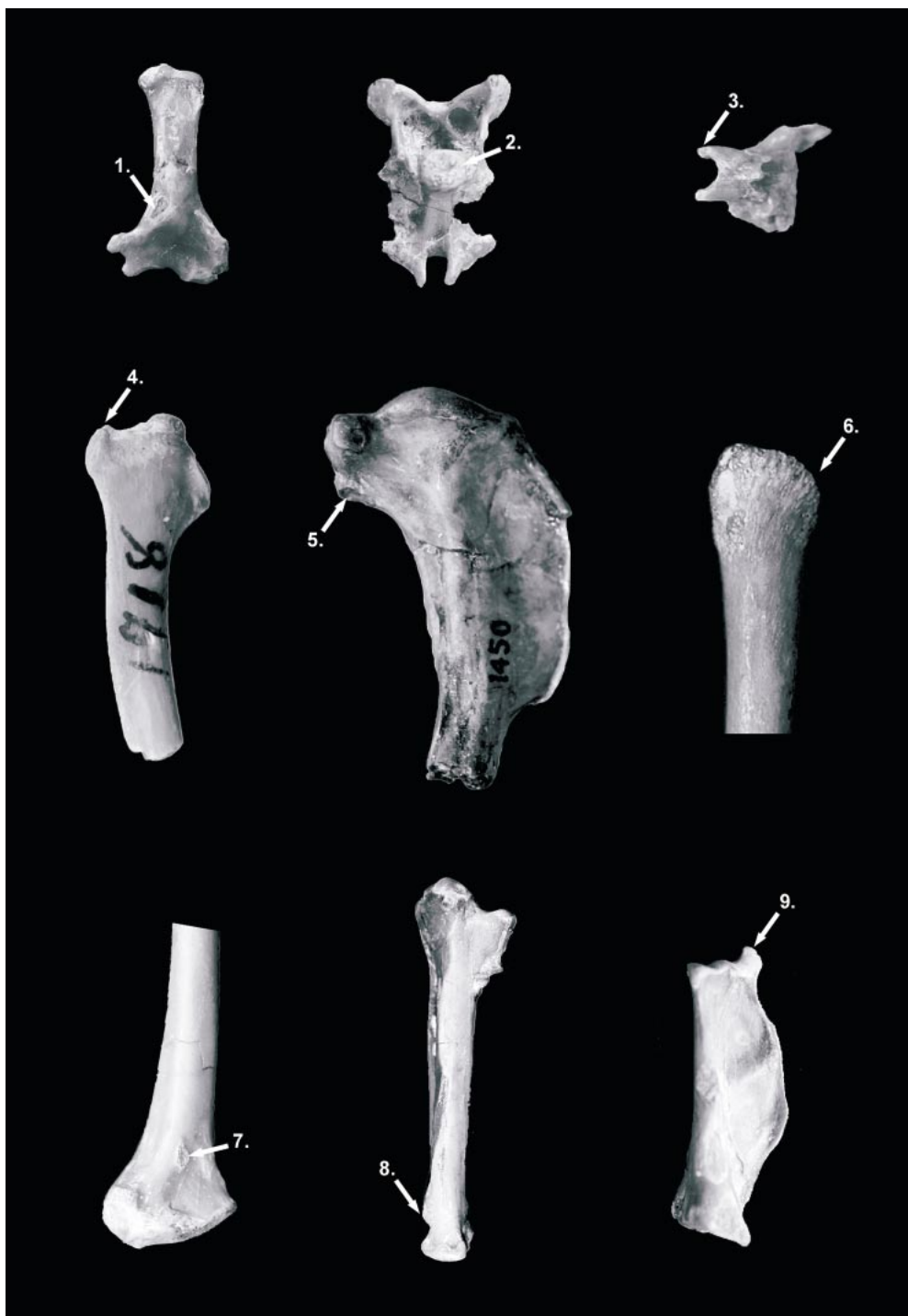


Fig. 4. Apomorphies of *Ichthyornis dispar*. Numbers 1–9 correspond to the characters used in the diagnosis and are indicated for the following specimens: (1) YPM 1775, left quadrate, anterior view; (2) YPM 1733, a posterior cervical vertebrae, posteroventral view; (3) YPM 1732 caudal vertebrae, dorsal view; (4) YPM 1718, right scapula, dorsal view; (5) YPM 1450, left humerus, posterior view; (6) YPM 1450, right humerus, posterior view; (7) YPM 1450, right radius, anterior view; (8) YPM 1450, right ulna, anterior view; (9) YPM 1450, right radius, posterior view.

constitutes the “strongly developed crest” (Harrison, 1973) illustrated for a neoavian remains difficult to assess, as it appears to be a complex of distinct characters. Certainly, the “small” bicipital crest, seen in nonavian theropods (e.g., *Deinonychus antirrhopus*; Ostrom, 1969) and all other basal avialans (e.g., *Confuciusornis sanctus*, *Enantiornithes*, *Apsaravis ukhaana*) is also a plesiomorphy retained in *Ichthyornis*. What characters comprise the derived “strongly developed” condition and when these characters arose remain to be investigated.

Each of the nine characters identified here as diagnosing *Ichthyornis* are commented on in more detail in the body of the Anatomical Description and/or in appendix 1. The figures of the anatomy of *Ichthyornis* that illustrate the morphologies discussed in this diagnosis are numbered to correspond to the organization of the body of the anatomical description. Several of these characters are proposed as local autapomorphies and not as features known only from *Ichthyornis* (e.g., the position of the quadrate pneumatic foramen, development of a condylar pterygoid articulation on the quadrate, and an internal index process on Phalanx II: 1). As opposed to those characters unique to *Ichthyornis*, these characters’ optimizations as locally autapomorphic will be affected by resolution of basal neoavian relationships. Characters found to be ancestral for Neoaves could make characters currently found to be derived for *Ichthyornis* ambiguously optimized. After surveying galloanserines and palaeognaths, considered to represent the two most basal divergences within the crown clade, as well as more basal avialans, a determination of the primitive condition was hazarded for some characters not included in the phylogenetic analyses. Of the following proposed diagnostic characters of *Ichthyornis*, those that were evaluated in the phylogenetic analyses and additionally commented on in Part II (Results) are indicated with an asterisk:

1. Quadrate: single large pneumatic foramen

located on the anteromedial surface of the corpus of the quadrate, lying close to the pterygoid articulation (“1” in fig. 4). This condition is not encompassed by either character 39 or 40 (appendix 1) as it was not observed in any of the other included taxa (although per the recommendation in Part II, Methods, it will be included in subsequent analyses). The anteromedial position of the foramen (close to the pterygoid articulation) is considered a local autapomorphy of *Ichthyornis* (contra Witmer, 1990) with this condition also observed in some Neoaves (Witmer, 1990).

- 2*. Cervical vertebrae: amphicoelous or “biconcave”. The conformation of the articular surfaces of the cervical vertebral centra in *Ichthyornis* is unambiguously optimized as derived (“2” in fig. 4). While amphicoelous cervical articulations are developed in nonavian theropods and *Archaeopteryx*, the cervical articular surfaces are heterocoelous in *Patagopteryx deferrariisi*, *Hesperornis regalis*, *Baptornis advenus*, *Apsaravis ukhaana*, *Lithornis*, and Aves. Other basal avialan taxa (e.g., *Confuciusornis sanctus*) exhibit an intermediate condition (appendix 2, character 52).

The cervical articulations in *Ichthyornis* (described in detail in the Anatomical Description) are optimized not as homologous with the amphicoely in more basal theropods, but as a unique transformation of a heterocoelous conformation. However, both the anterior and posterior articular surfaces of all cervical vertebrae are ovoid and flat with a central concavity (fitting the definition of amphicoely). By contrast, heterocoelous articulations involve an anterior surface that is broadly concave mediolaterally but convex dorsoventrally and a posterior surface convex mediolaterally and concave dorsoventrally.

- 3*. Caudal vertebrae: anterior free caudal vertebrae with well-developed prezygapophyses clasping the dorsal surface of preceding vertebra (“3” in fig. 4; appendix 1, char-

←

(6) YPM 1740, right ulna, dorsal view; (7) YPM 1741, right radius, posteroventral view; (8) YPM 1724, right carpometacarpus, dorsal view; (9) YPM 1726, right manual phalanx II:1, dorsal view. Elements not to scale.

acter 66:2). As Marsh (1880) noted, in *Ichthyornis* a reverse of the typical zygapophyseal articulation is developed with elongate prezygapophyses clasping the dorsal surface of the preceding vertebra in the anterior caudal vertebrae. The postzygapophyses, by contrast, are extremely weakly developed. They are flat facets on the posterodorsal surface of the neural arch that are in contact with the ventral surface of the prezygapophysis of the succeeding vertebra. By contrast, well-developed pre- and postzygapophyses (appendix 1, character 66:0) are present in the anterior caudal vertebrae of the outgroups and *Confuciusornis sanctus*. Both the pre- and postzygapophyses are short (even apparently noncontacting in the avian taxa included in this analysis as well as in *Hesperornis regalis*; appendix 1, character 66:1) but show no sign of a reverse articulation. In *Ichthyornis*, the pre- and postzygapophyses are short relative to the outgroup condition, but have a reverse articulation developed. This conformation is also observed within Neoaves (e.g., Charadriiformes such as *Vanellus melanopterus*). And, while its distribution deserves further scrutiny, it is not present in any taxa included in this analysis other than *Ichthyornis*. Even if development of a reverse articulation is found to be ancestral to Neoaves, it would remain most parsimoniously optimized as an autapomorphy of *Ichthyornis*.

4*. Scapula: The presence of an extremely diminutive acromion process ("4" in fig. 4) is unambiguously optimized as an autapomorphy of *Ichthyornis*. The acromion in *Ichthyornis* is minute (fig. 37); it does not extend anteriorly beyond the bosslike articular surface for the coracoid (appendix 1, character 103:0). The acromion also does not extend anterior to this articulation in *Chauna torquata* in what is optimized as a separate evolution of this morphology. In all other included taxa for which this character could be scored, the acromion extends well anterior to the articular surface for the coracoid (see appendix 1, character 103, regarding outgroup condition and Hesperornithes).

5. Humerus, bicipital crest, pit-shaped fossa for muscular attachment located directly at the distal end of the bicipital crest ("5" in fig. 4): The condition in *Ichthyornis* is cur-

rently not seen in any other avialan taxa. Considering the fossa/scar seen in Enantiornithes, *Apsaravis ukhaana*, *Ichthyornis*, and Aves on the bicipital crest (see appendix 1, character 115) as potential homologues is different from specifying a transformation series for this morphology. The latter would require that the directly distal position seen only in *Ichthyornis* is a necessary intermediate condition between an anterodistal position seen in more basal taxa (see appendix 1, characters 115, 116) and the posterodistal position in Aves. As the condition in *Ichthyornis dispar* is seen in no other taxon, it is used in the diagnosis. However, because this optimization is currently ambiguous (due to missing data in *Limenavis patagonica* and *Gansus yumenensis* and of uncertain homology with the highly transformed condition in Hesperornithes), this character is not used in the definition of the clade name "*Ichthyornis*" although it is preserved in the holotype of *Ichthyornis dispar* (YPM 1450).

6*. Ulna: the dimensions of the dorsal condyle (appendix 1, character 132) are such that the length of the trochlear surface along the posterior surface of the distal ulna is approximately equal to the width of the trochlear surface taken across its distal end ("6" in fig. 4). While these dimensions are also seen developed within Neoaves (Clarke and Chiappe, 2001) as well as apparently in *Gobipteryx minuta* (Kurochkin, 1996; although this morphology is extremely poorly preserved in that taxon), this character is unambiguously optimized as a local autapomorphy of *Ichthyornis*. All included taxa for which this character could be scored have a dorsal condyle with the posterior extent of the trochlear surface less than its distal width. In the outgroup taxa, the trochlear surface has no extension up the posterior edge of the ulna (see appendix 1, characters 131, 132).

7. Radius: an oval scar located on the posteroventral surface of the distal radius, in the center of a depression (depressio ligamentosa in Aves; Baumel and Witmer, 1993). The depression is also seen in *Ichthyornis*, but no conspicuous oval scar is developed in the included Aves. The ovoid scar ("7" in fig. 4) was not observed in any other avialans. However the posteroventral surface of the

distal radius is not visible in *Apsaravis ukhaana* and not preserved in *Patagopteryx deferrariisi*. A scar appears to be absent in *Baptornis advenus* and *Confuciusornis sanctus*.

8. Carpometacarpus: A large tubercle is developed close to the articular surface for the first phalanx of the second digit where the deep tendinal groove for the m. extensor digitorum communis ends as this tendon passes distally to insert on the first phalanx in the crown clade (Stegmann, 1978). This robust tubercle ("8" in fig. 4) is not present in any of the included Aves, YPM 1734, *Limenavis patagonica*, or more basal taxa where this portion of metacarpal II is preserved (e.g., *Neuquenornis volans* or *Confuciusornis sanctus*). Some Charadriiformes (Stegmann, 1978) have a tubercle in approximately the same position as *Ichthyornis*. Stegmann (1978) related this feature to the attachment of part of the lig. digito-metacarpale, part of which constrains the passage of the m. extensor digitorum communis.

9*. Phalanx II:1: the presence of an internal index process (Stegmann, 1978; appendix 1, character 152:1). An internal index process ("9" in fig. 4) is seen within Neoaves (e.g., Charadriiformes; Stegmann, 1978) but not in any of the avian taxa included in the phylogenetic analyses (i.e., the galloanserine or palaeognath exemplars used; see Part II, Material and Methods). This process is not present in *Iaceornis marshi* (YPM 1734; see below), *Limenavis patagonica* (Clarke and Chiappe, 2001), *Apsaravis ukhaana* (Norell and Clarke, 2001), or more basal taxa (e.g., *Confuciusornis sanctus*, Chiappe et al., 1999; see also appendix 1, character 152:1).

THE SPECIES QUESTION

Across the specimens here referred to *Ichthyornis dispar* (table 1), there is variation in size and in morphology. Future consideration of whether there is more than one species of *Ichthyornis* would depend on rejection of other explanations of the variation among these specimens. As mentioned, these possible explanations include: (1) anagenetic change in a single lineage, (2) sexual dimorphism, and (3) differences due to ontogenetic stage. I have concluded that these explana-

tions of the variation across material referred to *Ichthyornis* cannot currently be rejected. Variation in size and morphology will first be described, and then intralineaage explanations of this variation will be compared to the explanation of observed variation by the presence of distinct species.

VARIATION IN SIZE

There is a considerable range in the size of individuals represented by specimens referred to *Ichthyornis*, but the different sizes do not occur with the same frequency across the YPM material. Only two specimens (i.e., YPM 1738 and YPM 1765) are significantly smaller than the *Ichthyornis dispar* holotype (YPM 1450). And only four other specimens (i.e., YPM 1460, YPM 1462, YPM 1766, and YPM 9148) are approximately the same size as or just slightly smaller than the *Ichthyornis dispar* holotype. That is, of 77 specimens referred to *Ichthyornis*, only two specimens, or 2.6%, are notably smaller than the *Ichthyornis dispar* holotype, four specimens, or 5.2%, are the same size, and 92.2% are larger.

Those YPM specimens slightly larger than the *Ichthyornis dispar* holotype include, for example, YPM specimens 1730, 1733, 1749, 1756, and 1764. However, the majority (85.7%) of the YPM material referred to *Ichthyornis* is significantly larger than the *Ichthyornis dispar* holotype. Most of these specimens were previously referred to "*Ichthyornis victor*" and include, for example, YPM specimens 1447, 1452, 1457, 1461, 1720, 1721, 1722, 1725, 1729, 1737, 1741, 1742, 1747, 1748, 1750, 1755, 1757, 1762, 1763, 1773, and 1775.

The data presented in table 3 as well as figures 5–9 are not suggestive of the presence of distinct size classes, but rather a near continuum of differently sized individuals. A more detailed morphometric analysis would rigorously explore whether there are distinct size classes to be discriminated.

The width and depth of the distal humerus were compared for the only four undistorted YPM specimens (fig. 5). The smallest undistorted distal humerus (YPM 1738) measured (table 3) is one of the two YPM specimens significantly smaller than the *Ichthyornis dis-*

TABLE 3
Size of Specimens Referred to *Ichthyornis*: Measurements of the Humerus
in mm and as a Percentage of the Largest Individual

Specimen number	Total length (complete humeri only)		Maximum distal width (undistorted humeri only)		Maximum distal depth (undistorted humeri only)	
	mm	Percent of YPM 1742	mm	Percent of YPM 9685	mm	Percent of YPM 9685
YPM 1738	?	?	7.4	63%	4.3	65%
UA 18456	53.5	75%	?	?	?	?
YPM 9148	58	81%	?	?	?	?
YPM 1450	58.4	82%	9.4	80%	5	76%
YPM 1730	61.4	86%	?	?	?	?
YPM 1756	61.4	86%	?	?	?	?
TMM 42522-1	?	?	10.1	86%	?	?
YPM 1764	?	?	10.3	88%	5.7	86%
TMM 31051-25	62.5	87%	a	?	?	?
TMM 31051-24	63.8	89%	a	?	?	?
USNM 22820	?	?	10.5	90%	?	?
YPM 1447	71.1	99%	?	?	?	?
YPM 1742	71.5	100%	?	?	?	?
YPM 9685	?	?	11.7	100%	6.6	100%

^aMeasurements of “distal width” reported by Parris and Echols (1992) were not included as it is unclear whether they are equivalent to those taken here.

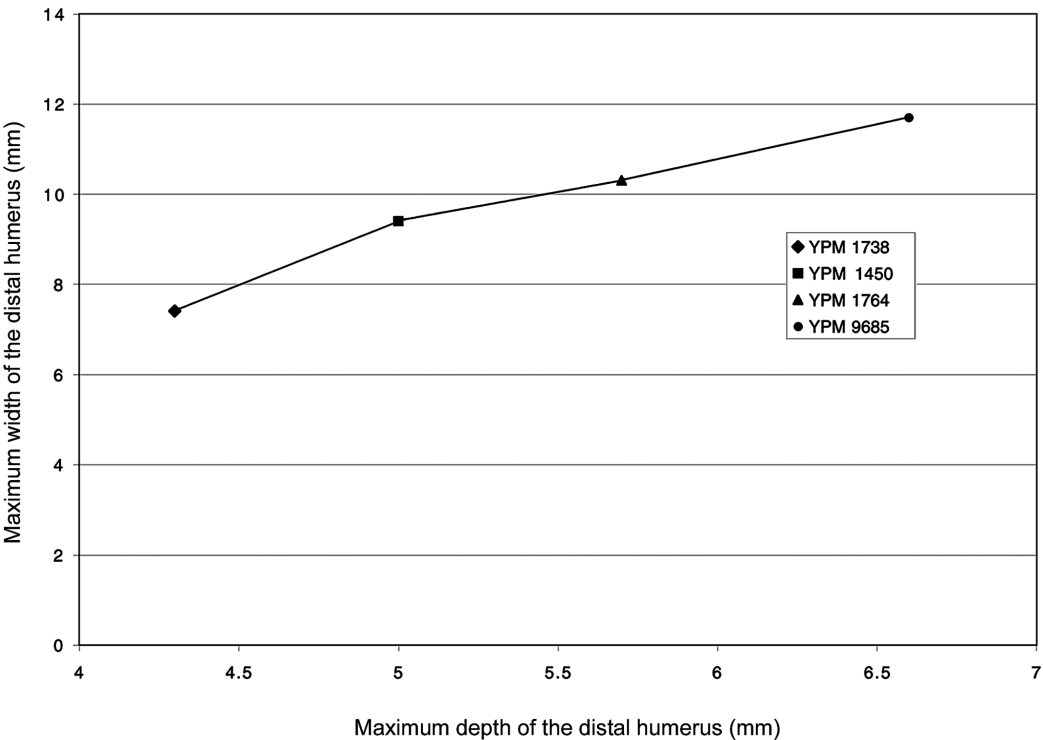


Fig. 5. Distal humeral dimensions (in millimeters) of four uncrushed YPM *Ichthyornis dispar* specimens (YPM 1450, YPM 1464, YPM 1738, YPM 9685).

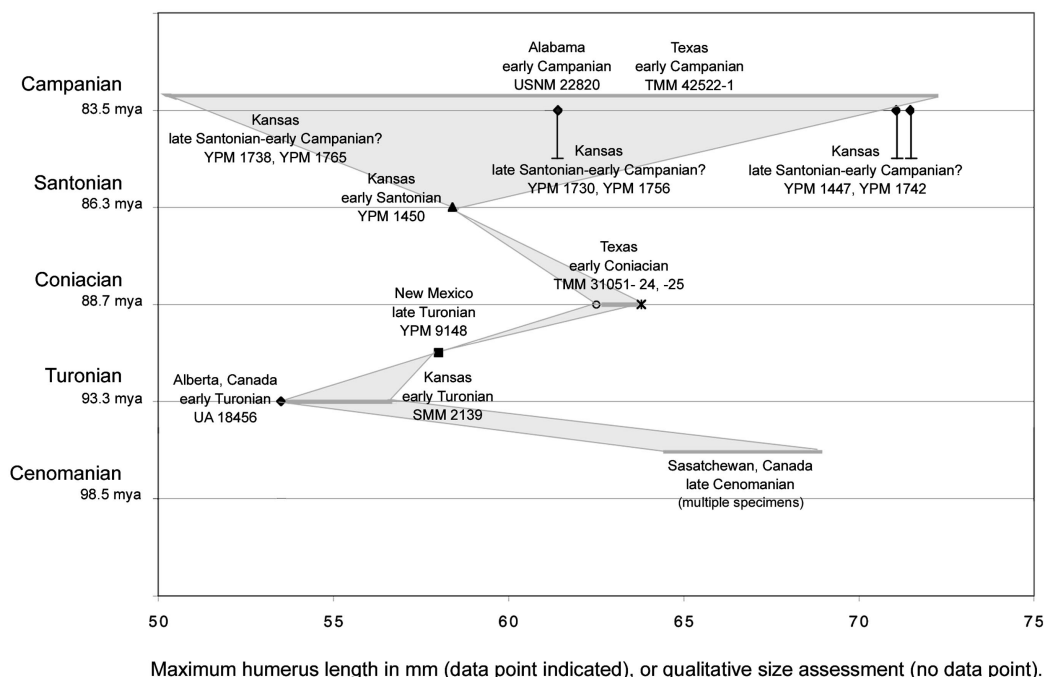


Fig. 6. Size and stratigraphic position of individuals referred to *Ichthyornis dispar* interpreted as anagenetic change. Data points represent total humerus length of the indicated specimen(s) in millimeters. The relative size of specimens without data points, those lacking complete humeri, was estimated (i.e., YPM 1738, 1765, SMM 2139, USNM 22820, TMM 42522-1, and Cenomanian specimens, SMNH P2077.67, SMNH P2077.111, SMNH P2077.112, SMNH P2487.5). Shaded regions indicate size variation for each time period interpreted as anagenetic change in a single lineage.

par holotype (YPM 1450). The undistorted humerus of YPM 1764 is slightly larger than the *Ichthyornis dispar* holotype; it plots between the holotype of *Ichthyornis dispar* (YPM 1450) and the largest undistorted specimen, YPM 9685 (table 3; fig. 5). YPM 9685 is approximately the same size as the majority of preserved YPM specimens. Based on comparison of the distal humeral dimensions of the two smallest undistorted humeri to the largest (YPM 9685), one of the two smallest specimens in the YPM material (YPM 1738) is 63–65% of the largest depending on what measurement is compared (table 3). By contrast, the *Ichthyornis dispar* holotype (YPM 1450) is 76–82% of the largest specimen compared (YPM 9685, or YPM 1742 in the case of total humeral length; table 3).

Placing the size of specimens in the context of time allows the investigation of anagenetic change as an explanation for some or

all of the size differences among the material. Specimens referred to *Ichthyornis* have been described from the late Cenomanian through the early Campanian, an interval of more than 10 million years. The specimens referred from the late Cenomanian (Tokaryk et al., 1997) are all significantly larger than the *Ichthyornis dispar* holotype. However, the three next oldest (Turonian) specimens referred to *Ichthyornis*, one from the early Turonian of Alberta (Fox, 1984) and Kansas (Martin and Stewart, 1982), as well as from the late Turonian of Texas (Lucas and Sullivan, 1982), are all notably smaller than or approximately the same size (figs. 6, 7) as the holotype of *Ichthyornis dispar* (YPM 1450). The oldest specimen is the smallest of the three (figs. 6, 7). Two slightly later specimens (TMM 31051-24, TMM 31051-25) from the early Coniacian of Texas (Parris and Echols, 1992; table 3) are slightly larger than YPM 1450. All of this material is smaller

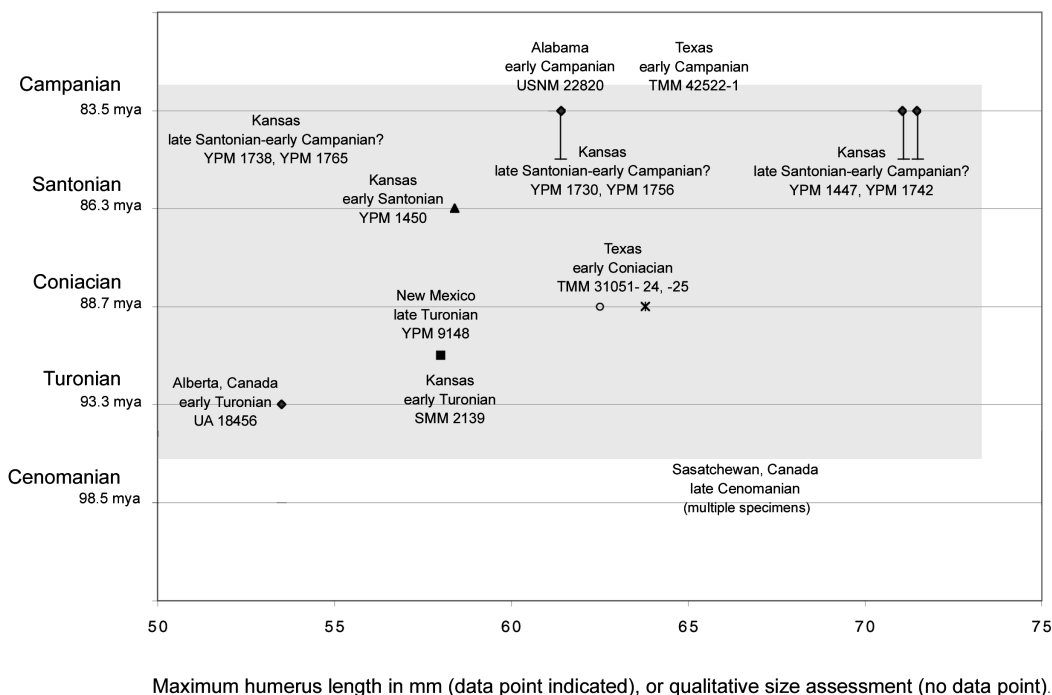


Fig. 7. Size and stratigraphic position of individuals referred to *Ichthyornis dispar* interpreted as variable sampling through time of a constant size range for a single species. Data points represent total humerus length of the indicated specimen(s) in millimeters. The relative size of specimens without data points, those lacking complete humeri, was estimated (i.e., YPM 1738, 1765, SMM 2139, USNM 22820, TMM 42522-1, and Cenomanian specimens, SMNH P2077.67, SMNH P2077.111, SMNH P2077.112, SMNH P2487.5). Shaded region indicates size variation interpreted as constant through time.

than the majority of the YPM material, for which more precise age estimates are generally not possible.

Unfortunately, there is almost no detailed stratigraphic information for the YPM *Ichthyornis* material collected from the Smoky Hill Chalk Member. Only a few YPM specimens referred to *Ichthyornis* have locality information more detailed than, for example, “Wallace County, Kansas” (YPM VP Catalogue). The entire Smoky Hill Chalk Member of the Niobrara Formation is upper Coniacian–lower Campanian in age (Stewart et al., 1990), and specimens of *Ichthyornis* have been estimated to be present in all recognized intervals of the Chalk (Stewart, 1990). However, Bennett (1990) concluded that, historically, nearly all of the fossil vertebrates, including the YPM material, were collected in the upper part of Smoky Hill Chalk Member from between Marker Unit 15 and 20 of Hattin (1982). Stewart (1990) estimated the in-

terval containing Hattin’s (1982) Marker Units 8–10 to be upper Santonian in age. Marker Units 15–20 must therefore be, at the earliest, from later in the upper Santonian through the early Campanian. Thus, the majority of the YPM material would appear to be from the late Santonian–early Campanian.

By contrast, the holotype of *Ichthyornis dispar* (YPM 1450) appears to be early Santonian in age: Bardack (1965) specified the locality of the holotype within Rooks County (see *Ichthyornis dispar* below), and this locality was mapped in the *Cladoceramus undulatoplicatus* by Stewart (1988). The “Zone of *Cladoceramus undulatoplicatus*” was given as early Santonian in age by Stewart (1990: 22). The top of this zone was dated more precisely by $^{40}\text{Ar}/^{39}\text{Ar}$ as 84.88 ± 0.28 Ma, which is in the late Santonian (Obadovich, 1993). Thus, more than 80% of the YPM *Ichthyornis* material is significantly

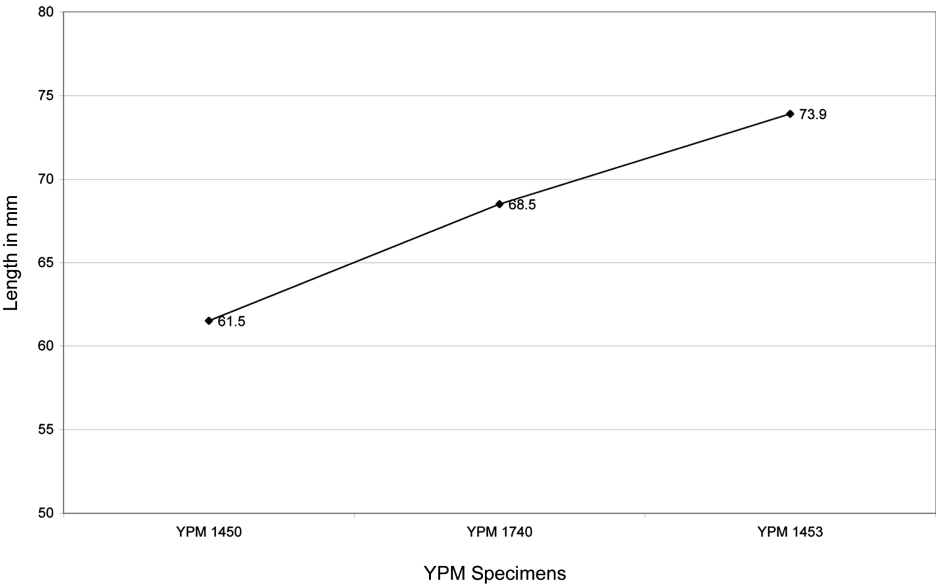


Fig. 8. Total ulnar length (in millimeters) compared for the only complete YPM *Ichthyornis dispar* ulnae (YPM 1450, YPM 1453, YPM 1740).

larger, and inferred as younger, than the holotype of *Ichthyornis dispar*.

Figures 5–7 summarize the data discussed above. Shading in figure 6 illustrates an explanation of the size-through-time data as anagenetic change, and figure 7 illustrates this

data as differential sampling through time of a consistent size range. Measurements of the six complete humeri in the YPM collection were taken (table 3). These measurements, taken from the material itself, differ from those given in Marsh (1880) and Lucas and

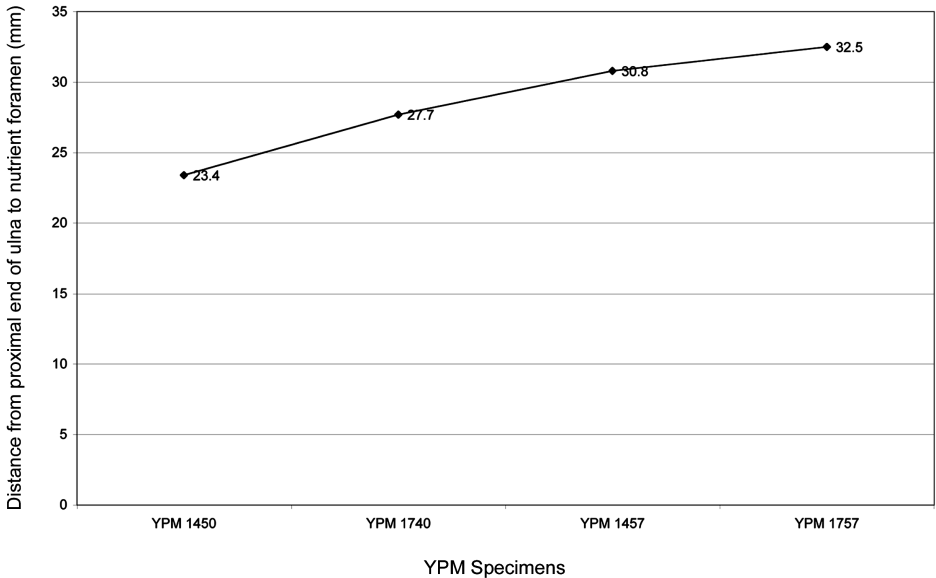


Fig. 9. Distance from the proximal end of the *Ichthyornis dispar* ulna (YPM 1450, YPM 1453, YPM 1740, YPM 1757) to the nutrient foramen (in millimeters).

Sullivan (1982). Other published measurements of complete humeri referred to *Ichthyornis* from the other localities mentioned above were also included (i.e., Fox, 1984; Parris and Echols, 1992). Further, qualitative estimates of the size of several additional specimens referred to *Ichthyornis* that do not include complete humeri but have comparatively good constraint on their age were also included. For example, a proximal carpo-metacarpus (SMM 2139) referred to *Ichthyornis* (although it preserves no apomorphies) from the early Turonian of Kansas (Martin and Stewart, 1982) was included. It is approximately the size of the *Ichthyornis dispar* holotype (YPM 1450; Clarke, personal obs.). The comparative sizes of the holotype of *Ichthyornis antecessor* from the Campanian of Alabama (Olson, 1975) and two specimens referred to that taxon from the Campanian of Texas (Parris and Echols, 1992) plotted in figures 6 and 7 were based on comparisons of published measurements for the distal humeri that comprise these specimens to comparable measurements of complete YPM humeri.

There is also slightly more precise locality data for one of the four specimens the size of the *Ichthyornis dispar* holotype. This specimen, YPM 1460, was collected at Twin Butte Creek, a well-known locality representative of the upper part of the Smoky Hill Chalk Member (Stewart et al., 1990). Bennett (1990) measured seven stratigraphic sections along Twin Butte Creek and identified the interval represented to be between Marker Unit 15 and 19 of Hattin (1982); this is the same interval as the majority of vertebrates from the Chalk (Bennett, 1990) and, presumably, the majority of the YPM *Ichthyornis* material. Indeed, YPM 1209 is approximately the size of 80% of the YPM material and also was also collected at Twin Butte Creek (e.g., Marsh, 1880).

Stewart (1990: 22) reported *Ichthyornis* "c.f. *Ichthyornis anceps*" and a "smaller species" as present in his late Coniacian "*Spinaptychus* n. sp." zone. This reference is cryptic, as the holotype of "*Ichthyornis anceps*" is a specimen from a large individual comparable in size to most of the YPM material. However, the one specimen referred to "*Ichthyornis anceps*" is from an individ-

ual midsize between the *Ichthyornis dispar* holotype and the size of most of the YPM material. All that can be gleaned from this information is that individuals of different sizes are present at this earlier time as well (i.e., lower in the Smoky Hill Chalk Member). However, measurements of these individuals were not reported in Stewart (1990).

In sum, there appears to be no evidence of individuals as large as more than 80% of the YPM *Ichthyornis* material from older deposits from the Smoky Hill Chalk Member (figs. 6, 7). There is some evidence that smaller individuals (i.e., the size of the *Ichthyornis dispar* holotype), in low abundance, are present in the upper part of the Smoky Hill Chalk Member where most of the material is large. The only known Cenomanian specimens (Tokaryk et al., 1997) are significantly larger than the *Ichthyornis dispar* holotype, while all of the Turonian specimens (Lucas and Sullivan, 1982; Fox, 1984; Clarke, personal obs.) are smaller than or the same size as the early Santonian *Ichthyornis dispar* holotype.

VARIATION IN MORPHOLOGY

YPM specimens showing morphological differences from the holotype of *Ichthyornis dispar* were divided into two kinds: (1) difference in specimens otherwise supported by other evidence as part of *Ichthyornis* and (2) difference in specimens not supported by other evidence as part of *Ichthyornis*. For the four YPM specimens not supported as part of *Ichthyornis* (table 2), noted differences were used to identify specimens for inclusion as separate terminal taxa in the phylogenetic analyses (Part II). A description of these four specimens (listed in table 2) and evaluation of their taxonomic status is provided below in the Taxonomic Revision.

Subtle variation that appears to represent intraspecific variation is seen among specimens referred to *Ichthyornis*. A large ovoid scar on the distal end of the anterior surface of the deltopectoral crest (e.g., YPM 1461, YPM 1720, YPM 1742) and a smaller scar just anterodorsal to the humeral head appear to be more pronounced in larger specimens (e.g., YPM 1742) as does a scar on the distal radius, character 7 from the diagnosis of *Ich-*

thyornis. These scars are commented on in more detail in the Anatomical Description. In addition, Olson (1975) reported a nutrient foramen just proximal to the dorsal condyle of the humerus in *Ichthyornis dispar* and *Ichthyornis antecessor*. It is also developed in other YPM humeri (e.g., YPM 1748, YPM 1764) but may not be present in all (e.g., YPM 9685) and can vary slightly in position and development. In the *Ichthyornis dispar* holotype, the foramen is conspicuous on the right but not on the left humerus. These subtle differences were observed in multiple YPM specimens.

The only other morphological variation observed in YPM material referred to *Ichthyornis* was observed only in single specimens. Nine YPM specimens show such differences. These specimens, the morphological differences noted, and the basis for referral to *Ichthyornis dispar* are listed in table 4. Unfinished bone at the ends of the ulna that comprises YPM 1740 suggests that it may be an immature individual. It is intermediate in size between the *Ichthyornis dispar* holotype and the large specimens that are the majority of the YPM material. YPM 1774 is a large coracoid (i.e., the size of the majority of the material) with what appears to be a pathology; the glenoid facet has an irregular boss of bone on its posterolateral edge and slopes smoothly into the corpus.

EVIDENCE FOR THE PRESENCE OF DISTINCT ONTOGENETIC STAGES

There is some evidence for the presence of individuals of different ontogenetic stages in the YPM material referred to *Ichthyornis*. In the *Ichthyornis dispar* holotype, septa between most of the posterior alveoli of the mandible are thickened and completely formed. By contrast, in several specimens larger than the *Ichthyornis dispar* holotype, these septa are thin or apparently absent (e.g., YPM 1735, YPM 1749, SMM 2503). However, in both the *Ichthyornis dispar* holotype and in these larger specimens, most of the bones of the mandible appear to be fused.

In YPM 1733, a midsized specimen larger than the *Ichthyornis dispar* holotype but smaller than the majority of the YPM material, the intercentrum of the atlas is complete-

ly fused to the body of the axis: No suture is visible. However, in the larger YPM 1775, which is the same size as the majority of the YPM *Ichthyornis* material, this suture is incompletely obliterated. Finally, as mentioned above, YPM 1740 is an ulna intermediate in size between the *Ichthyornis dispar* holotype and larger individuals, and is possibly subadult, based on the bone surface texture of its ends.

All specimens (with the exception of YPM 1740) appear to be adult. Muscle scars are well developed on all bones and some, as noted, appear more pronounced in the material larger than the *Ichthyornis dispar* holotype. All known carpometacarpi, tibiotarsi, and tarsometatarsi are completely fused. All skull bones, with the possible exception of the frontoparietal contact, are fused in both the *Ichthyornis dispar* holotype and the apparently just slightly larger YPM 1728.

CONCLUSIONS

Several possible conclusions can be drawn about the number of species represented in the *Ichthyornis* material from the variation in size, morphology, and ontogenetic stage. First, it must be emphasized again that the specimens referred to *Ichthyornis* do not sample contemporaneous individuals. Specimens referred to *Ichthyornis* have been described from the late Cenomanian–lower Campanian, a period of approximately 15 million years. Furthermore, even if the majority of the YPM specimens are only from the upper Santonian–lower Campanian, this interval still represents several million years. The individual represented in the holotype of *Ichthyornis dispar*, collected from the lower Santonian, may have existed as many as a million years earlier than the majority of YPM specimens.

Explanation of some of the observed variation in size by anagenetic change may be supported by apparent size variation across time (fig. 6; although see an alternative explanation of the data as differential sampling through time [fig. 7]). While the distribution of referred material from the Cenomanian is all significantly larger than the early Santonian holotype of *Ichthyornis dispar*, all Turonian referred specimens are smaller than or the

TABLE 4
Nine YPM Specimens Exhibiting Morphological Differences from the Holotype of *Ichthyornis dispar* and/or Other Specimens Referred on the Basis of Apomorphy

Specimen number	Morphological difference	Size	Support for referral to <i>Ichthyornis dispar</i> ^a
YPM 1446	groove developed at medial exit of <i>n. supracoracoideus</i> foramen; sculptured bone at glenoid and scapular cotyla; lack of strong groove at posterodorsal exit of <i>n. supracoracoideus</i> foramen	largest coracoid represented	morphological correspondence
YPM 1732	twelve sacral vertebrae	large pelvis and hind limb	morphological correspondence
YPM 1738	<i>m. scapulotriceps</i> groove may be slightly more developed for its size	smallest humerus represented	morphological correspondence
YPM 1745	no nutrient foramen in dorsal surface of coracoid	large coracoid	morphological correspondence
YPM 1749	mandible may be more delicate than in the specifier of <i>Ichthyornis</i> with smaller alveoli although it is associated with a humerus slightly larger than the holotype of <i>Ichthyornis dispar</i>	humerus slightly larger than the holotype of <i>Ichthyornis dispar</i>	5
YPM 1755	carpometacarpus may be disproportionately short for size of individual	large humerus	5, 6, 8
YPM 1765	the medial margin of the dorsal surface has a slightly more projected mark at what is interpreted as part of the attachment of the sternocoracoclavicular membrane (Baumel and Raikow, 1993) than in the holotype of <i>Ichthyornis dispar</i>	smallest coracoid represented	morphological correspondence
YPM 1766	the facet for articulation with the sternum appears to extend farther up the ventral surface and is slightly more curved than in the holotype of <i>Ichthyornis dispar</i>	slightly smaller than the holotype of <i>Ichthyornis dispar</i>	morphological correspondence
YPM 1774	irregular boss of bone on edge of glenoid facet; deformation of the edge of the glenoid facet	large coracoid	morphological correspondence

^aNumbers 5, 6, and 8 refer to numbered apomorphies of *Ichthyornis dispar* listed in the Diagnosis.

same size as the *Ichthyornis dispar* holotype. The latest specimens (late Santonian–early Campanian) include the largest specimens, which are significantly larger than the holotype of *Ichthyornis dispar*. If the Cenomanian-referred material is borne out as *Ichthyornis*, there may be a sharp decrease in size across the Cenomanian–Turonian boundary. This may be consistent with anagenetic change tracking environmental degradation associated with a global biotic event that has been recognized in marine environments (Raup and Stepkoski, 1986) and isotopic ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) fluctuations (Kyser et al., 1993).

However, within the comparatively short period of time represented in the Smoky Hill

Chalk Member, there is variation in size: A small individual, approximately the size of the *Ichthyornis dispar* holotype, and a larger one the size of the majority of referred specimens are copresent in the upper part of the Smoky Hill Chalk Member, and two specimens in the YPM Smoky Hill material are smaller than the earlier (Turonian) material. Anagenetic change within a single lineage, thus, does not appear sufficient to explain all observed variation in size.

This “residual” variation may be explained by the presence of more than one species of *Ichthyornis* or as intraspecific variation. At this time, the latter explanation cannot be rejected. Indeed, because of the distribution of morphological differences

among the YPM specimens referred to *Ichthyornis*, and because other Mesozoic avialan species show gross differences in size among referred individuals (Houck et al., 1990; Chiappe et al., 1999), this hypothesis is currently considered the more strongly supported.

Two forms of intraspecific variation are specifically considered here: difference due to ontogenetic stage and due to sexual dimorphism. Generally, there is little information on intraspecific variation in size or morphology (polymorphism) for Mesozoic avialan species to contextualize the variation seen in *Ichthyornis* because most of these species are known from single specimens. However, for the few species that are known from multiple specimens, considerable variation in size among individuals has been described. For example, both *Archaeopteryx lithographica* (Houck et al., 1990) and *Confuciusornis sanctus* (Chiappe et al., 1999) are known from multiple specimens that show a considerable range in size. In *Archaeopteryx lithographica*, the largest (Solnhofen) exemplar is roughly twice the size of the smallest (Eichstätt; Houck et al., 1990). In *Confuciusornis sanctus*, Chiappe et al. (1999) noted that the length of the humerus from the smallest specimen sampled was approximately 60% the length of the humerus of the largest specimen considered. The smallest humerus of the YPM specimens (table 3) is approximately 63% percent of the largest while that of the *Ichthyornis dispar* holotype is approximately 80% of the largest individual measured (table 3). However, only 2 specimens of the total 77 referred are this small, while most of the variation is between 80% and 100% of the largest specimen. Thus, while size variation as extreme as that observed in *Confuciusornis sanctus* is represented in the YPM material, the majority of the variation is less extreme than in that taxon or in *Archaeopteryx*.

Houck et al. (1990) explained the variation in *Archaeopteryx* as a growth series by presenting morphometric data, indicating that the known specimens scale allometrically. These authors further suggested that all *Archaeopteryx* specimens might represent subadult individuals, as all lack the compliment of fusions seen in adult coelurosaurs (Houck

et al., 1990). Chiappe et al. (1999) also considered the size variation in *Confuciusornis sanctus* to represent a growth series. Other authors, with reference to the *Ichthyornis* material, have considered individuals even slightly different in size to be parts of distinct species (e.g., Olson, 1975). Apparently, this is because a comparatively minute difference in size is all that appears to distinguish some crown clade species, and size within species is often assumed to be near invariant for adults of crown clade species. It has also been generalized that birds reach adult size in weeks to months after hatching (de Ricqlès et al., 2001). However, because *Ichthyornis* lies outside the avian crown clade it cannot, without additional evidence, be justifiably inferred to have grown like a living bird (Gauthier and de Queiroz, 2001). That certain muscle impressions in the YPM *Ichthyornis* material appear more strongly developed in larger specimens appears consistent with these larger individuals being more mature. Furthermore, plots (figs. 5, 8, 9) of the differently sized individuals in *Ichthyornis* appear closer to a continuum than to support the presence of distinct size classes.

As noted above, nearly all of the *Ichthyornis* specimens appear adult or nearly adult as indicated by the fused elements, muscle impressions, and bone texture that subadult Aves often lack. Wang et al. (2000) conducted a statistical analysis of several hundred specimens of *Confuciusornis sanctus* and concluded that all of these specimens were of adult individuals. These observations would appear inconsistent with the interpretation of the variation in size in both taxa as representing a growth series.

Some histological studies have been taken to indicate that a shift to an avian pattern of rapid sustained growth occurred phylogenetically after *Patagopteryx deferrariisi* (as well as *Enantiornithes* and *Confuciusornis sanctus*), and before *Hesperornis regalis* and *Ichthyornis* (Chinsamy et al., 1998). This conclusion was based on the apparent absence in *Hesperornis regalis* and *Ichthyornis* of lines of arrested development (LAGs) and on the presence of highly vascular primary bone (Chinsamy et al., 1998). At least one LAG was interpreted as present in *Patagopteryx deferrariisi* and a sampled enantiornithine

(Chinsamy et al., 1995). However, this hypothesis has been critiqued more recently, as the significance of LAGs, as well as their known distribution, has been reappraised (de Ricqlés et al., 2001). Furthermore, the notion that an avian growth pattern is seen in *Hesperornis regalis* and *Ichthyornis* is considered speculative (Castanet et al., 2000). Complicating the interpretation of the data from histological studies, the single humerus of *Ichthyornis* so far sampled has been considered possibly subadult (Chinsamy et al., 1998; de Ricqlés et al., 2001). Indeed, that this element was apparently not assessed to be subadult (which would make it less than ideal for sampling) based on morphology alone is suggestive that other *Ichthyornis* specimens, previously assumed to be fully mature individuals, may also be subadult.

Rapid rates of growth during some part of ontogeny have been associated with highly vascularized primary bone that is seen not only in basal avian taxa (Castanet et al., 1996, 2000) but in nonavian dinosaurs (Horner et al., 2001). However, it has been postulated that histological evidence from basal avialans suggests that some part of their ontogeny involved a slow growth phase and that they may have taken longer to reach adult size (de Ricqlés et al., 2001). This conclusion is consistent with the size ranges described for *Archaeopteryx* and *Confuciusornis sanctus* (de Ricqlés et al., 2000, 2001) and might explain the size variation observed in *Ichthyornis*. We appear to be early in developing understanding of the evolution of dinosaur ontogeny, and further study of the histology of noncrown clade avialans is necessary to document the changes that occur in growth pattern (de Ricqlés et al., 2001). Planned future histological work investigating samples from *Ichthyornis* should provide key insights into whether small and large individuals are, indeed, all adult. This data is essential to resolving the number of species represented in the YPM *Ichthyornis* material and to determining when, phylogenetically, the growth pattern seen in Aves (in which adult size is achieved in a matter of weeks to months) arose. Currently, the explanation of the variation in size present among the YPM *Ichthyornis* material as distinct growth stages, perhaps within a protracted slow

growth phase, fits histological data and is consistent with data from more basal Mesozoic avialans. If minute variation in size is considered to distinguish distinct species, it is not currently clear where the lines distinguishing these size classes could be meaningfully drawn.

While the variation in size among the YPM specimens appears largely explained by some anagenetic change and by individuals at different growth stages, it may not explain the three cases described above: (1) the axis is preserved in two specimens, and the larger of the two (YPM 1775) has an open suture that is closed in a slightly smaller specimen (YPM 1733); and (2) the septa separating the posterior alveoli of the dentary tooth row in the *Ichthyornis dispar* holotype are fully formed while in larger specimens (e.g., YPM 1735), they appear slightly more weakly developed or absent. Finally, unfinished bone at the ends of an ulna (YPM 1740) suggest it is from a very young individual, but the ulna is larger than that of the *Ichthyornis dispar* holotype. These data may suggest the presence of at least two species. However, we do not have data that any of the mentioned specimens represent nearly contemporaneous individuals. Furthermore, to compare the case of the axis and the ulna: The first case involves a specimen that falls nearly exactly intermediate in size between the *Ichthyornis dispar* holotype and the majority of the YPM *Ichthyornis* material and that appears adult relative to a larger individual. In the case of the ulna, a specimen that is, again, squarely intermediate in size appears to be from a very young individual. Thus, the signal from these cases is not clear. Even if two species were present, intermediary-sized material could potentially belong to either, and for other specimens, ontogenetic clues are not available. It is also possible that this variation is anagenetic at a finer scale than that discussed, with small scale climatic variation causing fluctuations in adult size or growth rates. On the basis of geochemical (%CaCO₃, %Al, %organic carbon) logs, gamma-ray logs, and bedding couplets, Pratt et al. (1993) identified four cycles in Niobrara Formation (Fort Hays Limestone and Smoky Hill Chalk Members) with estimated periodicities of 1.7 m.y. (30-m cycles),

280 k.y. (5-m cycles), and 100 k.y. (2-m cycles) and 41 k.y. for the bedding couplets. The 41 k.y. and the 100 k.y. periodicities are close to expected periodicities of the precession and eccentricity of the earth's orbit (Pratt et al., 1993) and may reflect cyclic variation in the depositional environment. Pratt et al. (1993) concluded that proximate causes of such cycles transcribed in the sediment record were changes in regional climate and paleo-oceanographic conditions, both of which would be expected to impact the local fauna; food supply and surface water temperatures have been shown to relate to intraspecific differences in adult body size in an array of avian taxa (e.g., Graves, 1991; Leafloor et al., 1998). However, even if the YPM specimens are assumed to represent contemporaneous individuals (contra limited stratigraphic information available), an explanation other than the presence of more than one species lineage is plausible.

Sexual dimorphism in size is a widespread phenomenon in Aves, having arisen many times and ranging from minor to extreme difference in size. Although sexual size dimorphism appears highly homoplastic across Aves, the presence of dimorphism in size in palaeognaths and galloanserines (del Hoyo et al., 1992–1999) suggests it may be ancestral to Aves. Furthermore, although dimorphism in size has not been investigated for *Confuciusornis sanctus*, there is evidence of sexual dimorphism in plumage (Chiappe et al., 1999). A variety of nonavian dinosaurs has also been described as possibly sexually dimorphic in the development of particular morphologies or as having gracile and robust morphs (e.g., Chapman et al., 1997). Sexual dimorphism in growth rates and growth duration is frequently documented in birds (reviewed in Teather and Weatherhead, 1994). Recent studies have found that in avian species in which males are larger than females, they may reach adult size after females (Badyaev et al., 2001). The growth rates of different traits and the duration of different growth phases varied in their relative time of onset between males and females (Badyaev et al., 2001).

The difference in size between the *Ichthyornis* individuals discussed is comparatively minimal. In the more extreme of the two cas-

es discussed, the axis with the closed suture is approximately 85% the size of that of the larger individual. This would yield a difference between these individuals in a ratio of larger/smaller of 1.18. This is well below the most extreme instances of dimorphism in Aves where, for example, in one icterid (Paseriformes) the male/female ratio for wing measurements is 1.33 (Webster, 1997), a value approached by a variety of other avian taxa (e.g., *Tetrao urogallus*, Galliformes: 1.30 for the wing and *Otis tarda*: Gruiformes: 1.27 for the wing; K. Zyskowski, personal commun.). Sexual size dimorphism in the extinct dodo (*Raphus cucullatus*) and solitary (*Pezophaps solitaria*; Livezey, 1993: table V) is also close to or exceeds size difference among *Ichthyornis* specimens (e.g., ratio of humerus length in “males”/“females”: 1.10 and 1.30, respectively) and these differences were similarly considered by some early workers to be evidence of distinct species (Livezey, 1993).

The morphological variation noted in single specimens (table 4) is not considered sufficient to merit the recognition of distinct species. Discovery in additional specimens of any of the morphological variants described, especially if associated with additional differences from the morphologies of the holotype of *Ichthyornis dispar*, may form the basis for recognizing distinct species of *Ichthyornis*. Variation in a variety of morphological characters has been noted across *Confuciusornis sanctus* specimens (e.g., in the development of the sternal midline ridge, fusion of the dentaries, and possible presence of uncinat processes; Chiappe et al., 1999). These differences, like those observed in the *Ichthyornis* material, may be related to the presence of individuals of differing ontogenetic stages or sexes among the material. To assume that in a sample of specimens representing individuals from across millions of years there would be no variation, even as minor as that described, would seem unrealistic.

Two previously named species referred to the genus *Ichthyornis* (Marsh, 1880) are not part of the clade *Ichthyornis* (see Part II, Results). *Apatornis celer* Marsh, 1873a (Marsh, 1873b) is recognized as a valid taxon. The holotypes of *Ichthyornis tener* Marsh, 1880,

Ichthyornis lentus Marsh, 1877b (Marsh, 1880), and *Apatornis celer* Marsh, 1873a (Marsh, 1873b), are differentiated from *Ichthyornis dispar* and were discovered more closely related to or part of Aves or placed as part of Aves in the phylogenetic analyses (Part II, results). The species epithets “*tener*”, “*lentus*”, and “*celer*” as well as the name “*Apatornis*” are converted in the context of a system of phylogenetic taxonomy (de Queiroz and Gauthier, 1990, 1992; Cantino and de Queiroz, 2000). Two new clades are named to which *tener* and *lentus* are designated internal specifiers. The one specimen previously referred to *Apatornis celer* (YPM 1734) cannot be compared to the holotype of *Apatornis celer* (YPM 1451) and is designated as the holotype of a new species. The five remaining previously named species of *Ichthyornis* are junior synonyms of *Ichthyornis dispar*, as mentioned above. Descriptions are provided of the holotypes of all previously named and newly identified species. Commentary is provided on the prior referral of specimens to these species. With reference to previously-named species that are recognized as junior synonyms of *Ichthyornis dispar*, the descriptions and commentary given support the synonymy of these species and serve as a resource for future work.

Most specimens previously referred to species of *Ichthyornis* and *Apatornis* cannot be compared to the holotypes of these species. Indeed, many of the referrals appear to have been largely arbitrary. Even if some of the species names synonymized with *Ichthyornis dispar* are found to be valid, almost without exception, the previous referral of specimens to these taxa will not. Size appears to have been the basis for the referral of the majority of specimens to *Ichthyornis victor*; however, even this criterion appears to have been inconsistently applied. For example, Marsh (1880) referred YPM 1733 to *Ichthyornis victor*, while a specimen of approximately the same size (YPM 1764) was referred to *Ichthyornis dispar* (Olson, 1975).

SPECIES RECOGNIZED AS JUNIOR SYNONYMS
OF *ICHTHYORNIS DISPAR* MARSH 1872b

Ichthyornis anceps

Graculavus anceps (Marsh, 1872a) was named several months before *Ichthyornis*

dispar (1872b) and was later referred to *Ichthyornis* (Marsh, 1880). *Graculavus anceps* is not the name-bearer of the taxon “*Graculavus*” and, thus, the name of the species was changed to *Ichthyornis anceps* (Marsh, 1880). The specimen number of the holotype was not given in the original publication but was later specified (Marsh, 1880).

HOLOTYPE SPECIMEN: YPM 1208 is a poorly preserved distal end of a left carpometacarpus (fig. 10A).

LOCALITY AND HORIZON: Marsh (1872a) indicated that the holotype was collected on the North Fork of the Smoky Hill River. Marsh (1880: 198) later specified that he collected the holotype in 1870 on the North Fork “about twelve miles east of Fort Wallace, Kansas.” Bardack (1965) gave its provenance as Section 11 or 13, Township 13 S, Range 36 W. Again, it is unclear how this more precise information was ascertained.

DISCUSSION: A brief description of the specimen was provided when it was named as the holotype specimen of *Graculavus anceps* (Marsh, 1872a). *Graculavus* was a genus Marsh (1872a) allied with extant cormorants (Phalacrocoracidae). *Graculavus anceps* was supposed to be differentiated from *Graculavus velox*, the type species of *Graculavus*, by the articular surface for the “external digit [metacarpal II] broader and nearly flat”, that of the “internal digit [metacarpal III] considerably smaller and oval in outline”, and the “intervening tubercle [which would be part of the articular surface for metacarpal II] more prominent” (Marsh, 1872a: 364). This specimen corresponds in all preserved morphologies, including those mentioned in Marsh’s (1872a) differentia above, to those preserved in the holotype of *Ichthyornis dispar*. The specimen also has a diagnostic character preserved in the holotype of *Ichthyornis dispar* (Diagnosis, character 8). For these reasons, and because it differs only in size from the holotype of *Ichthyornis dispar*, it is recognized as a junior synonym of that taxon. Size is not considered sufficient to diagnose distinct species in this analysis.

If, however, *Ichthyornis victor* (a taxon here also synonymized with *Ichthyornis dispar*, see below) were determined in the future to be a valid species with one of its an-

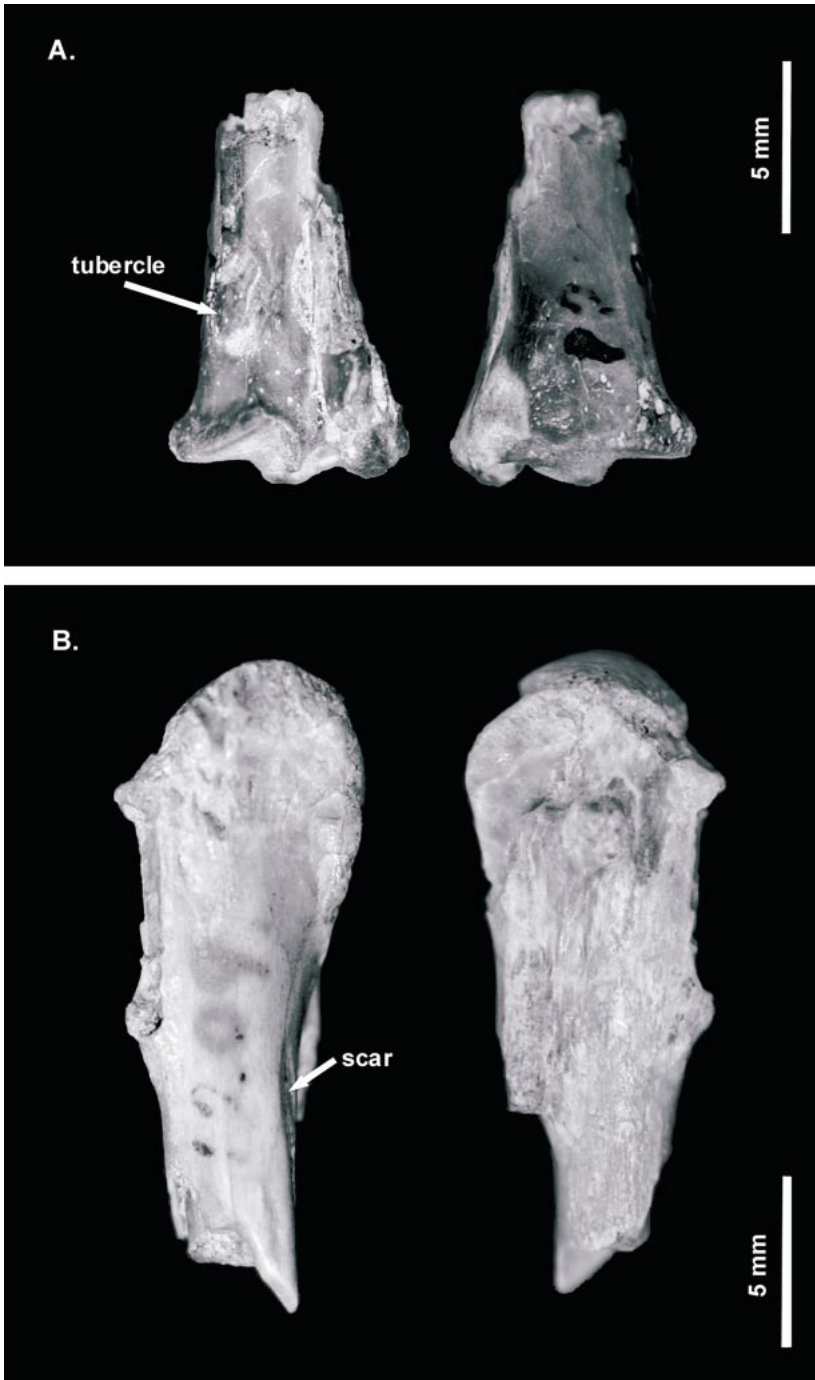


Fig. 10. The (A) *Ichthyornis anceps* (YPM 1208) and (B) *Ichthyornis agilis* (YPM 1209) holotype specimens in dorsal (right) and ventral (left) views. YPM 1208 and YPM 1209 are partial distal and proximal carpometacarpi, respectively.

cillary diagnostic features being larger size, *Ichthyornis anceps* must be a junior synonym of that taxon. Marsh (1880) published measurements of the holotype specimen that appear to have been intended to discriminate it based on size from *Ichthyornis victor*. The difference in the “greatest diameter of the distal end” (Marsh, 1880:156) was given as 6.75 for YPM 1208 and 7.6 for that referred to *Ichthyornis victor* (YPM 1724; Marsh, 1880). However, YPM 1208 is badly crushed and missing most of the distal portion of metacarpal III, making this comparison meaningless. Indeed, if the anteroposterior width of the relatively undistorted midpoint of the distal end is compared instead, the specimens are nearly identical in size (3.4 mm for YPM 1208 vs. 3.5 mm for YPM 1724). The dorsal process of the holotype is broken, leading to an apparent, but artificial, difference in the development of the anterodorsal edge of the trochlea of metacarpal II.

REFERRED SPECIMENS: The only specimen referred to *Ichthyornis anceps* is YPM 1749 (Marsh, 1880: 124). As YPM 1749 consists only of a partial humerus and mandible that cannot be compared to the carpometacarpus holotype of *Ichthyornis anceps*, this referral is considered baseless.

Ichthyornis agilis

Graculavus agilis (Marsh, 1873c) was named shortly after *Ichthyornis dispar* (Marsh, 1872b) and was subsequently referred to *Ichthyornis* (Marsh, 1880). It was described in two short sentences, and a holotype specimen was not named in the publication. The holotype specimen was not mentioned to be a proximal carpometacarpus, and the differentiation provided of *Graculavus agilis* from *Graculavus anceps* (Marsh, 1873c) is unsupported, primarily because the two holotypes are nonoverlapping parts of a left carpometacarpus that cannot be directly compared.

HOLOTYPE SPECIMEN: YPM 1209, a proximal left carpometacarpus lacking metacarpal I (fig. 10B).

LOCALITY AND HORIZON: Marsh (1880) specified that he collected YPM 1208 from Butte Creek in 1872. Butte Creek, also

known as Twin Butte Creek, is a well-known locality of what is now Logan County, Kansas, in the Smoky Hill Chalk Member, Niobrara Formation (Stewart et al., 1990), representing beds between Marker Units 15 and 19 (Bennett, 1990) of Hattin (1982). Stewart (1990) estimated that the interval containing Hattin’s (1982) Marker Units 8–10 to be upper Santonian in age. Thus, because Marker Units 15–19 are above these units, they must be from, at the earliest, later in the upper Santonian (than Marker Units 8–10) or from the lower Campanian. The top of the Smoky Hill Chalk Member is early Campanian in age (Stewart et al., 1990).

DISCUSSION: Marsh (1873c: 230) originally distinguished *Graculavus agilis* as a somewhat smaller species than *Graculavus anceps* with more “slender” metacarpals and lacking a “carpal fossa”. The holotype, however, does not appear to be smaller or more delicately built than the holotype of *Ichthyornis anceps*, so far as the widths of the metacarpals can be compared. As mentioned above, however, no part of the holotype of *Ichthyornis agilis* can be directly compared with the holotype of *Ichthyornis anceps*, which is a distal, as opposed to a proximal, carpometacarpus.

There are no identified diagnostic characters from the proximal end of the carpometacarpus identified for *Ichthyornis dispar*; thus, as indicated in table 1, YPM 1209 is referred by morphological correspondence. The morphologies of the pisiform process, as well as the configuration of muscle scars on the posterior surface of metacarpal II and anteroventral surface of metacarpal III, correspond with those preserved in the other carpometacarpi referred to *Ichthyornis dispar* (see table 1). The carpal trochlea superficially appears shorter anteroposteriorly and wider than in the best preserved referred carpometacarpus, YPM 1724. However, the proximal end of YPM 1724 is crushed dorsoventrally, while the *Ichthyornis agilis* holotype is crushed in the opposite direction, as betrayed by a prominent ridge visible crossing the carpal trochlea dorsoventrally. The *Ichthyornis dispar* holotype itself does not preserve the proximal end of the carpometacarpus.

The *Ichthyornis agilis* specimen differs in

size from *Ichthyornis dispar*. It is approximately the size of specimens referred to *Ichthyornis dispar* by apomorphy that are, by comparison, as large as the individual represented by the holotype of the synonymized *Ichthyornis victor*. For example, the dorso-ventral width of the shaft of metacarpal II is 3.9 mm both for the holotype of *Ichthyornis agilis* and for a specimen here referred by apomorphy to *Ichthyornis dispar* (but previously referred to *Ichthyornis victor*; YPM 1724). However, as discussed above, size is not considered to diagnose distinct species of *Ichthyornis* without further information on, for example, the ontogenetic stage and stratigraphic position of the preserved individuals. If, in the future, *Ichthyornis victor* were recognized as a valid taxon, with larger size as an accessory diagnostic character, the holotypes of *Ichthyornis victor* and *Ichthyornis agilis* would both appear to be specifiers of the same species (distinct from *Ichthyornis dispar*). In that case, the following question would have to be resolved: the name “*Ichthyornis agilis*” (Marsh, 1873c) was coined prior to “*Ichthyornis victor*” (1876), but may be *nomen dubium* because of a lack of diagnostic features and the invalid differentia used at its naming (Marsh, 1873c).

REFERRED SPECIMENS: Marsh (1880) referred only an isolated ulna (YPM 1453) to this taxon. As this specimen cannot be compared to the holotype, there is no evidence to support this referral.

Ichthyornis victor

Ichthyornis victor was named by Marsh (1876) and differentiated from the holotype of *Ichthyornis dispar* (YPM 1450) as being one-third larger than that species (Marsh, 1876).

HOLOTYPE SPECIMEN: YPM 1452 includes a proximal right coracoid, proximal right scapula, and three fragments of a poorly preserved left humerus (fig. 11). As discussed in the Historical Background, some or all of the material incorporated into the YPM *Ichthyornis victor* panel mount frequently appears to have been mistaken for holotype of *Ichthyornis victor*. The YPM Catalogue entry for YPM 1452 included the phrase “Ma-



Fig. 11. The *Ichthyornis victor* holotype (YPM 1452), which includes (A) two fragments of the left humerus (anterior view), (B) the left proximal scapula (dorsal view), and (C) the left proximal coracoid in medial view.

por portions of skeleton” for most of the 20th century.

LOCALITY AND HORIZON: Marsh (1880: 199) reported that YPM 1452 was “found in May 1876, by Mr. H. A. Brous, in Wallace County, Kansas.” No locality information was given in the original description of the species (Marsh, 1876), while the listing in Marsh (1880) was repeated in Brodkorb (1967).

DISCUSSION: Several morphologies described for the holotype (Marsh, 1876) but not used to differentiate it are also present in the holotype of *Ichthyornis dispar*. These are now known to be ancestral for more inclusive avialan clades (e.g., expanded deltopectoral crest and dorsal humerus condyle larger than the ventral; see appendix 1: characters



Fig. 12. The *Ichthyornis validus* holotype (YPM 1740), a right ulna: (A) the distal end in dorsal view and (B) the complete element in ventral view.

113, 125). Only humeri can be directly compared between the holotypes of *Ichthyornis dispar* and *Ichthyornis victor* and, while they are different in size, there are no appreciable differences in morphology. The morphology of YPM 1452 is discussed in the Anatomical Description.

REFERRED SPECIMENS: The majority of YPM specimens were referred (Marsh, 1880) to this species (see table 1).

Ichthyornis validus

Ichthyornis validus was named in *Odonotornithes*. The holotype was not described, differentiated, or diagnosed, although it was figured (Marsh, 1880: pl. XXX, figs. 11–14).

HOLOTYPE SPECIMEN: YPM 1740 is a nearly complete right ulna (fig. 12). Brodkorb (1967) noted the holotype to be comprised of an ulna and radius; however, no radius is currently known to exist for this specimen. Marsh (1880) also did not mention a radius as part of this specimen. Additionally, the original YPM label of the specimen mentions only an ulna, as does the unpublished YPM catalogue undertaken by Thorpe (1937).

LOCALITY AND HORIZON: The holotype is described (Marsh, 1880: 198) as being “discovered in September, 1877, by Mr. S. W. Williston, near the Solomon River in north-

western Kansas.” Brodkorb (1967) further specified that it was from Graham County, Kansas, information also listed as part of the original label associated with the specimen.

DISCUSSION: The holotype of *Ichthyornis validus* (YPM 1740) is considered subadult primarily because of the unfinished bone on the epiphyses. Compatible with this interpretation are the comparatively weakly developed follicular ligament scars and lack of detail in the morphology of the distal condyles and muscular attachments. It is intermediate in size between specimens corresponding to the majority of the YPM material and the holotype of *Ichthyornis dispar* (figs. 9, 10). This intermediate size can clearly be seen if the distance between the nutrient foramen and the proximal tip of the olecranon is compared or if total ulnar length is compared (fig. 10). The length of the ulna in *Ichthyornis dispar* is 61.5 mm (Marsh, 1880, reported 62.0 mm); in YPM 1740 it is 68.5 mm (consistent with Marsh, 1880); and YPM 1453 measures 73.8 mm (Marsh, 1880, reported 75.0; fig. 9). YPM 1453, an isolated ulna, is inferred to be the size of the *Ichthyornis victor* holotype, and the size of the majority of the YPM specimens through comparison with a third specimen, YPM 1757, which has elements overlapping those of the *Ichthyornis victor* holotype that are the same size.

If a larger species is recognized associated with further evidence concerning how *Ichthyornis* grew, the holotype of *Ichthyornis validus*, as a subadult individual of a larger species, would probably be recommended as a junior synonym of the named larger species (e.g., *Ichthyornis victor*). Further discussion of the significance of this specimen is presented in the Taxonomic Revision, in the section Evidence for the Presence of Distinct Ontogenetic Stages.

REFERRED SPECIMENS: An isolated partial coracoid (YPM 1446) was referred to this taxon. There is no evidence to support this referral to *Ichthyornis validus* as it cannot be compared to the holotype. This large coracoid is notably larger than the holotype of *Ichthyornis validus*. Thus, these two specimens do not have even relative size in common.

Ichthyornis antecessor

Plegadornis antecessor was named by Wetmore (1962) based on a distal humerus. Kashin (1972) noted that *Plegadornis* was preoccupied, and changed the name to *Angelinornis antecessor*. Olson (1975) used characters shared by *Ichthyornis* and *Angelinornis antecessor* to synonymize the latter genus and refer the specimen to *Ichthyornis*, but still recognized it as a valid species, *Ichthyornis antecessor*.

HOLOTYPE SPECIMEN: USNM 22820 is a left distal humerus and was illustrated in Olson (1975).

LOCALITY AND HORIZON: USNM 22820 is from the top of the Mooreville Formation just below the base of the Arcola Limestone Member (Selma Group; Wetmore, 1962) at Hewletts Farm, Greene County, Alabama (Parris and Echols, 1992). The Mooreville Formation has been inferred to be approximately the same age as or slightly younger than the uppermost deposits represented in the Niobrara Formation (Martin and Stewart, 1982) and early Campanian in age (Parris and Echols, 1992).

DISCUSSION: Olson (1975) listed characters differentiating *Ichthyornis antecessor* relative to a specimen he referred to *Ichthyornis dispar* (YPM 1764), pending a revision of *Ichthyornis* he mentioned as being undertak-

en by Pierce Brodkorb (Olson, 1975). Such revision was never completed. The differentia from YPM 1764 consisted of the following: shaft of *Ichthyornis antecessor* not as heavy; brachial depression shallower and slightly more distal; dorsal supracondylar process more prominent and a pit at its base, shallower (Olson, 1975). The attachment of the anterior articular ligament (lig. collaterale ventrale) was also, tentatively, considered to be different.

However, YPM 1764 clearly differs in size and several minor features of muscular attachment (like those mentioned in the differentia of *Ichthyornis antecessor*) from the holotype of *Ichthyornis dispar* (YPM 1450). Thus, it is a less than ideal proxy to have been used for the holotype of *Ichthyornis dispar*. The shaft of the holotype of *Ichthyornis dispar* is also more slender, or less "heavy", than YPM 1764. The distal width in YPM 1450 is 9.4 mm as opposed to the 10.5 mm of YPM 1764 and USNM 22820. The other characters noted in the differentia are very minor differences in muscular attachments that could be attributed to intraspecific variation. A pit at the base of the dorsal supracondylar process described of *Ichthyornis antecessor* is present in the *Ichthyornis dispar* holotype and other referred YPM *Ichthyornis dispar* specimens. Because the holotype of *Ichthyornis dispar* is from the Santonian, while that of *Ichthyornis antecessor* is from the Campanian, it is possible that slight differences in muscular attachment (if they can be confirmed to be other than individual variation) are due to anagenetic change within a single lineage. *Ichthyornis antecessor* is, therefore, considered a junior synonym of *Ichthyornis dispar*.

REFERRED MATERIAL: TMM 42522-1 is a distal humerus referred to *Ichthyornis antecessor* (Parris and Echols, 1992). It seems to have been referred to *Ichthyornis antecessor* because it was approximately the same age as the holotype (Campanian), but it was also judged to match closely the morphology of the holotype. However, on the points of morphological comparison noted, the specimen is equally like the holotype of *Ichthyornis dispar* and specimens referred to that species. TMM 42522-1 is smaller than the holotype of *Ichthyornis antecessor*; the measure of the

width of the distal end is 10.1 mm as opposed to 10.5 mm in the holotype. The same measure of the holotype of *Ichthyornis dispar* is 9.5 mm, making TMM 42522-1 intermediate in size between the holotype of *Ichthyornis dispar* and that of *Ichthyornis antecessor*.

ET 4396 (L85-6) is a proximal left carpo-metacarpus described by Parris and Echols (1992). As these authors mentioned, it cannot be compared to the holotype of *Ichthyornis antecessor*. It was referred to *Ichthyornis antecessor* because the humerus from the same formation was referred to that species and is from younger deposits than all named *Ichthyornis* species other than *Ichthyornis antecessor* (Parris and Echols, 1992). The fragment was also supposed to differ from other *Ichthyornis* material in several features of metacarpal I. However, nearly half of metacarpal I is missing and the mentioned attributes could not be confirmed. The carpo-metacarpus was also supposed to be more gracile than the Niobrara *Ichthyornis* material to which it was compared (although this material is not identified). The other noted differences between the figured specimen and YPM specimens, here referred to *Ichthyornis dispar*, were not confirmed. The absence of a groove on the carpal trochlea and other figured morphologies correspond with those in YPM specimens referred to *Ichthyornis* by apomorphy, but it does not preserve any characters used in the diagnosis of *Ichthyornis dispar*.

OTHER VALID SPECIES NOT SUPPORTED AS PART OF *ICHTHYORNIS* OR *ICHTHYORNITHES*

Guildavis (new clade name)

DEFINITION: “*Guildavis*” is here defined as a stem-based name (de Queiroz and Gauthier, 1992) for the clade including all taxa/specimens more closely related to YPM 1760 (*tener* Marsh, 1880, holotype specimen) than to *Ichthyornis dispar* or the following internal specifiers of Aves (Gauthier and de Queiroz, 2001; see Introduction): *Vultur gryphus*, *Struthio camelus* Linnaeus, 1758, *Tetrao* [*Tinamus*] *major* Gmelin, 1789, and *Vultur gryphus* Linnaeus, 1758.

ETYMOLOGY: “*Guildavis*” is a combination of “Guild”, for E. W. Guild, who col-

lected the holotype of *tener* and internal specifier, YPM 1760, and “*avis*”, the Latin for bird.

tener Marsh, 1880 (converted species name)

DEFINITION: The name “*tener*” Marsh, 1880 is converted and defined as the name for the species that includes YPM 1760 (see the Introduction of the Taxonomic Revision for the definition of “species” used). With its clade address (sensu Cantino et al., 1999), the converted name of this species is “*Guildavis tener*”. The name “*tener*” was originally published in the combination “*Ichthyornis tener*” (Marsh, 1880).

HOLOTYPE SPECIMEN: A specimen indicated by Marsh as the holotype was never figured, described, or diagnosed. YPM 1760, a sacrum (fig. 13), was specified in the following way: “The type specimen (number 1760) of the present species [*Ichthyornis tener*] was found in 1879, by Mr. E. W. Guild in Wallace County, Kansas.” (Marsh, 1880: 198). The locality, date of collection, and collector are that of YPM 1760, which is comprised of the sacrum. However, a humerus (YPM 1738) was figured in *Odontornithes* (Marsh, 1880: pl. XXX, fig. 8) with the name “*Ichthyornis tener*” applied to it and this figure is referenced under the heading “*Ichthyornis tener*” where the species is named (Marsh, 1880: 198). The specimen number of the humerus was not mentioned in the text (Marsh, 1880) as either the holotype or as referred to *Ichthyornis tener*, although another specimen (a coracoid; YPM 1766) was mentioned as referred (Marsh, 1880: 198). The humerus was collected by S. W. Williston in 1877 and, thus, does match the description of the intended type specimen.

Brodkorb (1967) listed YPM 1760, the specimen mentioned by Marsh (1880), as the holotype, but incorrectly described it as an isolated distal humerus. Presumably, Brodkorb (1967) thought that the figured distal humerus (YPM 1738) in *Odontornithes* (Marsh, 1880: pl. XXX, fig. 8), with the name “*Ichthyornis tener*” applied to it, was YPM 1760, as nowhere in the text is it mentioned that YPM 1760 is a sacrum. This confusion points to a fundamental taxonomic

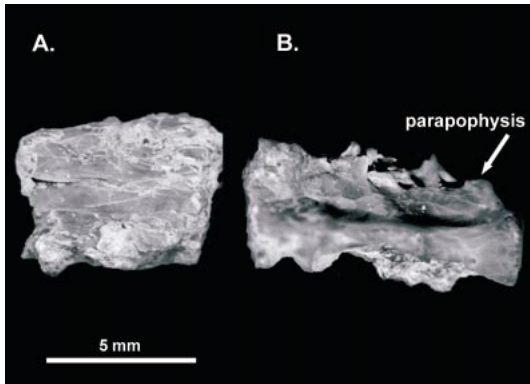


Fig. 13. The holotype specimen of *Ichthyornis* (Guildavis) *tener* (YPM 1760). The holotype is a partial sacrum comprised of crushed portions of (A) the midsacral series (in dorsal view) and (B) the anterior end (in oblique ventrolateral view).

question: whether the name “*tener*” is available and, if so, if it is tied to the humerus figured (YPM 1738) and not to the sacrum (YPM 1760) Marsh (1880) designated as the holotype. Under the ICZN (International Commission on Zoological Nomenclature, 1999; the PhyloCode does not yet address species level names) the name “*Ichthyornis tener*” would be available; its publication satisfies the provisions of Articles 11 and 12. However, it is less clear whether the name is tied to the figured humerus (the illustration clearly constituting an “indication” under Article 12.2.7; International Commission on Zoological Nomenclature, 1999) or the sacrum the specimen number of which is referred to explicitly as the holotype specimen and additionally specified by locality, collection year, and collector.

Here, the explicit designation by Marsh (1880) of YPM 1760 as the holotype of *tener* was followed in the choice of the internal specifier for both “*Guildavis*” and “*tener*” and considered the valid name-bearing specimen under the ICZN (International Commission on Zoological Nomenclature, 1999). While the humerus is supported by morphological correspondence as a part of *Ichthyornis dispar*, the sacrum can be differentiated from *Ichthyornis dispar* and is placed in the phylogenetic analyses as more closely related to Aves than to *Ichthyornis dispar*.

YPM 1760 consists solely of two fragments of a tiny sacrum. One fragment, from the anterior end, preserves the anterior articular surface and the three anteriormost ankylosed vertebrae. The second fragment is from the middle of the sacral series. It is crushed dorsoventrally and no morphologies could be discerned.

LOCALITY AND HORIZON: Marsh (1880: 198) mentioned that YPM 1760 was “found in 1879 by Mr. E. W. Guild in Wallace County, Kansas.” No locality information other than “Cretaceous, Kansas” is provided on the original label associated with the specimen. The humerus (YPM 1738), figured as *Ichthyornis tener* in *Odontornithes* (Marsh, 1880: pl. XXX, fig. 8), but never mentioned in the text as referred to *Ichthyornis tener*, was collected by S. W. Williston “near Monument Rock” two years earlier (i.e., in 1877).

DISCUSSION: *Guildavis tener* is differentiated from the holotype of *Ichthyornis dispar* by the presence of a parapophysis visible on the left side of the completely fused first sacral vertebra. The widths of the iliosynsacral sulci appear greater than in the holotype of *Ichthyornis dispar*. The subcircular anterior articular surface and lateral excavations in the first sacral are shared with the holotype of *Ichthyornis dispar* and referred specimens. YPM 1760 is significantly smaller than the holotype of *Ichthyornis dispar*; the diameter of the anterior articular surface of the first sacral is approximately two-thirds that of the *Ichthyornis dispar* holotype. It is also smaller than the holotype of *Apatornis celer*. However, YPM 1760 cannot otherwise be differentiated relative to *Apatornis celer*; these specimens cannot be compared directly, as the holotype of *Apatornis celer* lacks at least one vertebra from the anterior end of the sacrum and is strongly crushed mediolaterally.

REFERRED SPECIMENS: Marsh (1880: 198) referred a coracoid (YPM 1766) to this taxon and figured a humerus (YPM 1738; Marsh, 1880: pl. XXX, fig. 8) with the name “*Ichthyornis tener*” applied to it. These referrals are considered unsupported as neither specimen can be compared to the holotype. The only feature that the humerus and the holotype share is that they are both conspicuously smaller than *Ichthyornis dispar*. By contrast,

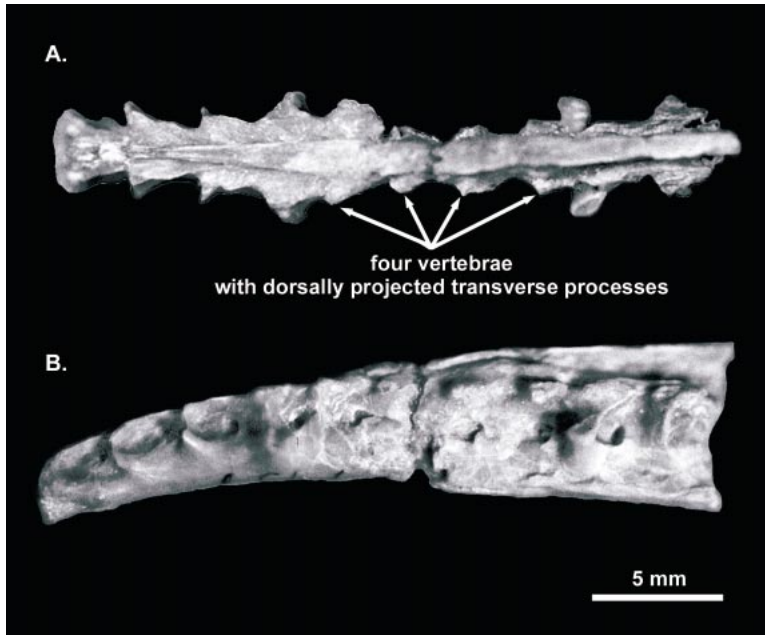


Fig. 14. The *Apatornis celer* holotype (a sacrum; YPM 1451) in (A) dorsal and (B) right lateral views. The sacral series is proximally incomplete.

the coracoid is approximately the same size as that of *Ichthyornis dispar*.

Furthermore, the holotype is not placed as part of *Ichthyornis* when included in analysis (Part II, Results), while the humerus and coracoid are referred to *Ichthyornis dispar* based on the correspondence of preserved morphologies. In the case of the humerus, several correspondent features include: hypertrophied muscle insertions on the dorsal supracondylar process and a narrow intercondylar groove consistent with referral to *Ichthyornis*.

Apatornis Marsh, 1873b (converted clade name)

DEFINITION: “*Apatornis*” Marsh, 1873b is here converted to a stem-based name (de Queiroz and Gauthier, 1992) for the clade including all taxa/specimens more closely related to YPM 1451 (*celer* Marsh, 1873a holotype specimen) than to *Ichthyornis dispar* or the following internal specifiers of Aves (Gauthier and de Queiroz, 2001; see Introduction): *Vultur gryphus*, *Struthio camelus* Linnaeus, 1758, *Tetrao* [*Tinamus*] *major*

Gmelin, 1789, and *Vultur gryphus* Linnaeus, 1758.

celer Marsh, 1873a (converted species name)

DEFINITION: The name “*celer*” Marsh, 1873a is converted and defined as the species that includes YPM 1451 (see the Introduction of the Taxonomic Revision for the definition of “species” used). With its clade address (sensu Cantino et al., 1999), the converted name of this species is “*Apatornis celer*”. This name was originally published in the combination “*Ichthyornis celer*” (Marsh, 1873a) and later in the combination, “*Apatornis celer*” (Marsh, 1873b), when the species was identified as the type species of the genus *Apatornis* (Marsh, 1873b).

HOLOTYPE SPECIMEN: YPM 1451 is a sacrum lacking its proximal end (Marsh, 1880; fig. 14).

LOCALITY AND HORIZON: Marsh (1880: 192) specified that he collected the specimen in October 1872, from Butte Creek, a locality discussed with reference to *Ichthyornis agilis*. Butte Creek, also known as Twin Butte

Creek, is a well-known locality of Logan County, Kansas, in the Smoky Hill Chalk Member, Niobrara Formation (Stewart et al., 1990), representing (Bennett, 1990) beds between Marker Units 15 and 19 of Hattin (1982). Stewart (1990) estimated that the interval containing Hattin's (1982) Marker Units 8–10 was upper Santonian in age. Thus, Marker Units 15–19 must represent, at the earliest, a period of time later in the late Santonian through the early Campanian. The top of the Smoky Hill Chalk Member, close to Marker Unit 23 of Hattin (1982), is in the early Campanian (Stewart et al., 1990).

DISCUSSION: Marsh (1873a) originally differentiated the holotype (YPM 1451) from *Ichthyornis dispar* by more slender proportions and a more deeply concave posterior articular surface on the last vertebra of the sacrum. Neither of these characters was confirmed to differ discernibly in the holotype of *Ichthyornis dispar*. Marsh (1880), however, noted three additional differences from *Ichthyornis dispar* that are confirmed here. First, while both holotypes preserve 10 remnants of transverse processes, indicating the presence of 10 fused sacral vertebrae, that of *Apatornis celer* is incomplete anteriorly (Marsh, 1880: 162). The sacrum of *Apatornis celer* had at least one more fused sacral vertebrae than *Ichthyornis dispar*. Spinal nerve openings visible on the anterior edge of the first preserved vertebra indicate that the series continued anteriorly.

Marsh also commented on a difference in the number of vertebrae with a particular morphology that occurs in approximately the middle of the sacral series (Marsh, 1880: 162–163). There is a difference in the number of sacral vertebrae appearing to lack transverse processes in the middle of the series. The transverse processes appear to be oriented directly dorsally (appendix 1, character 62). *Apatornis celer* has four such sacra between a short, blunt, morphologically distinct transverse process anteriorly and a costal strut at the level of the acetabulum, while *Ichthyornis* (YPM 1450; YPM 1732) has three. In a preliminary survey of extant birds, this count appeared even more conservative than total sacral number.

Finally, Marsh (1880: 163) noted that the *Apatornis celer* holotype does not have co-

ossified tendons expanding “posteriorly over as broad a region [of the dorsal surface of the sacrum] as in *Ichthyornis*.” The last noted difference could also be described as the absence of a fan of ossified tendons in *Apatornis celer* that covers the posterior half of the dorsal surface of the *Ichthyornis dispar* holotype sacrum.

Based on these three characters from Marsh (1880), *Apatornis celer* can be differentiated from *Ichthyornis dispar*. However, the few characters preserved, rather than suggesting that *Apatornis celer* is particularly close to *Ichthyornis dispar* as originally proposed (Marsh, 1873b), place *Apatornis celer* more closely to Aves than to *Ichthyornis* (Part II, Results).

REFERRED SPECIMENS: One specimen (YPM 1734) was referred to *Apatornis celer* (Marsh, 1880). This specimen, because of its completeness, has formed the basis for nearly all of (1) the description of *Apatornis celer* in *Odontornithes* (Marsh, 1880), and (2) the subsequent treatment of *Apatornis celer* in the literature. As no part of YPM 1734 currently overlaps the holotype, there is no evidence to support referral of YPM 1734 to *Apatornis celer* (Clarke, 2000a). YPM 1734 was collected five years after the holotype. The two specimens were found by different collectors in different localities near the Smoky Hill River in western Kansas; the holotype was collected by Marsh from Butte Creek in what is currently called Logan County, while YPM 1734 was collected by F. H. Williston five years later from Gove County (Marsh, 1880: 192).

The pelvis from YPM 1734 is missing and cannot be compared to the holotype. Furthermore, it appears that it was never able to be compared because it is not clear that sacral vertebrae were ever preserved with the pelvis (a situation that occurs with some frequency in basal avialans). The depicted pelvis is shown in lateral view (Marsh, 1880: pl. XXXII, fig. 1) with no part of the sacral vertebrae visible. Thus, even this representation (fig. 15) cannot be compared to the holotype of *Apatornis celer*. Two characters, however, can be compared for the two specimens. Ilium length in YPM 1734 can be roughly compared with the length of the pelvis in the *Apatornis celer* holotype and ap-

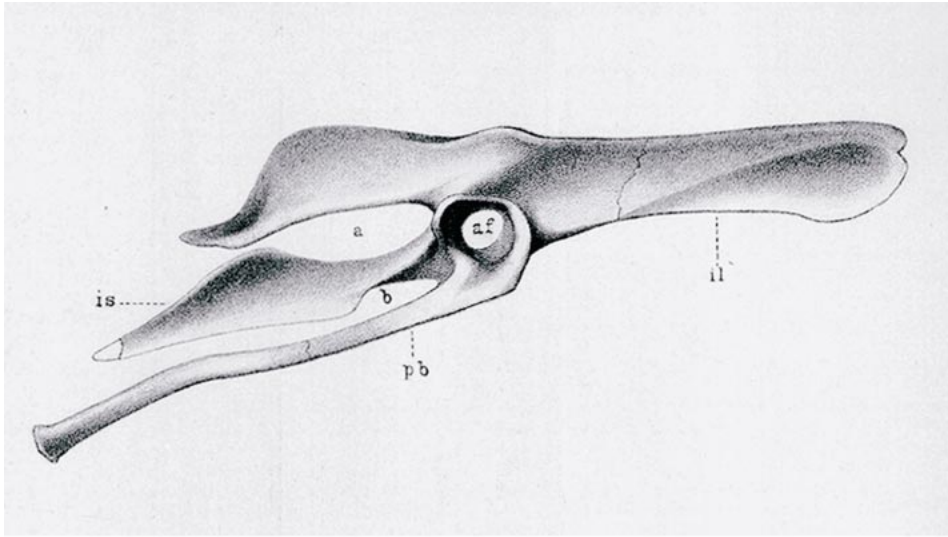


Fig. 15. The pelvic bones of a specimen previously referred to *Apatornis celer* (YPM 1734; the *Iaceornis marshi* holotype) as originally illustrated in right lateral view (Marsh, 1880: pl. XXXII). These elements are missing and could not be examined. Anatomical abbreviations original to Marsh (1880; a: Ischio-sciatic interval, b: obturator interval, af: acetabular foramen, il: ilium, is: ischium, pb: pubis). Figure not to scale.

pears notably longer than the holotype of *Apatornis celer*. The *Apatornis celer* holotype was differentiated from that of *Ichthyornis dispar* by the presence of at least one additional anterior sacral, and Marsh (1880) identified the preacetabular ilium as longer in the pictured pelvis of “*Apatornis*” (i.e., the referred specimen, YPM 1734) than in *Ichthyornis dispar* (YPM 1732). However, even elongation of the preacetabular ilium or anterior part of the sacrum (if these measures are justifiably compared) would not be an apomorphy allying YPM 1734 with *Apatornis celer*; an increase in preacetabular ilium length appears to be an apomorphy of Aves relative to *Ichthyornis* and more basal avian taxa.

Furthermore, measurements were given only from the pelvic bones of YPM 1734, and no sacral vertebrae are mentioned in the text (Marsh, 1880). Whether there was a basis for Marsh’s referral of YPM 1734 to *Apatornis celer* cannot be assessed. Marsh (1880) did not list characters shared by the holotype and YPM 1734 to identify this specimen as a part of *Apatornis celer*. Given that nearly all of the referrals Marsh (1880) made were of specimens that could not be

compared to the holotypes of the species to which they were referred, YPM 1734 might, similarly, not have had any preserved elements in common with the holotype of *Apatornis celer*.

The referral of YPM 1734 to *Apatornis celer* is here considered unsupported, and this specimen is named as the holotype of a new species, *Iaceornis marshi*.

Iaceornis (new clade name)

DEFINITION: “*Iaceornis*” is here defined as a stem-based name (de Queiroz and Gauthier, 1992) for the clade including all taxa/specimens more closely related to YPM 1451 than to *Ichthyornis dispar* or the following internal specifiers of Aves (Gauthier and de Queiroz, 2001; see Introduction): *Vultur gryphus*, *Struthio camelus* Linnaeus, 1758, *Tetrao* [*Tinamus*] *major* Gmelin, 1789, and *Vultur gryphus* Linnaeus, 1758.

ETYMOLOGY: “*Iaceornis*” is a combination of the Latin “*Iaceo*,” figurative for “to be neglected”; “*ornis*” the Greek for bird.

marshi (new species name)

DEFINITION: The name “*marshi*” is defined as the species that includes YPM 1734 (see

the Introduction of the Taxonomic Revision for the definition of “species” used). With its clade address (sensu Cantino et al., 1999), the converted name of this species is “*Iaceornis marshi*”.

ETYMOLOGY: The name “*marshi*” is latinized “Marsh” for O. C. Marsh, who originally described the holotype specimen (Marsh, 1880).

HOLOTYPE SPECIMEN: YPM 1734 includes many postcranial elements: pelvis, both coracoids, both scapulae, proximal end of left clavicle, proximal end of left radius, left ulna and radiale, right carpometacarpus, right phalanges 1 and 2 of manual digit II, proximal and distal fragments of left femur, distal right tibiotarsus, a rib, and miscellaneous unidentifiable fragments (fig. 16). Many of these elements are figured throughout *Odontornithes* and the elements generally match their representations. However, the preservation of material differs from its representation in the following ways: on the sternum, the posterior end of the keel is not preserved, and the posterior margin is almost entirely missing; the right coracoid is missing the prominent lateral process figured; and the left scapula lacks its distal end.

Additionally, neither the right fibula (Marsh, 1880: pl. XXXIII, fig. 5) nor the complete pelvis figured by Marsh (1880: pl. XXXII, fig. 1) are currently among the YPM 1734 material. These elements were not located during an inventory of all *Ichthyornis* and *Apatornis* YPM specimens. Elzanowski (1995) noted that the pelvis was not among the YPM 1734 material, and it seems that the element was missing by the time of Hildegaard Howard’s (1955) publication on *Telmabates antiquus*. That is, Howard (1955: 6) refers to the now missing pelvis “as depicted by Marsh” while her comments on other elements indicate direct examination of the original material (e.g., Howard, 1955: 17).

Martin (1987) described the humerus in “*Apatornis*” and features it shared with that of *Ambiortus dementjevi*; however, no humerus is known, or was ever described, for either the holotype of *Apatornis celer* or for the previously referred YPM 1734. Martin (1987) also discussed amphicoelous cervical vertebrae in *Apatornis celer*; however, no

cervical vertebrae are known from either the holotype of that species or from YPM 1734.

DIAGNOSIS: Two autapomorphies were identified in the phylogenetic analysis: a strongly tapering, or pointed, omal tip of the furcula (character 82) and a hooked scapular acromion process (character 104). Character 82 is also seen within Aves (e.g., in *Anseriformes*) and character 104 is seen in *Apsaravis ukhaana* (Norell and Clarke, 2001) and *Lithornis* (Houde, 1988). See appendix 1 for further commentary on the distribution of these characters.

DIFFERENTIA: *Iaceornis marshi* is differentiated from *Ichthyornis dispar* (see specimen numbers listed in the Anatomical Description of *Ichthyornis dispar* below) by the following characters. (These are intended to serve as a preliminary description of the specimen.)

Sternum (fig. 16B): By contrast to the sternum in *Ichthyornis dispar*, conspicuous raised intermuscular ridges are developed parallel to the midline keel although these are not visible in the illustration in *Odontornithes* (Marsh, 1880: pl. XXIX, fig. 8). The coracoidal sulci are crossed but do not overlap as extensively as in *Ichthyornis dispar* (Marsh, 1880). The midline anterior edge of the sternum (i.e., the sternal rostrum) is markedly less projected than in *Ichthyornis dispar*.

Coracoid (fig. 16A): The glenoid facet is more concave rather than flat and located entirely anterodorsal to the scapular cotyla. Contra illustrations in Marsh (1880), the shaft of the coracoid does not appear strongly deflected medially (e.g., Marsh, 1880: pl. XXIX, figs. 5, 6). The area of the dorsal surface of the coracoid, which serves as the attachment of the m. sternocoracoideus in Aves (Baumel and Witmer, 1993), is markedly more concave.

Scapula (fig. 16D): The acromion process is elongate, with a small lateral projection at its tip (not figured in *Odontornithes*). The shaft tapers much more distinctly posteriorly (Marsh, 1880: pl. XXXIX, figs. 1–3).

Radius (fig. 16G): Matches closely its illustration in *Odontornithes* (Marsh, 1880: pl. XXX, figs. 1–4). The area of the insertion of the m. biceps brachii in Aves (Baumel and Raikow, 1993) is conspicuously more prox-

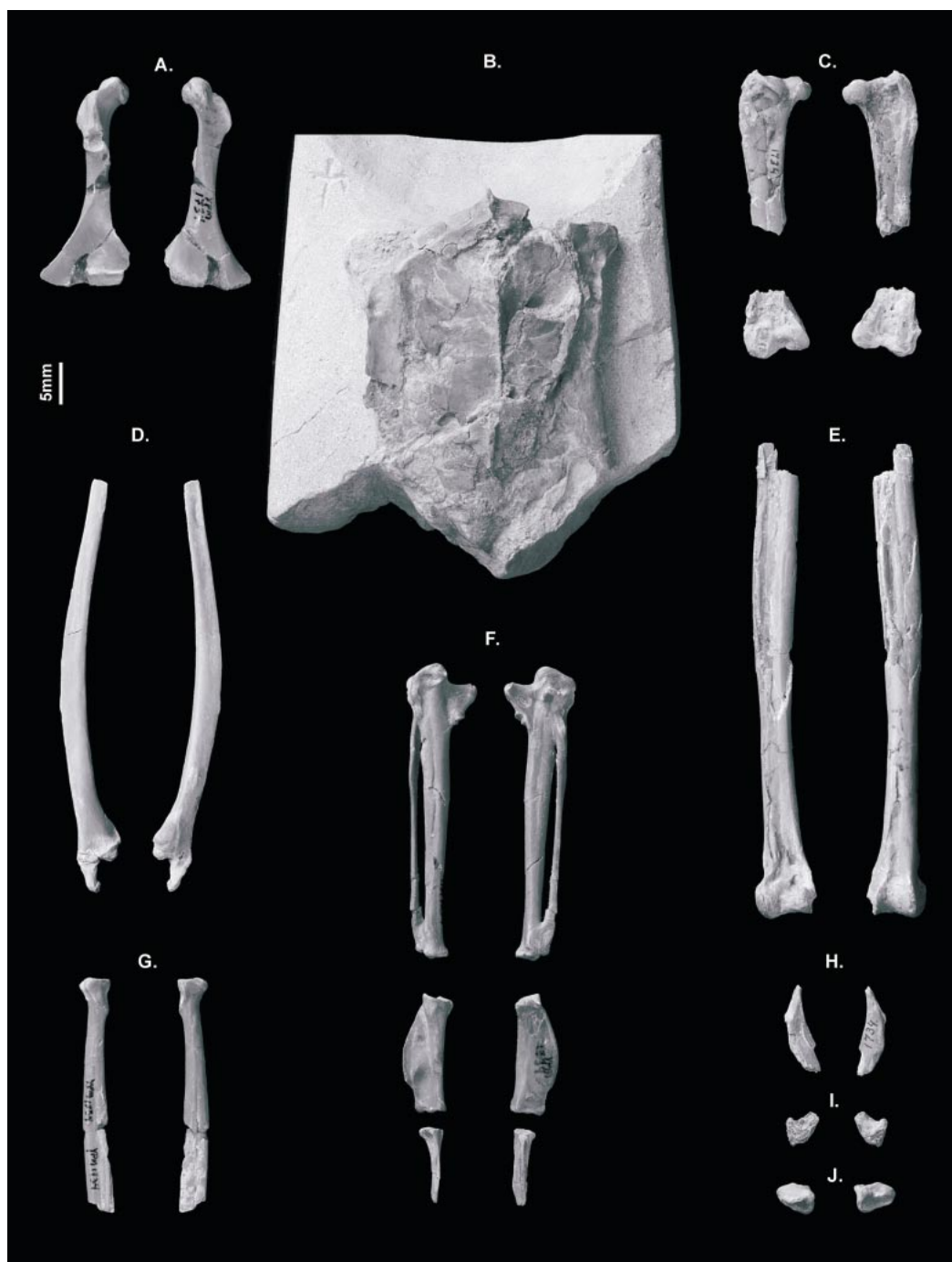


Fig. 16. The holotype specimen of *Iaceornis marshi* (YPM 1734) is comprised of a partial postcranium: (A) left coracoid in (left) dorsal and (right) ventral views, (B) sternum in ventral view, (C) proximal and distal ends of left femur in (left) posterior and (right) anterior views, (D) left scapula in (left) dorsal and (right) ventral views, (E) right tibiotarsus in (left) anterior and (right) posterior views, (F) right carpometacarpus, manual phalanges II:1 and II:2 in (left) dorsal and (right) ventral views, (G) left radius in (left) dorsal and (right) ventral views; (H) left omal tip of furcula; (I) left ulnare in (left) anterior and (right) posterior views; and (J) left radiale in (left) dorsal and (right) ventral views.

imally located. The proximal articular facet for the ulna is demarcated by a distal ridge. The capital tuberosity is smaller, nearer the humeral cotyla, and the muscular ridge that lies just distal to it is shorter.

Carpometacarpus (fig. 16F): Metacarpal I (Marsh, 1880: pl. XXXI, figs. 1–4) is proportionally shorter than the corresponding element in *Ichthyornis dispar*. The carpal trochlea is grooved posteriorly. The proximal end of metacarpal I projects anteriorly a distance approaching the anteroposterior width of the carpal trochlea. By contrast, *Ichthyornis dispar* has metacarpal I projected less than the anteroposterior width of the carpal trochlea. The extensor process is more pointed and projects anteriorly well past the distal articular surface for manual phalanx I:1. The extensor groove does not curve markedly posteriorly and its distal terminus is not demarcated by a large tubercle. The dorsal process is not as well projected as *Ichthyornis dispar*. Neither the prominent intermuscular ridge on the anteroventral edge of metacarpal II nor the ovoid scar on the proximodorsal surface of this element is developed.

Manual phalanx II:1 (fig. 16F): The internal index process developed in *Ichthyornis dispar* is absent (Marsh, 1880: pl. XXXI, figs. 5–8), and the posterior edge of this element is slightly notched distally. The more proximal of the two prominent scars on the dorsal surface of the anterior edge is only slightly demarcated, unlike the conspicuous ovoid scar in *Ichthyornis dispar*.

Pelvis (fig. 15): In the brief description of the missing pelvis, Marsh (1880: 164) remarked that it was generally similar in “form and proportions” to that of *Ichthyornis dispar*, as represented by YPM 1732, but that the pubis was longer than in *Ichthyornis dispar* (Marsh, 1880: 164). Currently, however, the pubis is not preserved in any YPM *Ichthyornis dispar* specimen and could not be compared even to the figure of the YPM 1734 pelvis. The following aspects of the pelvis commented on in *Odontornithes* (Marsh, 1880) do not, however, differentiate the specimen from *Ichthyornis dispar* and could not be confirmed: preacetabular ilium longer than the postacetabular, the acetabulum perforate, ilium and ischium not coossified to close the ilioischadic fenestra, and

pubis longer than the ischium. These morphologies are visible in the illustration of the pelvis (Marsh, 1880: pl. XXXII, fig. 1).

Femur (fig. 16C): As Marsh (1880) noted, the femur appears to have been more robust than in *Ichthyornis dispar*. It also differs from *Ichthyornis dispar* by the presence of a prominent, pit-shaped muscle scar on the lateral edge of the ventral surface proximal to the fibular trochlea. It may correspond to the insertion of the impression of the ansae iliofibularis in Aves (Baumel and Witmer, 1993).

Tibiotarsus (fig. 16E): The tibiotarsus is distinguished from that of *Ichthyornis dispar* by the presence of an ossified supratendinal bridge (contra Marsh, 1880; Martin, 1987). The illustration of the tibiotarsus in *Odontornithes* (Marsh, 1880: pl. XXXIII, figs. 1–4) does not show this ossified bridge.

When Martin (1987) remarked that the elongate acromion seen in *Apatornis celer* and *Ambiortus dementjevi* suggested that they may be closely related, he must have been referring to YPM 1734 (holotype of *Iaceornis marshi*) formerly referred to *Apatornis celer* (Marsh, 1880), as the *Apatornis celer* holotype does not include a scapula. In this context, it should be noted that *Iaceornis marshi* can also be differentiated from *Ap-saravis ukhaana* (Norell and Clarke, 2001), with which it shares the overall appearance of the scapula, remarked by Martin (1987), as well as from *Ambiortus dementjevi* (Kurochkin, 1985, 1999).

Iaceornis marshi is differentiated from *Ap-saravis ukhaana* (Norell and Clarke, 2001) by, for example, the presence of a procoracoid process, metacarpal II lying parallel to metacarpal III, a more pointed extensor process of metacarpal I, crossed coracoidal sulci, and many other characters (see Norell and Clarke, 2001). It is differentiated from *Ambiortus dementjevi* (Kurochkin, 1985, 1999) by the shape of the proximal end of the furcula, which is pointed and has a coracoidal tubercle, unlike the blunt omal ends lacking a coracoidal tubercle in *Ambiortus dementjevi* (Kurochkin, 1999). Further, although the carpometacarpus in *Ambiortus dementjevi* (Kurochkin, 1999) is poorly preserved, metacarpal I is almost as thick dorsoventrally as metacarpal II, whereas in *Iaceornis* it is

only approximately one-half that measure. Additionally, manual phalanx II:2 in *Iaceornis* is strongly compressed dorsoventrally and lacks a well-developed distal condyle for articulation of a claw, a feature present in *Ambiortus dementjevi* (Kurochkin, 1999). Finally, the illustrated shape of manual phalanx II:1 of *Ambiortus dementjevi* (Kurochkin, 1999) lacks the curved posterior margin present in *Iaceornis marshi*.

AVES LINNAEUS, 1758
PANGALLIFORMES
(NEW PROVISIONAL CLADE NAME)

Austinornis

(New provisional clade name)

DEFINITION: “Pangalliformes” is recommended to be used provisionally as a stem-based name (de Queiroz and Gauthier, 1992) for all taxa/specimens more closely related to *Phasianus* [*Gallus*] *gallus* Linnaeus, 1758 than to *Anas* [*Anser*] *anser* Linnaeus, 1758. See Gauthier and de Queiroz (2001: 24) for the form of this name and general rationale for the chosen specifiers. The definition of this name is provisional pending consensus regarding conversion of avian subclade names defined under previous codes and on the form of new major subclade names. *Austinornis lentus* is identified as a part of Pangalliformes in the phylogenetic analyses (Part II, Results).

DEFINITION: “*Austinornis*” is recommended to be used provisionally as a stem-based name (de Queiroz and Gauthier, 1992) for the clade comprised of all taxa more closely related to YPM 1796 (*lentus* Marsh, 1877b holotype specimen) than to *Phasianus* [*Gallus*] *gallus* Linnaeus, 1758, *Crax rubra* Linnaeus, 1758, and *Megapodius freycinet* Gaimard, 1823. The definition of this name is provisional pending (1) conversion of pangalliform subclade names defined under previous codes, (2) further phylogenetic analyses addressing YPM 1796’s position within Pangalliformes, and (3) implementation of a portion of the PhyloCode governing conversion of binomial species names (as are all other names defined and used in this document). The name is proposed for consistency in the application of the species + least inclusive clade couplet approach used here. The ap-

pearance of “*Austinornis*” and the form of clade + species couplets used generally was elected out of awareness that these names will be published during an awkward transitional period prior to decisions concerning conversion of binomial species names from previous codes and prior to the official start date of the PhyloCode. The form of the names is intended to facilitate use by taxonomists during the period prior to the start date of the PhyloCode. This clade would not have been named here had *lentus* not already been named. Further analysis of pangalliform interrelationships may suggest that *lentus* should be *nominum dubium*, and that YPM 1796 is undiagnostic. In that case, both names taking this specimen as a specifier would no longer be valid.

It should also be noted that because YPM 1796 is highly incomplete, its phylogenetic position within Pangalliformes may not be able to be resolved unless further material is discovered. Pending decisions on treatment of such issues in the context of a system of phylogenetic nomenclature, it may be that use of constructions like “*Pangalliformes lentus*” will be formally recommended, and creation of names like *Austinornis* deemed unnecessary and redundant.

lentus Marsh, 1877b

(converted species name)

DEFINITION: The name “*lentus*” Marsh, 1877b is converted and defined as the species that includes YPM 1796 (see the Introduction of the Taxonomic Revision for the definition of “species” used). With its clade address (sensu Cantino et al., 1999), the converted name of this species is “*Austinornis lentus*”. The name was originally published in the combination “*Graculavus lentus*” (Marsh, 1877b) and later in the combination “*Ichthyornis lentus*” (Marsh, 1880).

HOLOTYPE SPECIMEN: YPM 1796 is a well-preserved distal left tarsometatarsus (fig. 17).

LOCALITY AND HORIZON: Marsh (1880: 198) described the holotype specimen as collected by B. F. Mudge near Fort McKinney, Texas, in 1876. Brodkorb (1967: 178) specified that it was from the Austin Chalk from “Colling” County (misprint of Collin County; Parris and Echols, 1992) near Fort Mc-

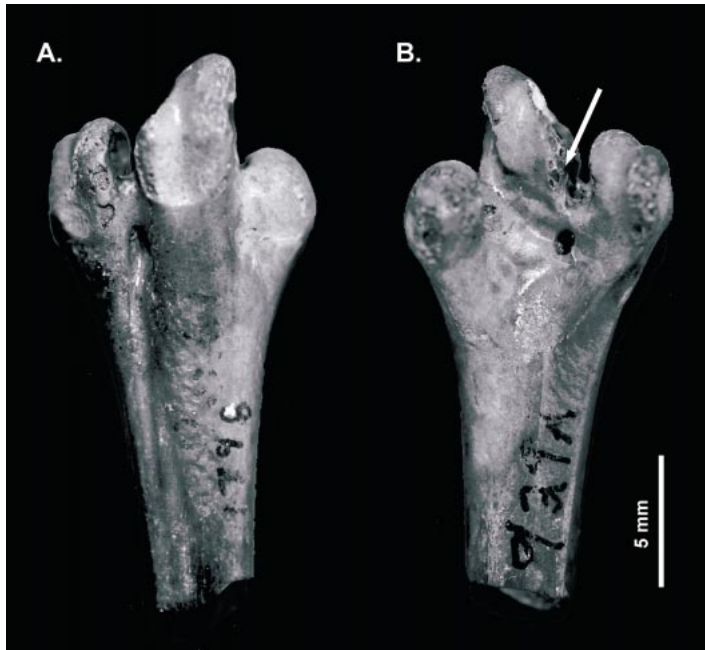


Fig. 17. The holotype specimen of *Ichthyornis* (*Austinornis*) *lentus* (YPM 1796; a right distal tarsometatarsus) in (A) dorsal and (B) plantar views. The asymmetrical development of the trochlea of metatarsal III is indicated.

Kinney. There is no more precise stratigraphic or locality data available. Its provenance should be further investigated.

DISCUSSION: *Graculavus* (*Ichthyornis*) *lentus* Marsh (1877b) is removed from *Ichthyornis*. It is placed phylogenetically as part of Aves rather than part of *Ichthyornis* (Part II, Results). Removal from *Ichthyornis* was suggested by Martin and Stewart (1982: 325), although no evidence was given as a basis for this recommendation. Shufeldt (1915: 76) also remarked in passing that *Graculavus lentus* (*Ichthyornis lentus* of Marsh, 1880) was “some tetraonine species” (Galliformes, Tetraonidae: Grouse) which is consistent with the identification made here.

The holotype differs in nearly all anatomical features that could be compared between it and *Ichthyornis dispar* (as represented by referred YPM tarsometatarsi, i.e., YPM 1456, YPM 1464, YPM 1739, YPM 1771; see table 1 for the basis of referral). A tarsometatarsus is not preserved in the *Ichthyornis dispar* holotype. Unlike other specimens referred to *Ichthyornis dispar*, a slight groove extends proximally from the juncture

of metatarsals II and III on the dorsal surface of the tarsometatarsus. Also on the dorsal surface, a distinct groove extends proximally from the distal vascular foramen. This vascular foramen also has a much more solid distal enclosure than in *Ichthyornis dispar*. Metatarsal II approaches IV in distal extent as opposed to being much shorter than IV in *Ichthyornis dispar*. The trochlea of metatarsal II is strongly rounded as opposed to ginglymoid in *Ichthyornis dispar*. The metatarsal I fossa is slightly more proximally situated than in *Ichthyornis dispar* and better developed. On the distal plantar surface, intermuscular lines are well developed while these are not marked in *Ichthyornis dispar*. One is located along the lateral edge of the shaft and a second slightly more medially positioned, parallel to the first, and extending toward metatarsal IV. Finally, the trochlear surface of metatarsal III is asymmetrically developed with the lateral edge of this trochlea extending distinctively proximal to the medial; in *Ichthyornis dispar* the edges of the trochlea are symmetrical.

The last mentioned morphology was re-

cently described for a taxon (i.e., *Paraortygoides messelensis*, Mayr, 2000) identified as most closely related to crown clade Galliformes and suggested to be a derived character of that taxon + crown clade galliforms (Mayr, 2000). The other morphologies described in the differentia (e.g., the strength of the fossa metatarsi I and plantar intermuscular lines) are consistent with the development of these features in other galliforms surveyed (e.g., *Alectura lathami*, *Meleagris gallopavo*), but their distribution needs to be further evaluated.

REFERRED SPECIMENS: No specimens have been referred to this taxon.

ANATOMICAL DESCRIPTION OF *ICHTHYORNIS DISPAR*

The description of *Ichthyornis dispar* is based upon the holotype of *Ichthyornis dispar* (YPM 1450) and referred specimens (see table 1 for YPM specimens and the Taxonomic Revision for the basis of the referral of these specimens, and for several others from the BMNH, SMM, and USNM). The description is organized into subsections by element or an anatomical subregion, beginning with parts of the cranium and proceeding through elements of the axial skeleton, pectoral girdle (and limbs) to the pelvic girdle (and limbs).

In each subsection, the YPM numbers inferred for the specimens figured in Marsh (1880) are given, as well as the basis for these inferences. Commentary is made on the correspondence (or fidelity) of the plates in *Odontornithes* (Marsh, 1880) and the description of the element by Marsh and other authors to the material as preserved. The specimen numbers of all YPM specimens in which the element is represented are listed. Several elements are described for the first time, including most parts of the cranium, furcula, ulnare, and manual phalanges II:2 and III:1. Finally, the new description of each element, as a result of the dissertation analysis, is provided.

COMPARATIVE MATERIAL AND METHODS

Osteological, arthrological, and myological nomenclature partially follows Baumel and Witmer (1993), Baumel and Raikow

(1993), and Vanden Berge and Zweers (1993), where possible. When these authors did not name osteological structures or discuss muscles, terms from other sources are used and cited or new terms are proposed. English equivalents of the Latin osteological nomenclature of all authors are used although in most cases the Latin equivalent is also given. The terms of orientation for the anatomical position of a bird, as specified by Clark (1993), are used.

However, “anterior” and “posterior” are used rather than “cranial” (and “rostral”) and “caudal” as proposed by Clark (1993). Clark (1993) suggested that cranial and caudal should be preferred to the time-honored terms of zoological nomenclature anterior and posterior because of past confusion arising from the fact that these terms correspond to the “dorsal” and “ventral” of human anatomy (Clark, 1993). While this clarity is an admirable aim, the creation of a special, unique terminology for Aves (or operationally, Avialae) among all vertebrates has been the *de facto* result of the relatively limited influence of the *Handbook of Avian Anatomy: Nomina Anatomica Avium* (Baumel et al., 1993).

The creation of special terminologies, as evidenced by the example of that from human anatomy given by Clark (1993), can obscure attempts to trace the history of anatomical traits into more basal tetrapods (see also Rowe, 1986) where the terms common to the zoological literature are generally employed. Thus, here “anterior” and “posterior” are used.

Further, anatomical terms historically unique to the avian literature (defined exclusively with respect to avian morphologies) such as “carpometacarpus”, “pygostyle”, and “hypotarsus” are applied only to morphologies optimized as basal to the crown clade. The form–function complexes associated with these terms most often evolve the coossification of elements primitively separate. The ontogeny of these structures and the identity of incorporated elements as well as their functions can only be observed for the crown clade with few exceptions. Placing these terms on morphologies outside of the crown clade encourages potentially unjustified inferences about the identity of incor-

porated elements, their ontogeny, and, especially, their function in outgroups of Aves. Restriction of these terms to only those taxa for which there is evidence of the components of the morphology bracketed as ancestral to the crown clade allows the assembly of these complexes to be investigated (see further discussion in appendix 1). Morphologies of avian outgroups assessed by primary topological congruence to have the components of a “hypotarsus” as bracketed to be ancestral to Aves, and discovered to be homologous with it, may subsequently be discovered to lack some of the crown clade attributes of that structure; however, the possibility of unjustified inference (see Rowe, 1986) is much more constrained.

Comparisons made with avian taxa in the body of the description refer to specific YPM specimens used as exemplars for the named species and/or named higher taxa. These are the following: (1) Palaeognathae: *Crypturellus undulatus* (YPM 11564), *Crypturellus noctivagus* (YPM 2120, YPM 2121), *Nothoprocta perdicaria* (YPM 2040), *Nothura darwinii* (YPM 6697), *Eudromia elegans* (YPM 6706), *Apteryx australis* (YPM 13486), *Struthio camelus* (YPM 2126, YPM 16179, YPM 16184), *Struthio camelus*, juv. (YPM 16175), *Casuarius* sp. (YPM 2123), *Casuarius casuarius* (YPM 5954), *Casuarius casuarius*, juv. (YPM 6208), *Rhea americana* (YPM 11524); (2) Anseriformes: *Chauna torquata* (YPM 6046), *Anhima cornuta* (YPM 12385), *Anas platyrhynchos* (YPM 2230, YPM 14369, YPM 14344); (3) Galliformes: *Alectura lathamii* (YPM 12498), *Crax pauxi* (YPM 2104), *Gallus gallus* (YPM 2106, YPM 6705) juv. (YPM 14517), *Meleagris gallopavo* (YPM 361, YPM 9302); and (4) Neoaves: *Columba livia* (YPM 10077, YPM 11985), *Gavia stellata* (YPM 6073), *Sterna maxima* (YPM 10831), *Burhinus capensis* (YPM 14780, YPM 14781), *Vanellus armatus* (YPM 14785), *Vanellus melanopterus* (YPM 14796), *Numenius phaeopus* (YPM 396, YPM 14967). Marsh (1880) drew numerous comparisons between *Ichthyornis* and the “Royal Tern”, “*Sterna regia*” Gambel, 1848, which is a junior synonym of *Sterna maxima* Boddaert, 1783 (Ridgeway, 1919).

Comparisons are primarily drawn with

taxa of Palaeognathae and Galloanserae, which are supported as the two basal-most divergences of the crown clade (e.g., Cracraft, 1988; Sibley and Ahlquist, 1990; Groth and Barrowclough, 1999; van Tuinen et al., 2000; Cracraft and Clarke, 2001). Additionally, the included galloanserine species were chosen to sample basal divergences (i.e., *Chauna torquata*, *Anhima cornuta*, *Meleagris gallopavo*, and *Crax pauxi*) and deeply nested taxa (i.e., *Anas platyrhynchos*, *Alectura lathamii*, and *Gallus gallus*) from within Anseriformes and Galliformes based on previous phylogenetic hypotheses for these two clades (e.g., Holman, 1964; Sibley and Ahlquist, 1990; Livezey, 1997a, 1997b).

By contrast, there is no well-supported hypothesis of the lineages basal to Neoaves (e.g., Cracraft, 1988; Cracraft and Clarke, 2001). Further, many identified neoavian subclades lack well-supported hypotheses regarding the relationships of their component taxa. Of neoavian lineages, most comparisons are made with charadriiforms (e.g., *Sterna maxima*, *Burhinus capensis*, *Vanellus armatus*, *Numenius phaeopus*). Charadriiformes, the avian lineage of taxa commonly referred to as “shorebirds”, has alternatively been considered a basal divergence of the crown clade (e.g., Feduccia, 1995, 1996) or a relatively basal divergence of subsequent neognath diversification (e.g., Sibley and Ahlquist, 1990; Ericson, 1997; Groth and Barrowclough, 1999). Comparisons with charadriiforms are emphasized to shed light on the morphologies that formed the basis of the oft-hypothesized affinities of *Ichthyornis* to Charadriiformes (e.g., Marsh, 1880; Fürbringer, 1888; Brodkorb, 1963). The exemplars of Charadriiformes used were chosen to sample broadly across the clade based on recent hypotheses of its interrelationships (Sibley and Ahlquist, 1990; Chu, 1995). Species of *Burhinus* (Burhinidae) have been considered an aberrant primitive lineage similar in morphology to the Cretaceous “form family Graculavidae” (Olson and Parris, 1987). However, Chu (1995, 1998) suggested that *Vanellus* is actually a more basal divergence within a clade of “plover-like” birds that includes *Burhinus* (“thick knees”) as part of a clade that is sister to the terns (e.g., *Sterna maxima*) and gulls. *Numenius* is placed as

part of the sister group to the plover-like birds in a clade of “sandpiper-like birds” (Chu, 1995) with the divergence between these two large clades constituting the most basal one identified within Charadriiformes. The relationships among these taxa proposed by Chu (1995) is the same as that of Sibley and Ahlquist (1990), except that in their analysis *Burhinus* and *Vanellus* are placed as more closely related to each other than *Burhinus* is to *Sterna*. Several comparisons were also made with *Columba livia*; Columbiformes have been considered closely related to Charadriiformes (e.g., Cracraft, 1988), but members of this clade have a decidedly different range of ecologies, none of which has been considered to be “shorebird-like” (del Hoyo et al., 1992–1999).

With reference to more basal avialans, Enantiornithes is represented by the taxa considered to comprise it by previous authors (e.g., Zhou et al., 1992; Chiappe and Calvo, 1994; Sanz et al., 1995; Chiappe, 1995a, 1996; see also Part II, Materials and Methods) and *Confuciusornis sanctus* is represented primarily by specimens figured in Chiappe et al. (1999) and Hou (1997). A specimen number is given for fossil avialans when morphologies are noted that have not been previously described. Comments on the anatomy of *Apsaravis ukhaana*, *Hesperornis regalis*, and *Patagopteryx deferrariisi* refer to the material described in Norell and Clarke (2001), Marsh (1880), and Chiappe (1996), respectively, and may include observations of that material not described in the cited papers. References to *Baptornis advenus* are based on the description of that taxon in Martin and Tate (1976) and study of the holotype tarsometatarsus (YPM 1465).

SKULL

CRANIAL ELEMENTS

The description of the cranium (exclusive of the mandible) in *Odontornithes* (Marsh, 1880) is limited. It included measurements (Marsh, 1880: 125) of the holotype of *Ichthyornis dispar* (YPM 1450) and of a second specimen, YPM 1459. Marsh (1880: 124) also commented that two specimens were used to estimate the size of the *Ichthyornis*

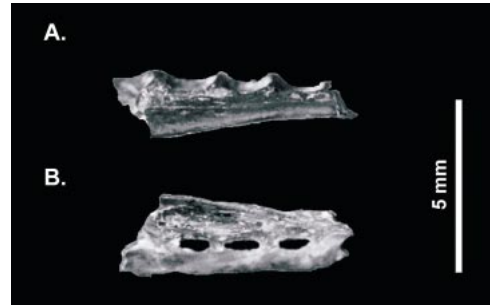


Fig. 18. Maxillary fragment from the *Ichthyornis dispar* holotype specimen (YPM 1450) in (A) ventrolateral view and in (B) mediodorsal view. Illustrations of the maxilla in Marsh (1880) are mirror images of the element.

brain, but did not indicate which specimens these two were.

Cranial material incorporated in the *Ichthyornis dispar* panel mount (YPM 1450; fig. 1) is comprised of one partial cranium and one fragment of the tooth-bearing portion of the left maxilla (fig. 18). However, we can only surmise the specimen numbers of three cranial fragments in the *Ichthyornis victor* mount (fig. 19A). Henry Gibb's notes (fig. 3) placed a single arrow applying the number “[YPM] 1728” to the illustration of the cranium on the annotated copy of the reconstruction of *Ichthyornis victor* (Marsh, 1880: pl. XXXVI) that he used to indicate the contents of the *Ichthyornis victor* mount. However, the single, large portion of the cranium illustrated (Marsh, 1880: pl. XXXVI, and copied in Gibb's notes, fig. 3) is simply an enlargement of the *Ichthyornis dispar* holotype skull (compare Marsh, 1880: pl. XXI), and not based on material referred to *Ichthyornis victor*. Further, Gibb (fig. 3) applied only one number (YPM 1728) to the *Ichthyornis victor* reconstruction that he annotated, while three separate cranial fragments were included in the *Ichthyornis victor* mount (fig. 19A).

In this section, the identity of the specimen(s) represented by the three skull parts in the *Ichthyornis victor* panel mount is discussed. Next, the basis for the referral of specimens known only from cranial material to *Ichthyornis dispar* is appraised. Finally, the morphology of the cranium is detailed, as inferred from the partial cranium of the *Ich-*

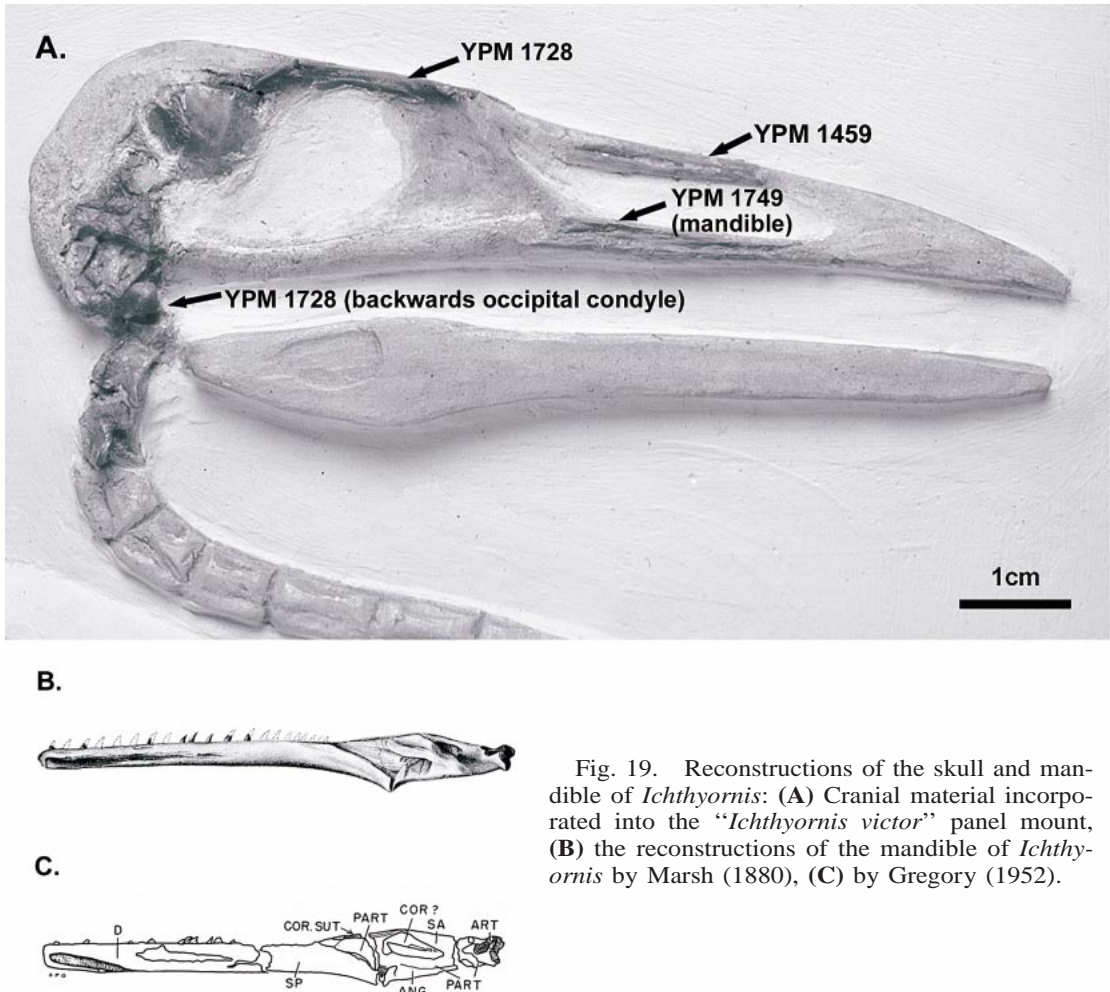


Fig. 19. Reconstructions of the skull and mandible of *Ichthyornis*: (A) Cranial material incorporated into the “*Ichthyornis victor*” panel mount, (B) the reconstructions of the mandible of *Ichthyornis* by Marsh (1880), (C) by Gregory (1952).

thyornis dispar holotype and specimens assessed to be reliably referred to this species.

The YPM 1728 specimen number is here applied to all of the cranial material from the *Ichthyornis victor* mount consistent with the label in Gibb’s notes. However, it is possible (but considered unlikely) that one of these fragments, which includes the occipital condyle (figs. 20–22), is part of specimen YPM 1459. Because the fragment in the mount is the only YPM specimen to preserve basicranial morphology other than the holotype of *Ichthyornis dispar* (YPM 1450), the specimen number of this fragment is nontrivial. Its identity determines which other material

is associated with it, either as part of YPM 1728 or YPM 1459.

Measurements were given (Marsh, 1880: 129) for a supposedly “cordate” (Marsh, 1880: 121) occipital condyle in YPM 1459 (i.e., transverse diameter: 3.0 mm; median vertical diameter: 2.2 mm). These dimensions are approximately the same as those of the basicranial fragment in the *Ichthyornis victor* mount identified by Gibb as YPM 1728 (i.e., 3.0 mm and 2.5 mm, respectively). Does this suggest that the mount specimen is YPM 1459? The dimensions of the frontals in YPM 1459 and those in a second part of the cranium in the *Ichthyornis victor*

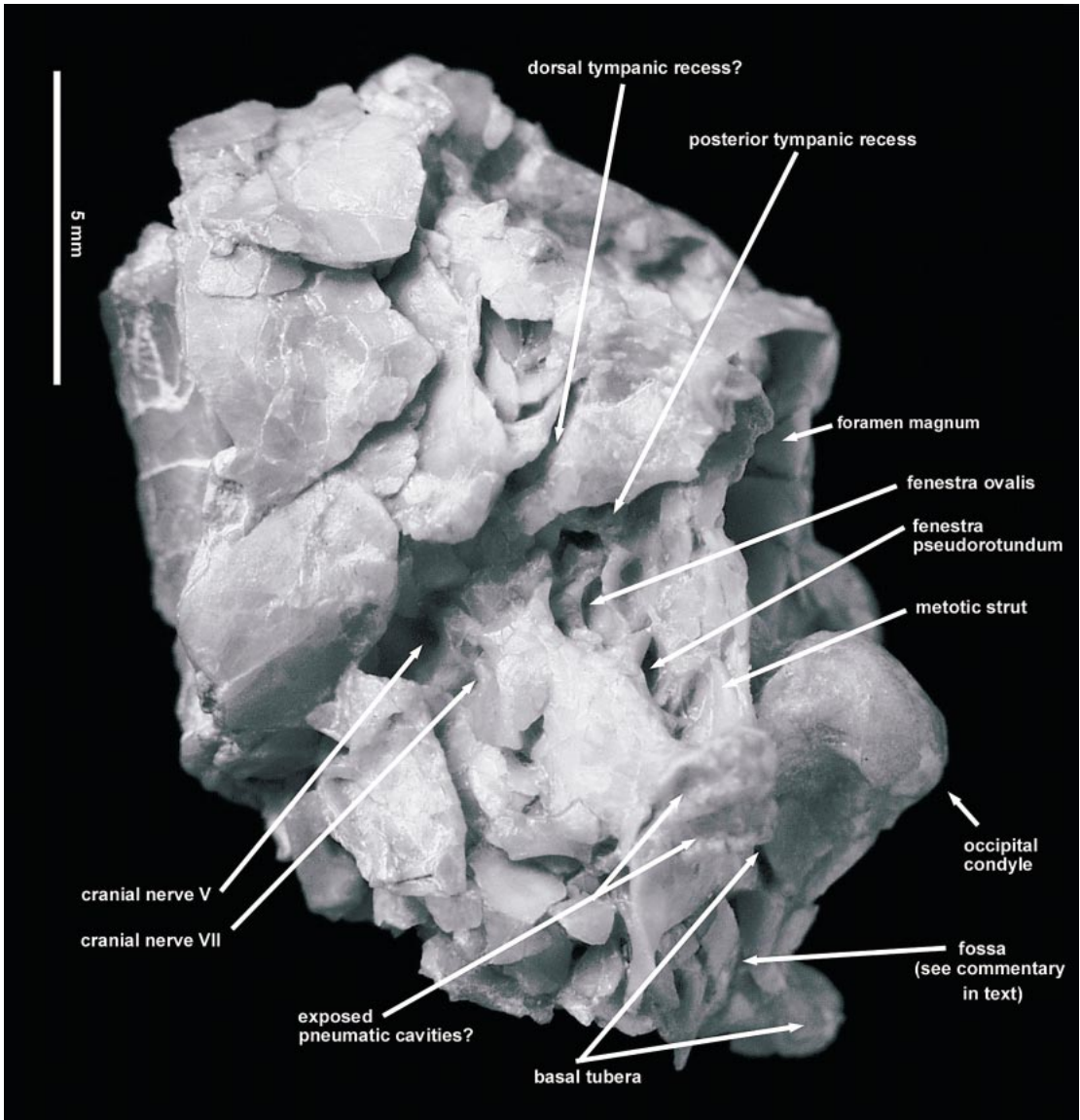


Fig. 20. The braincase of *Ichthyornis dispar* (YPM 1728) in left lateral view. This part of YPM 1728 was placed in the "*Ichthyornis victor*" panel mount.

mount (presumably YPM 1728) suggest they are from individuals of approximately the same size. Thus, the occipital condyle in the mount could be from the similarly sized YPM 1728 and, for this reason, closely matches Marsh's (1880) dimensions for YPM 1459. However, no occipital condyle appears currently among the YPM 1459 material; what did Marsh (1880) measure? It is possible that an occipital condyle was once

part of YPM 1459 and is now lost. Alternatively, Marsh (1880) could have identified a small, extremely crushed fragment from YPM 1459 as an occipital condyle; he identified such a condyle in the holotype of *Ichthyornis dispar* (Marsh, 1880: pl. XXI, "bo"), where no morphology resembling a condyle is present. In 1983, Whetstone identified an *Ichthyornis* braincase as YPM 1459 when describing anatomical details of the *fe*-

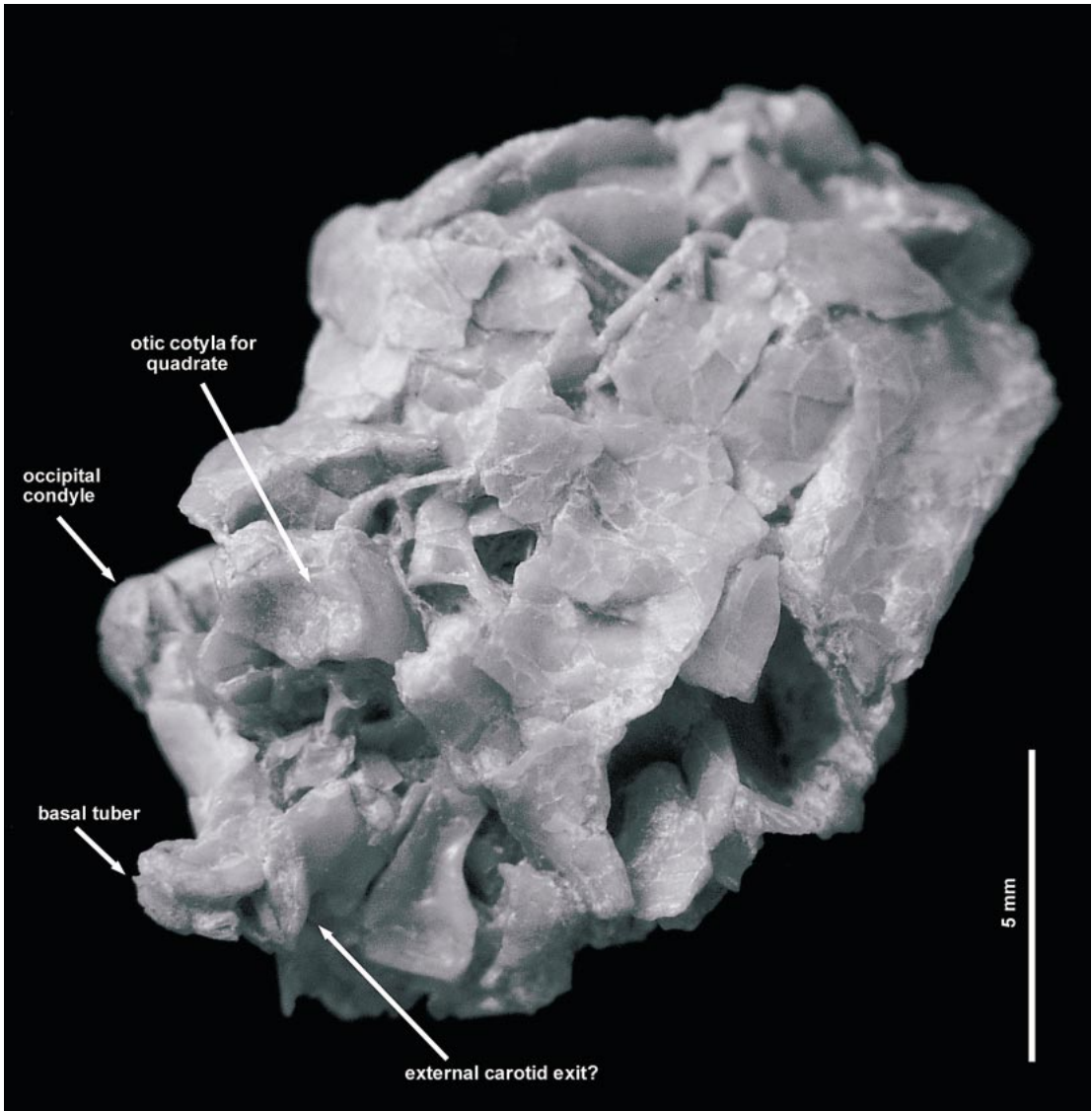


Fig. 21. The braincase of *Ichthyornis dispar* (YPM 1728) in right lateral view. This part of YPM 1728 was placed in the "*Ichthyornis victor*" panel mount.

nestra pseudorotunda and pneumatic features of the braincase. These morphologies are also not represented in material that is currently part of YPM 1459, although they are represented in the fragment included in the mount with the well-preserved occipital condyle.

The question of whether the partial basicranium in the *Ichthyornis victor* mount with the well-preserved occipital condyle is part

of YPM 1728 (per Gibb's notes) or a missing and measured part of YPM 1459 may never be known with complete certainty. In this paper, however, the decision was made to apply YPM 1728 to this specimen for three reasons. First, the positive identification of the cranial material in the mount as YPM 1728 in Gibb's notes is considered stronger evidence than the apparent lack of basicranial material in YPM 1459. Second, it seems that

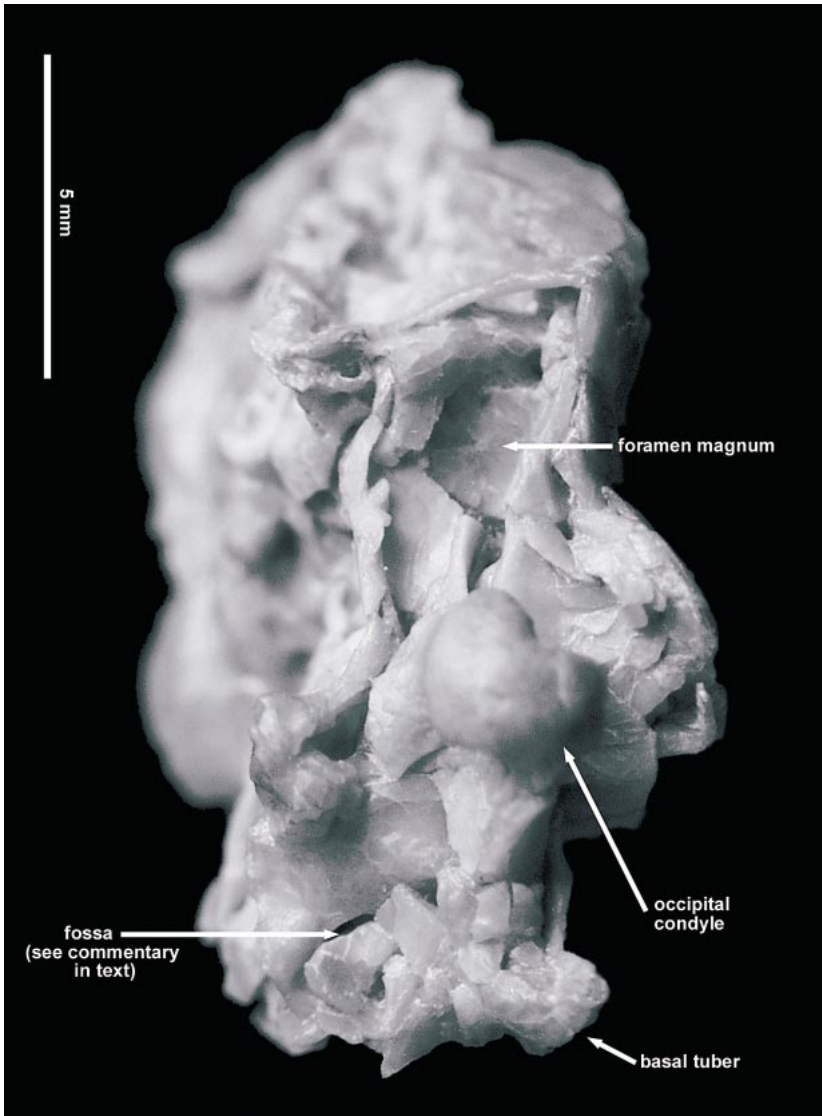


Fig. 22. The braincase of *Ichthyornis dispar* (YPM 1728) in posterior view. This part of YPM 1728 was placed in the "*Ichthyornis victor*" panel mount.

Whetstone (1983) simply assumed that the measurements given in Marsh (1880) pertained to the mount fragment and applied YPM 1459 to that specimen. Gibb's notes and other information on the composition of the mount were unknown at that time and would, thus, have been unavailable to Whetstone (1983). Finally, the pale yellow-orange color of the element removed from the mount matches the color of the other two cranial fragments removed from the *Ichthyornis vic-*

tor mount, while the YPM 1459 material has a slightly darker, yellow-gray tone.

Neither of the two YPM specimens referred to *Ichthyornis dispar* to include cranial material (i.e., YPM 1459 and YPM 1728) has associated postcranial material. Their identification as *Ichthyornis dispar* is only supported by morphological correspondence to the cranium of the *Ichthyornis dispar* holotype (YPM 1450).

YPM 1728 consists solely of parts of the

cranium (which accords with the original inventory of the material) and two fish teeth. YPM 1459 includes a fragment mounted as part of the premaxillae in the *Ichthyornis victor* mount (per Gibb's notes), an identification with which this reevaluation agrees. The rest of YPM 1459 includes a fragment (marked "YPM 1459A") labeled "fish", which is actually fused avian frontals (fig. 23B) for which the measurement of the "distance between upper margins of orbits" of *Ichthyornis victor* is given in *Odontornithes* (Marsh, 1880: 125). A final vial contains a proximal coracoid collected a year following the cranial material and not considered associated with it (see table 1). Thus, the morphology of the partial coracoid cannot be used to refer YPM 1459 to *Ichthyornis dispar*.

The frontals in YPM 1728 (fig. 23B), YPM 1459, and the holotype of *Ichthyornis dispar* (YPM 1450) correspond in the following details: (1) frontals fused; (2) paired shallow glandular depressions (i.e., fossae glandulae nasalis; Baumel and Witmer, 1993) on the dorsal supraorbital margins; (3) glandular depressions do not reach midline; (4) anteroventral midline of frontals fused with mesethmoid (only barely discernable in YPM 1450); (5) the position of the shallow groove for the olfactory nerve and ethmoid artery (i.e., sulcus n. olfactorii; Baumel and Witmer, 1993), which is developed in the angle between the interorbital septum and the dorsal lamina (Baumel and Witmer, 1993) of the mesethmoid (which is fused to the frontals). Morphology "5" is visible on the right side of the *Ichthyornis dispar* holotype (YPM 1450; fig. 24A) in ventral view and on both the right and left sides in YPM 1459 and YPM 1728. The correspondence of these morphologies is consistent with identification of the material to the same species, a conclusion supported by other similarities discussed below. These characters, however, are not considered demonstrated apomorphies of *Ichthyornis dispar*.

The nearly complete frontals from YPM 1728 preserve contacts with the nasals, premaxillae, and lacrimals (fig. 23B). On the dorsal midline of the anterior tip of the fragment, a tongue-shaped depression, underlain by the mesethmoid, is interpreted as a sur-

face for the articulation of the premaxillae (fig. 23B). There is no evidence (such as a midline ridge on the dorsal surface of the mesethmoid) to indicate that the premaxillae were unfused to each other posteriorly, although Marsh (1880: 121) described them as unfused.

Frontal processes of the premaxillae are known from YPM 1459 (previously incorporated in the *Ichthyornis victor* panel mount). The premaxillary portion of the facial margin has been reported to lack teeth (Lamb, 1997) but is not preserved in any of the YPM specimens. The section of the frontal processes preserved in YPM 1459 is incomplete proximally and distally (fig. 23A). The premaxillae are fused for the length of this section such that a midline ridge is seen in ventral view (YPM 1459; fig. 23A). The ventral surface is concave on either side of the midline ridge at the closed suture. The fragment is slightly broader and flatter at one end, interpreted as posterior. Dorsally, a styloid midline depression, not an open suture, is visible for approximately the posterior half of the fragment (fig. 23A). This line deepens into a pit at approximately the midpoint of the dorsal surface (fig. 23A).

Based on the following two morphologies, it is inferred that the fragment would have formed most of the dorsal margin of the external nares (its approximate position in the *Ichthyornis victor* mount): (1) the presence of a ventrally projected midline flange anteriorly, which in Aves extends toward the body of the premaxillae and sits just anterior to the external nares (fig. 23A); and (2) the slight posterior flattening that marks the nasofrontal hinge in Aves.

Based on the position of the nasals in *Hesperornis regalis* (Bühler et al., 1988) and the anteroventral midline flange, it may be that the preserved part of the premaxillae represents all or nearly all of the supranarial bar. If so, the supranarial bar would have been relatively thick dorsoventrally, as has been reported for *Hesperornis regalis* (Bühler et al., 1988). The nature of the premaxilla/nasal contact, and specifically the anterior extent of the nasals, is somewhat unclear. Two lateral flanges, which extend one-third of the length of the ventral surface of the fragment, are interpreted as representing the anterior

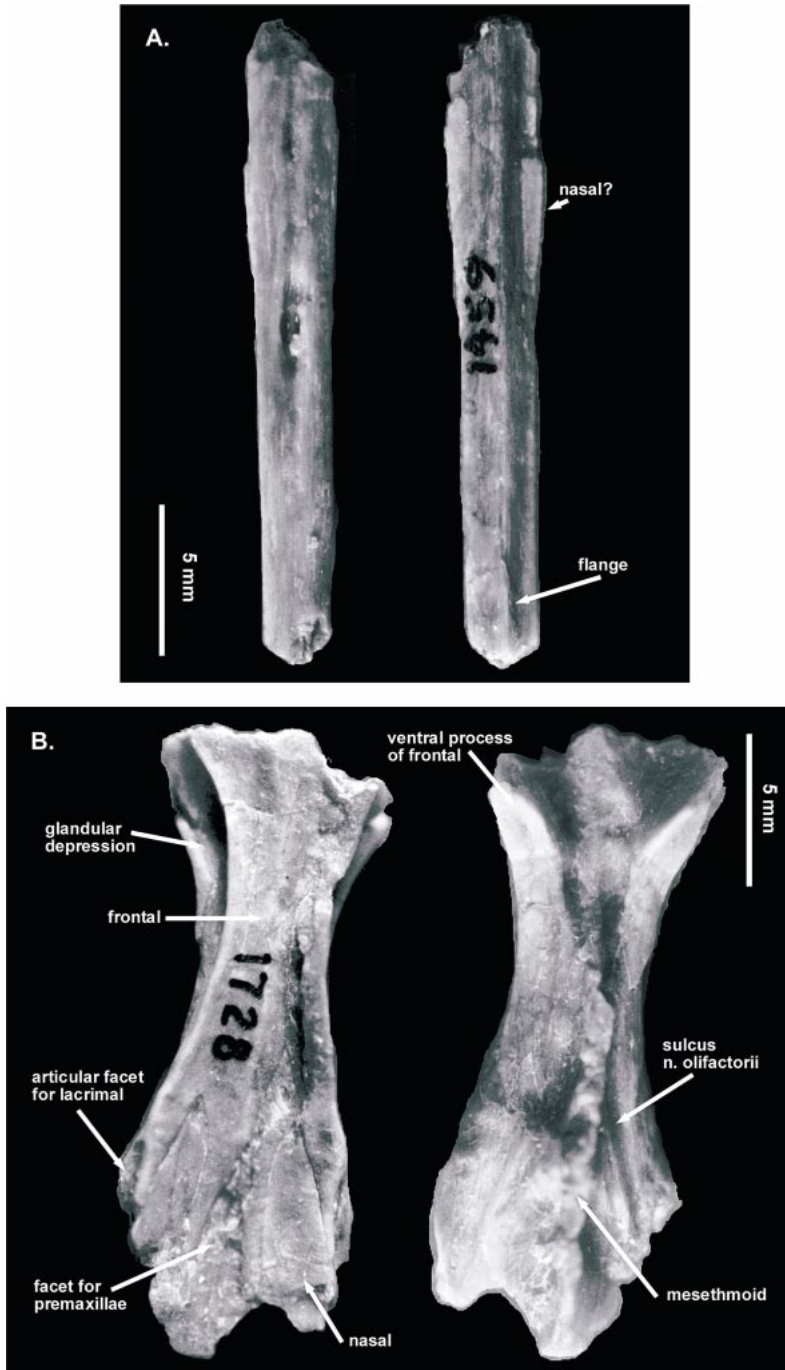


Fig. 23. The *Ichthyornis dispar* (A) premaxillae and (B) frontal/nasal contact (YPM 1459 and YPM 1728 shown, respectively). On the left the elements are shown in dorsal view and on the right, ventral.

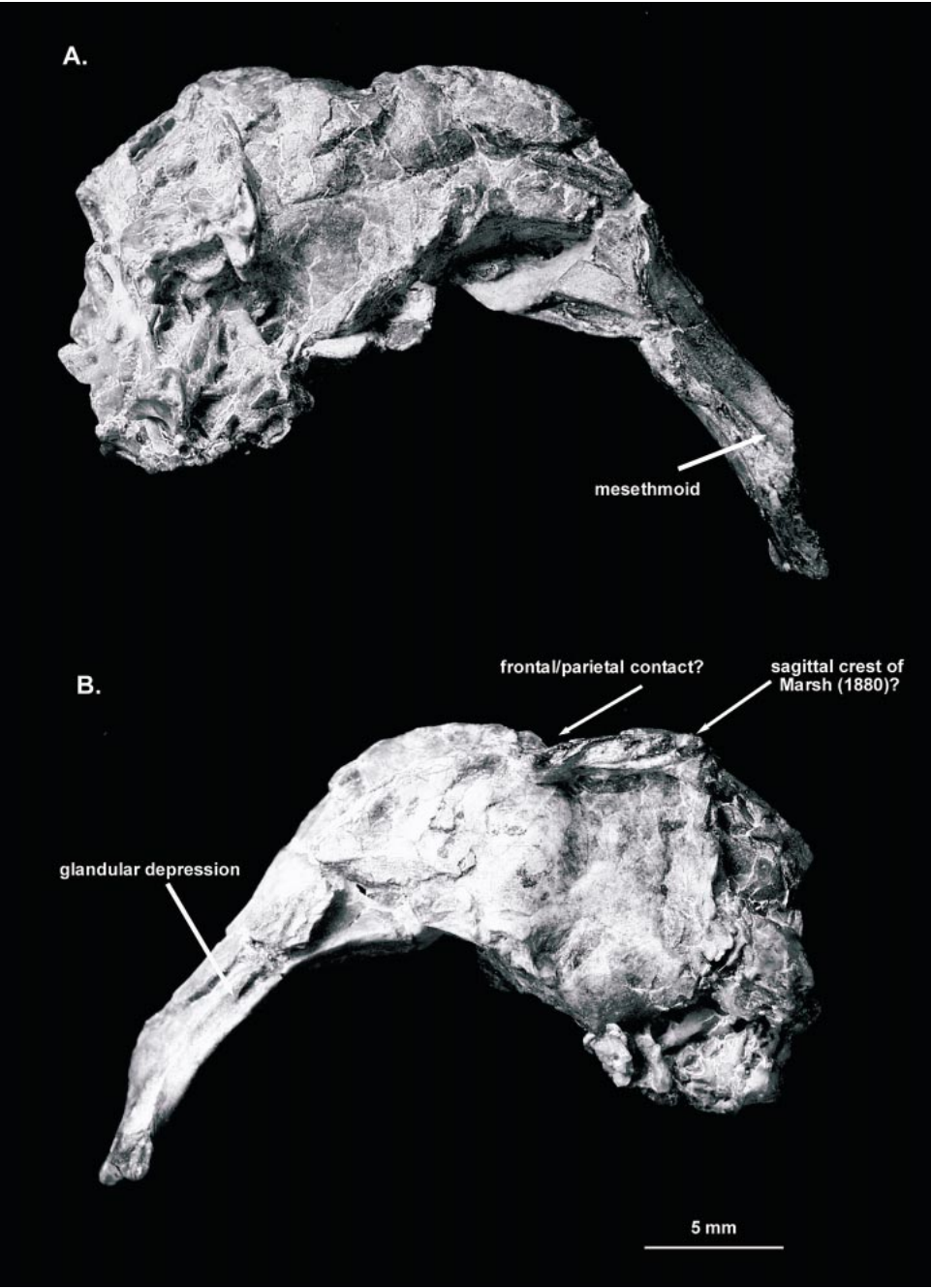


Fig. 24. The skull of the *Ichthyornis dispar* holotype (YPM 1450) in (A) right and (B) left lateral views.

tips of the nasals (fig. 23A). The nasals do not appear to have met or approached each other on the ventral midline, but rather to have only underlain posterolateral edges of the premaxillae (fig. 23A).

The posterior tips of the nasals do not contact the premaxillae. Narrow, tonguelike processes of the frontals lie between these bones and the nasals in dorsal view (YPM 1728; fig. 23B). Processes of the frontals also underlie and pass lateral to the nasals. These lateral processes bear well-developed facets for the lacrimals, the articular surfaces of which are perpendicular to the dorsal surface of the frontals (fig. 23B). The lacrimals may have also articulated with the nasals; the facets are incomplete anteriorly.

The presence of facets indicate that sutures between the lacrimals and frontals were not closed in *Ichthyornis dispar*. Lateral facets on the frontals in *Hesperornis regalis* (e.g., YPM 1206) indicate that, in this taxon, the lacrimals were also not fused to the frontals. By contrast, the two bones are often coossified in Aves (Cracraft, 1968), a feature that may be synapomorphic of that clade or derived within it.

In Aves, the lacrimal can articulate with (or coossify to) both the nasal and frontal, but may articulate exclusively with either of these two bones (Cracraft, 1968). In *Struthio camelus* and *Rhea americana*, for example, the lacrimal usually contacts only the nasal (Cracraft, 1968), unlike the condition in *Ichthyornis dispar*, while in tinamous, *Apteryx*, and *Gallus gallus*, it contacts the frontal and nasal (Cracraft, 1968). In Anhimidae, it also articulates exclusively with the nasal (Cracraft, 1968). *Hesperornis regalis* has the lacrimal primarily contacting the nasal, although also contacting the anterolateral portion of the frontal (Bühler et al., 1988).

As noted above, the nasals (from YPM 1459; fig. 23A) do not appear to have met on the ventral midline or to have extended under the premaxillae to approach the anterior margin of the external nares. These two morphologies appear also to be potential synapomorphies of Aves relative to *Ichthyornis dispar*, as the *Ichthyornis* condition is also present in *Hesperornis regalis* (e.g., Bühler et al., 1988).

While the mesethmoid in *Ichthyornis dis-*

par (YPM 1450, YPM 1459, YPM 1728) is fused to the frontals (fig. 23B), it did not form the complete or nearly complete inter-orbital septum seen in many adult avians. Posterodorsally, the unbroken ventral edges of the frontal indicate they did not contact the mesethmoid (fig. 23B). Thus, the ventral processes of the frontals did not meet to completely close the anterodorsal part of the cranial cavity; the mesethmoid contacts and fuses to the frontals only anteriorly. In Aves, this morphology would appear to be described as a broadly open, single foramen opticum (Baumel and Witmer, 1993). The mesethmoid may have extended posteriorly to contact the ventral processes of the frontals and/or part of the basicranium only ventrally, a condition that appears to be developed in *Hesperornis regalis* (see Bühler et al., 1988).

The mesethmoid is visible in YPM 1728 extending from anterior to the anterior edges of the ventrally projecting processes of the frontal to the anteriormost tip of the fragment (fig. 23B). It is fused indistinguishably with the frontals for the length of its preserved contact with them. The mesethmoid in *Hesperornis regalis* was not fused to the frontals (Bühler et al., 1988), unlike the condition in *Ichthyornis dispar* (YPM 1450, YPM 1459, YPM 1728).

The mesethmoid is interpreted as having been overlain by the premaxillae; its apparent dorsal exposure (fig. 23B) is here considered an artifact of preservation. Where the mesethmoid is exposed dorsally (e.g., Ratiatae; Cracraft, 1986), its dorsal surface is coplanar with the frontals, which is not the condition in YPM 1728 (fig. 23B). The thin and shallow sulcus for the olfactory nerve developed on the mesethmoid angles laterally at approximately the premaxilla/frontal contact, where the mesethmoid also broadens (fig. 23B). The anterior extent of the mesethmoid unfortunately cannot be ascertained from YPM 1728, but it may thin slightly (to taper out?) at the anteriormost tip of the fragment (fig. 23B).

The maxilla is represented only by a small, tooth-bearing fragment that is part of the holotype of *Ichthyornis dispar* (YPM 1450; fig. 18). It was described and figured in *Odonotornithes* (Marsh, 1880: pl. XXI, fig. 1); however, this fragment differs from Marsh's

(1880) illustration. Marsh (1880: pl. XXI, fig. 1b) indicated a thin sheet of bone covering the alveoli dorsally, but the alveoli in the preserved fragment are completely perforate (fig. 18). Further, Marsh (1880: pl. XXI, fig. 1a) illustrated a curved edge he interpreted as the medial edge of the left maxilla. However, the fragment is a mirror image of its representation in *Odontornithes* (Marsh, 1880: pl. XXI, fig. 1), the curved edge reported seen on the opposite side of the fragment (fig. 18), and is here interpreted as a dorsally projected flange (fig. 18B), laterally placed, and increasing in height posteriorly. That is to say, the fragment would be from the left maxilla where Marsh placed it in his reconstructed outline of the skull (Marsh, 1880: pl. XXI, fig. 1), but a dorsal flange that was not illustrated would have been visible in lateral view.

The straight medial edge of the maxilla has a slightly rounded edge, which does not bear any indication of articular surfaces for any palatal elements (fig. 18B). On this side of the alveolar surface, interpreted as medial (labial), minute foramina lie close and slightly posterior to the alveoli themselves. These foramina are not present in the dentaries (YPM 1450). Similar features are observed on the medial surface of the maxilla in crocodilians (J. Gauthier, personal obs.).

Marsh (1880: 124) interpreted the size of the maxillary teeth as larger than the dentary teeth that would have opposed them. However, the exact position of the maxillary fragment in the jaw is uncertain and the alveoli are not significantly larger than those in the lower jaw. Further, the posterior teeth that Marsh interpreted as smaller than those in the middle of the dentary tooth row may be simply in a different stage of replacement. *Hesperornis regalis* has been proposed to have a groove in the maxilla into which subnasal processes of the premaxillae/nasals contacted in a unique tongue and groove articulation (Bühler et al., 1988). This morphology is unfortunately missing data for the alveolar portion of the maxilla preserved in YPM 1450.

Severely crushed portions of the posterior part of the skull are preserved in the holotype of *Ichthyornis dispar* (YPM 1450; figs. 24, 25), and in YPM 1728 (figs. 20–22). Two relatively large portions of the skull roof

were removed from the *Ichthyornis victor* mount. These include the fragment with a well-preserved occipital condyle discussed above and identified as belonging to YPM 1728 (figs. 20–22) and one fragment explicitly marked with the specimen number “1728” (fig. 26). The anatomy of the posterior part of the skull in *Ichthyornis dispar* is described from these two specimens. It is inferred from comparison of features in the auditory region and frontals that there was no conspicuous difference in size between these two specimens (although YPM 1450 is the holotype of *Ichthyornis dispar*, and YPM 1728 was referred to *Ichthyornis victor* [Marsh, 1880]).

The larger fragment removed from the *Ichthyornis victor* mount and marked with “1728” is interpreted as part of the frontals (fig. 26). It is extremely thin, dorsally convex, and its arch is interpreted as preserving the contour of the right cerebral hemisphere (fig. 26). On the dorsal midline (fig. 26A), there is a moderately developed frontal depression (depressio frontalis; Baumel and Witmer, 1993). A faint ridge (crista temporalis; Baumel and Witmer, 1993) appears to border a shallowly depressed portion of the temporal fossa (fossa temporalis; Baumel and Witmer, 1993) surrounding the upper temporal fenestra (fig. 26A).

In ventral view, there is a ridge (crista frontalis interna, Baumel and Witmer, 1993) demarcating the virtually complete impression of the right cerebral hemisphere from the preserved portion of the left (fig. 26B). At the anteriormost edge of the fragment close to and subparallel with this ventral midline ridge is a short, low ridge (fig. 26B).

The frontal/parietal contact is not discernable in YPM 1459 or YPM 1728 but may be in YPM 1450 (fig. 24). If present in YPM 1450, the frontal/parietal suture appears obliterated or closed (fig. 24B). A transverse ridge possibly associated with the back of the skull at or near the supraoccipital/parietal contact (YPM 1450; fig. 24A,B). Anterior to this contact, the bone surface in left lateral view is smooth, and the faint contour of the cerebral hemisphere appears visible. Posterior to this contact there is a change in the slope of the dorsolateral surface of the skull (fig. 24B). This change in slope is also seen

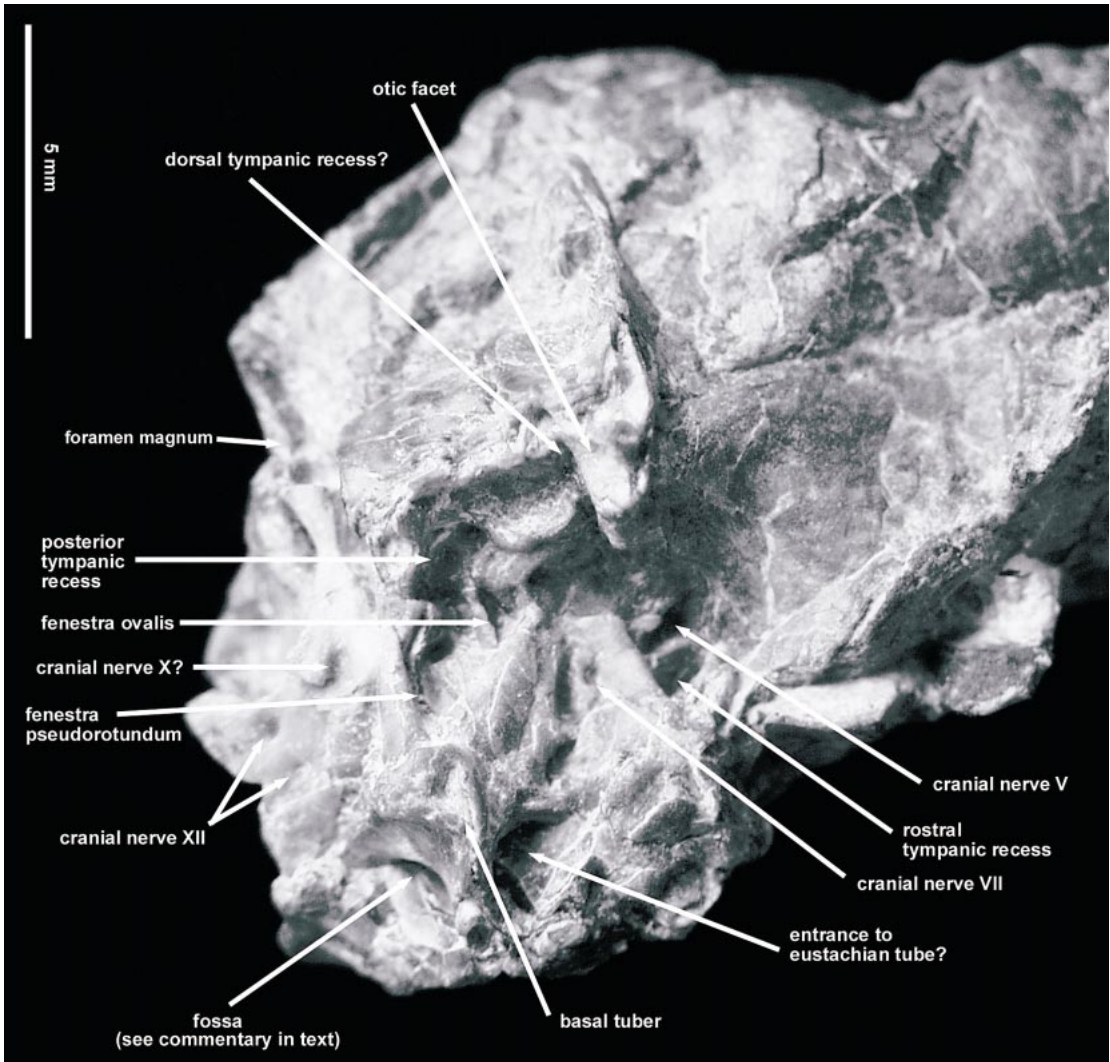


Fig. 25. The braincase of the *Ichthyornis dispar* holotype (YPM 1450) in right lateral view.

in many avians and can be observed in juveniles when the sutures are still open (e.g., *Gallus gallus*). Marsh (1880) described a sagittal crest in the holotype; however, this is an artifact of crushing (fig. 24B).

Marsh's (1880) interpretations of the size and shape of the brain in *Ichthyornis* must have been made from YPM 1728. Though Marsh comments that his reconstruction of the brain is based on two specimens (Marsh, 1880: 122), no other specimen was found that would appear informative about brain morphology. One possible exception is part of YPM 1773, which could be interpreted as

an endocast, but is not mentioned by number in *Odontornithes* (Marsh, 1880). While the estimate of the size of the cerebral hemispheres is partially discernable in YPM 1728, the rest of the reconstruction (e.g., of the cerebellum) must be considered highly, if not entirely, speculative.

The occipital condyle is well preserved in the second fragment removed from the *Ichthyornis victor* mount identified as belonging to YPM 1728 (see above) but not in the *Ichthyornis dispar* holotype (YPM 1450). The basioccipital and exoccipital components of the occipital condyle are fused (figs. 20, 22).

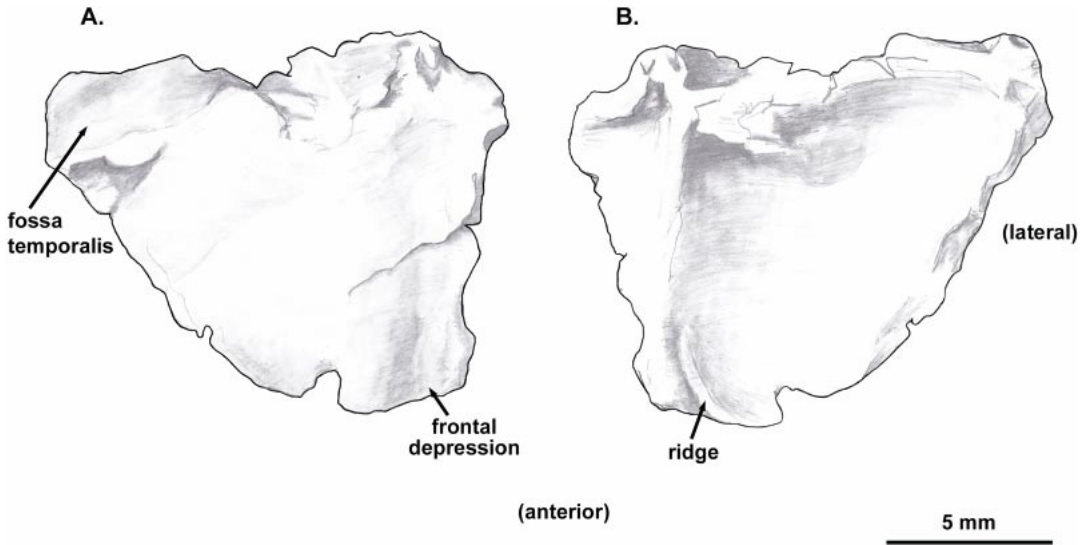


Fig. 26. A portion of the skull roof of *Ichthyornis dispar* (YPM 1728) in (A) dorsal and (B) ventral views.

The condyle appears to have been large relative to the size of the foramen magnum (fig. 22) compared to the condition in Aves. However, the size of the foramen magnum can only be roughly interpreted, as it is crushed in both YPM 1450 (fig. 24A) and YPM 1728 (fig. 22). The dorsal edge of the foramen magnum in YPM 1728 is relatively well preserved, although its lateral edges are fractured and crushed (figs. 20, 22). The occipital condyle in YPM 1728 is artifactually appressed to the left basal tuber. These tubera in both YPM 1450 (figs. 24A, 25) and YPM 1728 (figs. 20, 22) are conspicuously robust (figs. 20, 22).

The anterior portion of the auditory recess is clearly visible, as the ala parasphenoidalis (Baumel and Witmer, 1993) is apparently broken away from this region in both YPM 1450 (figs. 24A, 25) and YPM 1728 (fig. 20). In YPM 1728, the metotic strut (sensu Witmer, 1990) is visible in left ventrolateral view (fig. 20). Portions of the fenestra ovalis, fenestra pseudorotunda, and a depression interpreted as a part of the posterior tympanic recess are visible anterior to this strut (fig. 20). Whetstone (1983) identified a caudal (posterior) tympanic recess in a specimen he identified as YPM 1459; he appears, however, to have been referring to the specimen

from the *Ichthyornis victor* mount, which is YPM 1728. A conspicuous foramen lies anterior to and at about the same dorsal height as the fenestra ovalis (fig. 20); this feature is interpreted as the exit of the fifth cranial nerve (trigeminal; or foramen n. maxillo-mandibularis; Baumel and Witmer, 1993).

Paired large openings on the ventral surface of the basisphenoid plate visible in YPM 1450 (fig. 25) and to a lesser extent in YPM 1728 (figs. 20, 22) may be the openings of ossified eustachian tubes. Witmer (1990) describes paired foramina in *Enaliornis barretti* as such openings. On the right side of the preserved section of the basisphenoid plate in YPM 1728 and just ventral to the right basal tuber, a flat fragment that does not appear grossly displaced may be a part of the parasphenoid. A conspicuous foramen in this fragment is possibly the anterior exit of an external carotid (fig. 21). Below this relatively large opening is a straight fracture. On the ventrolateral surface of the left basal tuber, two oblong grooves are developed which appear to be artifactually exposed pneumatic cavities (fig. 20).

Most of the brief description of the skull of YPM 1450 (Marsh, 1880: 120) is inaccurate. However, it can be inferred, as Marsh (1880) suggested, that the rostrum in *Ichthy-*

ornis dispar is extremely long, based on the preserved length of the mandibles. Although, Marsh (1880) described the occipital condyle as “very small, and directed backward” in YPM 1450, it is not preserved. What was indicated as the occipital condyle (Marsh, 1880: pl. XXI) is a part of a flat piece of bone perforated by two foramina discussed below (figs. 24A, 25).

In YPM 1450, the fragment identified as bearing the occipital condyle by Marsh (1880: pl. XXI) is visible in right lateral view (fig. 25). This flat fragment appears to be a portion of the exoccipital. It is perforated by two foramina, the more dorsal of which is the larger (fig. 25). These foramina may represent two exits of the 12th cranial nerve (hypoglossal), but this identification, given the obvious displacement of the fragment, is tentative. Slightly anterodorsal to this fragment lies another that appears to preserve the margin of a third and larger foramen (fig. 25) that may represent the exit of the 10th cranial nerve (vagus). Anterior and slightly ventral to the above-described fragment lies a third that ventrally contacts the right basal tuber. It appears in approximately its natural position relative to the right basal tuber and is tentatively identified as the metotic strut (fig. 25).

Anterior to the metotic strut (sensu Witmer, 1990) an elongate, crushed fossa interpreted as representing both the fenestra pseudorotunda and fenestra ovalis is present (fig. 25). A posterior projection is interpreted as an incomplete portion of the bar that separated these two fenestrae (crista interfenestralis). Dorsal to these depressions and close to the preserved fragments of the paraoccipital process is a depression possibly representing the posterior (caudal) tympanic recess (fig. 25). Anterior to the area of the fenestra pseudorotunda and fenestra ovalis is a small foramen that may represent the exit of the seventh cranial nerve (facial), but it appears slightly ventral to its typical position at approximately the same level as the fenestra ovalis (fig. 25). The auditory region lacks the extreme pneumatization seen, for example, in Palaeognathae and Galliformes (Witmer, 1990).

Anterior to this foramen is a much larger, roughly ovoid, depression interpreted as the

exit of the fifth cranial nerve (trigeminal; foramen n. maxillomandibularis; Baumel and Witmer, 1993). Ventrally adjacent and just slightly anterior to this structure is an opening to an anteroventrally directed passage or pocket that may be the rostral tympanic recess (fig. 25). Ventral and slightly posterior to this structure is a depression (fig. 25) that could only be interpreted as a portion of the ossified eustachian tube entrance (comparing favorably with *Gavia stellata*, e.g.). The remains of the ala parasphenoidalis (see Baumel and Witmer, 1993, for a discussion of this structure, which has its own ossification center in Aves) are interpreted as present anteroventral to this structure. The ala parasphenoidalis shows no sign of being particularly large or thick, morphologies present in *Hesperornithes* (Witmer, 1990). No further morphologies of the parasphenoid could be discerned; basipterygoid processes, for example, are not preserved.

The articular cotylae for the quadrate are best preserved in the holotype of *Ichthyornis dispar*, YPM 1450 (fig. 25). The otic and squamosal cotylae for the quadrate appear separated by a very narrow incisure marking the entrance to the dorsal tympanic recess visible on the right side of YPM 1450 (fig. 25) and on the left in YPM 1728 (fig. 20). A diminutive entrance to the dorsal tympanic recess between the capituli is consistent with the slight separation of the two articular surfaces on the head of the quadrate (YPM 1775; fig. 27D). In YPM 1450, there is no evidence of an elongate ventral, or “zygomatic”, process of the squamosal, but the lateral surface of this element is poorly preserved (fig. 25).

The only quadrates known for *Ichthyornis dispar* belong to YPM 1775 (fig. 27), a specimen referred to *Ichthyornis dispar* on the basis of apomorphy (see table 1). The left quadrate was figured in relative detail in *Odontornithes* (Marsh, 1880); however, Marsh (1880) commented only on the braincase articulation, which he considered “single headed”. Witmer (1990) figured in stereo photographs and in a line drawing the complete left quadrate of YPM 1775. The otic process of the right quadrate is also preserved and has not been figured; it contains some additional information about the mor-

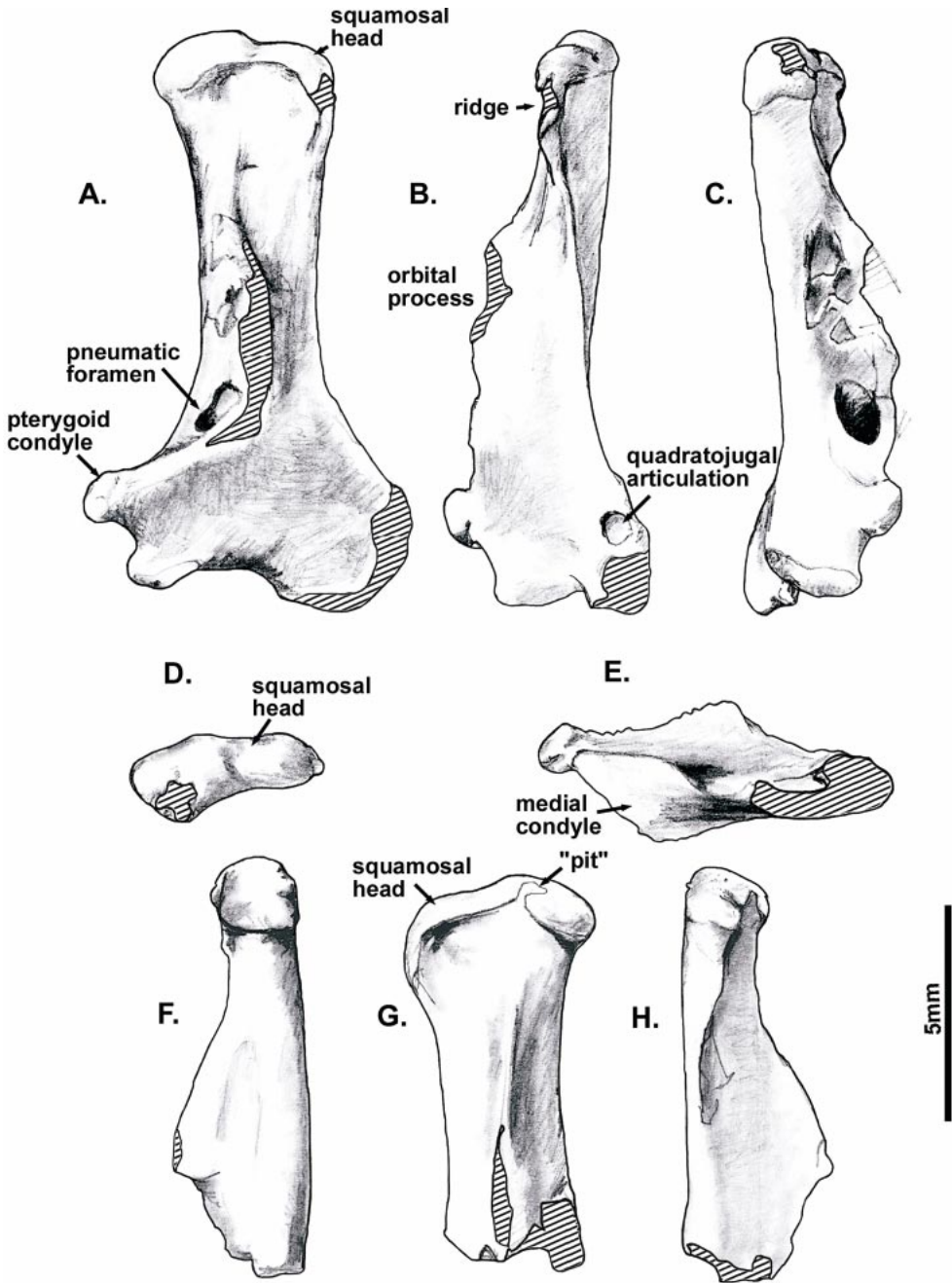


Fig. 27. The left (A–E) and right (F–H) quadrates of *Ichthyornis dispar* (YPM 1775) in (A, G) anterior, (B, H) lateral, (C, F) medial, (D) dorsal, and (E) ventral views.

phology of the head and the shape of the orbital process.

As described by Witmer (1990), the quadrate has a large pneumatic foramen lying

close to the pterygoid condyle on the ventro-medial surface of the shaft (fig. 27A,C). Witmer (1990) also noted that the position of the foramen is seen in some birds that were con-

sidered at one time “primitive” or basal within crown clade Aves (e.g., in the neoavian *Fregata minor*). The foramen in *Ichthyornis dispar* and these taxa, located close to the pterygoid articulation, differs, however, from the condition in the basal neognaths (i.e., galloanserines) surveyed for the phylogenetic analyses (see Part II, Materials and Methods), which have a foramen on the posterior surface of the shaft (see appendix 1). Further, the extremely dorsally located foramina in Palaeognathae are found to be non-homologous with the more basal foramina in the other included Aves because the two foramina co-occur at least in *Crypturellus undulatus* (appendix 1). They are only observed in the one crown clade palaeognath exemplar included and are, thus, optimized as an autapomorphy of that taxon (Part II, Results). They appear to be synapomorphies of crown clade Palaeognathae as Witmer (1990) suggested. The plesiomorphic position of a quadrate pneumatic foramen is ambiguously optimized (Part II and appendix 1).

The head of the quadrate is well preserved in both the right and left quadrates of YPM 1775 (fig. 27). The otic capitulum (articulating with an “otic cotyla”, or facet, variably of prootic or opisthotic; Baumel and Witmer, 1993) is more globose and projects farther dorsally than the squamosal capitulum. As noted by Witmer (1990) for *Hesperornis regalis* and figured for *Ichthyornis* (Witmer, 1990), the otic and squamosal capituli are distinct, separated by a nonarticulating shallow incisure. As also noted by Witmer (1990), this condition is distinct from that seen in extant Palaeognathae, in which there is no such incisure and the capituli are confluent. Both of these conditions are distinguished from the lack of an otic articulation, or “single headed” condition (Witmer, 1990), primitive to theropod dinosaurs.

The squamosal capitulum extends ventrally in a narrow ridge down the lateral edge of the otic process of the quadrate (fig. 27B). This feature is slightly broken on the left quadrate but is clearly seen on the right. The capitulum and ridge project slightly anteriorly to overhang the body of the otic process (fig. 27A,G). The otic capitulum has a slight anterodorsal indentation or pit (fig. 27G). A similar pit was described on the head of the

quadrate of *Potamornis skutchi* near the medial edge of its dorsal surface (Elzanowski et al., 2000). It was interpreted as an autapomorphy of that taxon and was considered to possibly delineate edges of the capituli that otherwise appear confluent in that taxon. A similar feature in *Ichthyornis dispar* in approximately the middle of the prootic capitulum suggests that this feature should not be taken to indicate the edge of a capitulum or to be homologous with the intercapitular incisure, because this feature co-occurs with an indentation in *Ichthyornis*.

The body of the otic process is only slightly narrower mediolaterally than the width of the head (fig. 27A). The process is virtually straight, although it bows slightly anteriorly close to its base. It is virtually unoutlined, lacking any muscular impressions (e.g., impressio medialis; Elzanowski et al., 2000) or processes (e.g., eminentia articularis; Lowe, 1926). The orbital process begins to rise below the head as a narrow ridge (fig. 27G). The dorsal portion of this low ridge of the process is better preserved on the right quadrate, which can be compared with the left to observe its relative extent down the body of the quadrate. The ventral portion of the process is missing. Posteromedial to the process, a slight depression is developed that deepens ventrally (fossa basiorbitalis; Elzanowski et al., 2000). At the broken base of the process is the large pneumatic foramen commented on above; a flat, dorsally facing surface lies between it and the pterygoid condyle (fig. 27A). The edges of the pterygoid articular surface are indistinct.

The pterygoid condyle is round, with a slightly constricted base (fig. 27A). It projects anteromedially well past the medial condyle and there is a cleft between it and the medial condyle. In *Ichthyornis dispar*, the pterygoid condyle is not an extension of a facet with a flat to concave dorsal surface and a projected edge (also a “pterygoid condyle” sensu Elzanowski et al., 2000), but rather it is a hemispherical, knoblike process (see appendix 1, character 32).

The maximum width of the ventral quadrate, with its condyles for articulation with the mandible, is more than half the maximum dorsal/ventral height. This finding is contra Elzanowski et al. (2000), who claimed the

width of the mandibular articulation was less than half the height of the quadrate, and considered that condition to be synapomorphic of a monophyletic “Odontognathae”, including *Ichthyornis* and *Hesperornithes*. This condition, by contrast, appears to be primitive to at least Avialae (see *Confuciusornis sanctus*, Chiappe et al., 1999).

Ichthyornis dispar (fig. 27E) and *Hesperornis regalis* have a medial condyle, with its long axis extending posterolaterally. In Palaeognathae and Galloanserae, it is the lateral condyle rather than the medial that angles posteriorly. The gain of a posteriorly projected lateral versus medial condyle may be a synapomorphy of Aves relative to *Ichthyornis*. Elzanowski et al. (2000) considered the condition in *Hesperornis regalis* and *Ichthyornis* to be a state in which the medial condyle is continuous with the “caudal condyle” and considered this morphology synapomorphic of a monophyletic Odontognathae. However, a posterior projection of the medial condyle is also present in *Confuciusornis sanctus*. Thus, this morphology does not appear synapomorphic but symplesiomorphic within Avialae, and it may be present in taxa still deeper within Theropoda.

It seems inappropriate to call the posterior continuation of single medial condylar surface a “caudal condyle”. The presence of a caudal condyle has been considered a synapomorphy of Aves relative to *Ichthyornis* (e.g., Cracraft, 1986). In palaeognaths and most neognaths (but not Galloanserae; reviewed in Cracraft and Clarke, 2001), the mandibular articulation of the quadrate has a triangular aspect in ventral view, with a posterior articular surface developed that is variably distinct. Elzanowski et al. (2000) describe *Ichthyornis* and *Hesperornis regalis* as having such an apomorphic posterior articulation and triangulate articular surface.

The highly recurved and large medial condyle in *Hesperornis regalis* is strikingly different from the flat and relatively shorter condyle in *Ichthyornis dispar* (fig. 27E). The ventral surface of the quadrate in *Hesperornis regalis* and *Confuciusornis sanctus* (Chiappe et al., 1999) could be described as “triangulate” (Elzanowski et al., 2000; with closely placed condyles and a posteriorly directed medial condyle). By contrast, the

broad, shallow separation between the medial and lateral condyles (sulcus intercondylaris; Baumel and Witmer, 1993), and the preserved morphology of the medial condyle (fig. 27A,E) do not confer a triangulate aspect on the ventral surface of the *Ichthyornis dispar* quadrate (fig. 27A,E).

Given the extensive range of conditions in Aves, which includes many cases in which the caudal condyle is virtually indistinguishable from the medial or, alternatively, the lateral condyle, or in which the caudal condyle is apparently secondarily lost, it is reasonable to presume that *Ichthyornis* and *Hesperornis regalis* might represent such a case outside of Aves. However, it is a less supported explanation given that the medial condyle in *Confuciusornis sanctus*, *Ichthyornis*, and *Hesperornis regalis* is a single surface with such a posterior component and no nonavian taxa are known to have a distinct caudal condyle. Additionally, none of the preserved mandibular fragments that are a part of the YPM material (i.e., 1450, 1761, 6264) indicate the presence of a distinct posterior facet (fig. 28). Neither in these *Ichthyornis dispar* exemplars nor in *Hesperornis regalis* (contra Elzanowski et al., 2000) is there any indication that the slight posterior component of the medial articulation is a separate articulation or condyle.

The quadratojugal articulation is shallow and dorsal to the lateral condyle (fig. 27B). This articulation has also been described as shallow in *Hesperornithes* and *Potamornis* (Elzanowski et al., 2000), but it is deeper in those taxa than in *Ichthyornis dispar* or *Confuciusornis sanctus* (Chiappe et al., 1999). The pit for the quadratojugal articulation also appears deeper in *Patagopteryx deferrariisi* (Chiappe, 1996) than in *Ichthyornis dispar*. Furthermore, in *Hesperornis regalis* and *Potamornis*, this pit lies close to the lateral condyle (Elzanowski et al., 2000), while it is distinctly dorsal to this condyle in *Ichthyornis dispar*.

MANDIBLE

Portions of the mandible are represented in the holotype of *Ichthyornis dispar* (YPM 1450) and in referred specimens YPM 1735, YPM 1749, YPM 1761, YPM 1775, and

YPM 6264, which are referred on the basis of apomorphy or morphological correspondence with the holotype (see table 1). The right mandible of YPM 1450 was mounted in the *Ichthyornis dispar* panel mount as the left (fig. 19A; as noted in Gregory, 1952, and in Gingerich, 1972). The partial left mandible from YPM 1749 was mounted in the *Ichthyornis victor* mount as the left maxilla (fig. 19A). It was identified as part of YPM 1749 with reference to Gibb's notes (fig. 3) and description of the material in *Odontornithes* (Marsh, 1880: 124–125). The mandible of YPM 1761 (fig. 28A) is larger than that of the holotype (YPM 1450) or YPM 6264 (fig. 28B).

Marsh (1880) commented on very few aspects of mandibular morphology. He considered there to be no ossified mandibular symphysis in *Ichthyornis* and no “distinct symphyseal surface” (Marsh, 1880: 123). He described the rami of the jaws as nearly straight, large and massive, and compressed mediolaterally, noting that nearly all sutures were closed with the exception of the splenial-angular intramandibular joint (Marsh, 1880: 123). Finally, he commented that the upper margin of the dentary was straight and that there was no mandibular foramen and no retroarticular process (i.e., that the jaw was “truncated” directly behind the articulation of the quadrate; Marsh, 1880: 123). As is further elaborated below, this analysis confirmed the lack of an ossified symphysis and several characters of the jaw Marsh (1880) described. Visible sutures in the jaw and a small mandibular fossa (contra Marsh, 1880) and previously undescribed morphologies are treated below.

Gregory (1952) was the only other worker to figure the jaw, hypothesizing the identity and topological relations among the bones that comprise it. Gingerich (1972) commented on the reconstruction by Gregory (1952) and discussed additional details of the articulation with the quadrate based particularly on a newly uncovered specimen (YPM 6264)

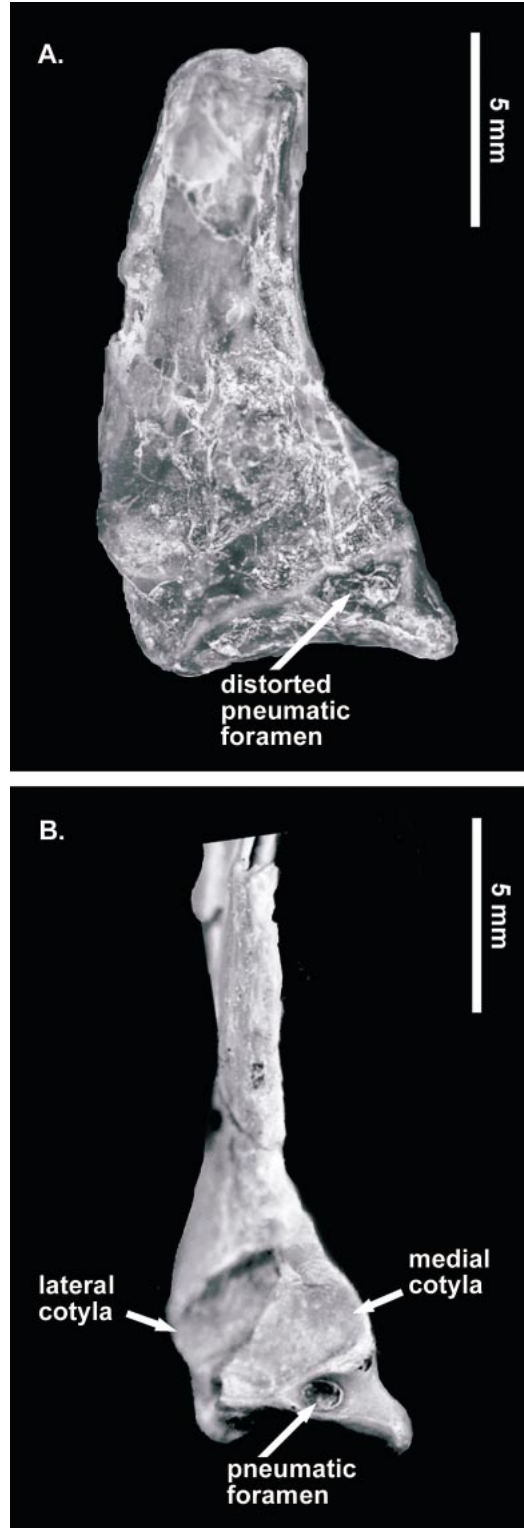


Fig. 28. The posterior portion of the mandible of *Ichthyornis dispar* in dorsal view: (A) YPM 1761 and (B) YPM 6264.

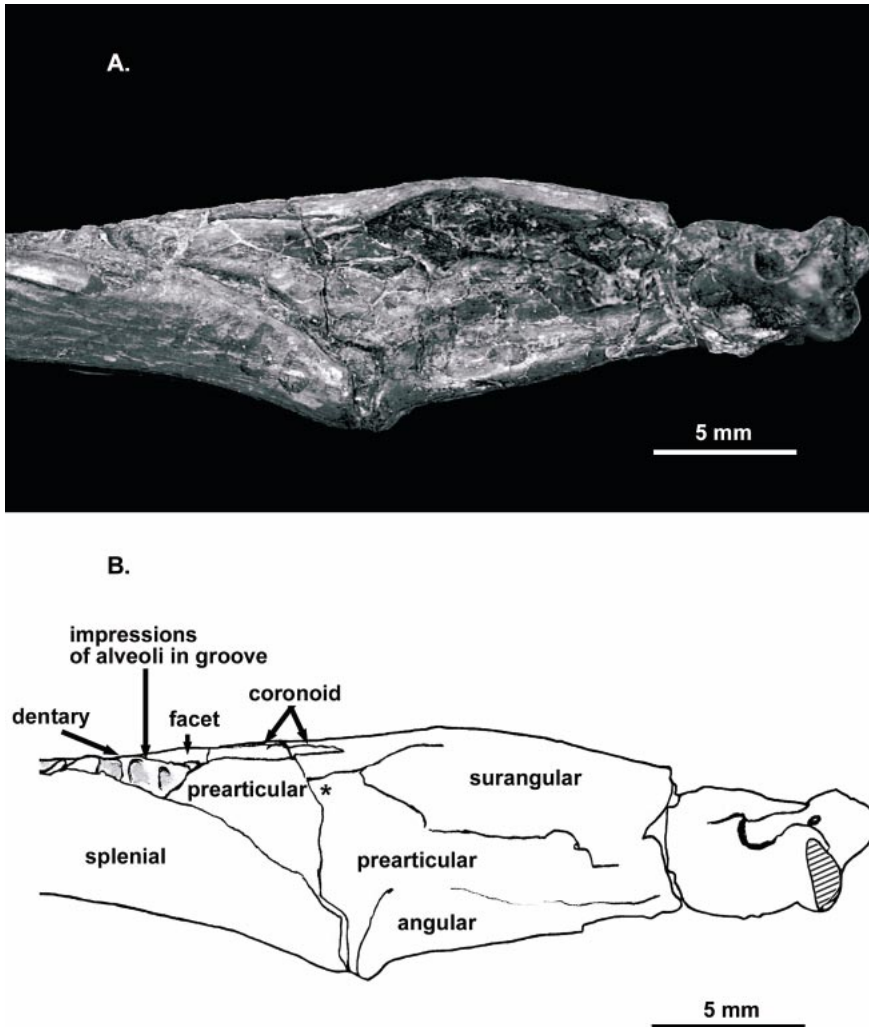


Fig. 29. The posterior portion of the right mandible of the *Ichthyornis dispar* holotype (YPM 1450) in (A, B) medial (internal) view. The prearticular/surangular suture appears distorted posterior to a prominent fracture (*).

that, among the YPM material, best preserves the posteriormost portion of the jaw (Gingerich, 1972). Figure 19B,C, and figures 28–32 compare representations and reconstructions of the jaw in *Odontornithes* (Marsh, 1880; fig. 19B), by Gregory (1952; fig. 19C), and by this analysis (figs. 28–32).

The posterior part of the mandible and the cotylae for the quadrate are represented in YPM 1450 (right side), YPM 1761 (fig. 28A), and YPM 6264 (fig. 28B). Gingerich (1972) described this portion of the jaw in

detail, and the present analysis largely agrees with his description. What was named the “anterior cotylus” by Gingerich (1972) corresponds to the lateral cotyla of other authors (cotyla lateralis; Baumel and Witmer, 1993) and the “posterior cotylus”, to the medial (cotyla medialis; Baumel and Witmer, 1993). The quadrate cotylae appear as two postero-laterally angled grooves and are best preserved in YPM 6264. Directly posterior to the medial cotyla is the pneumatic foramen (fig. 28) that was commented on by Ginger-

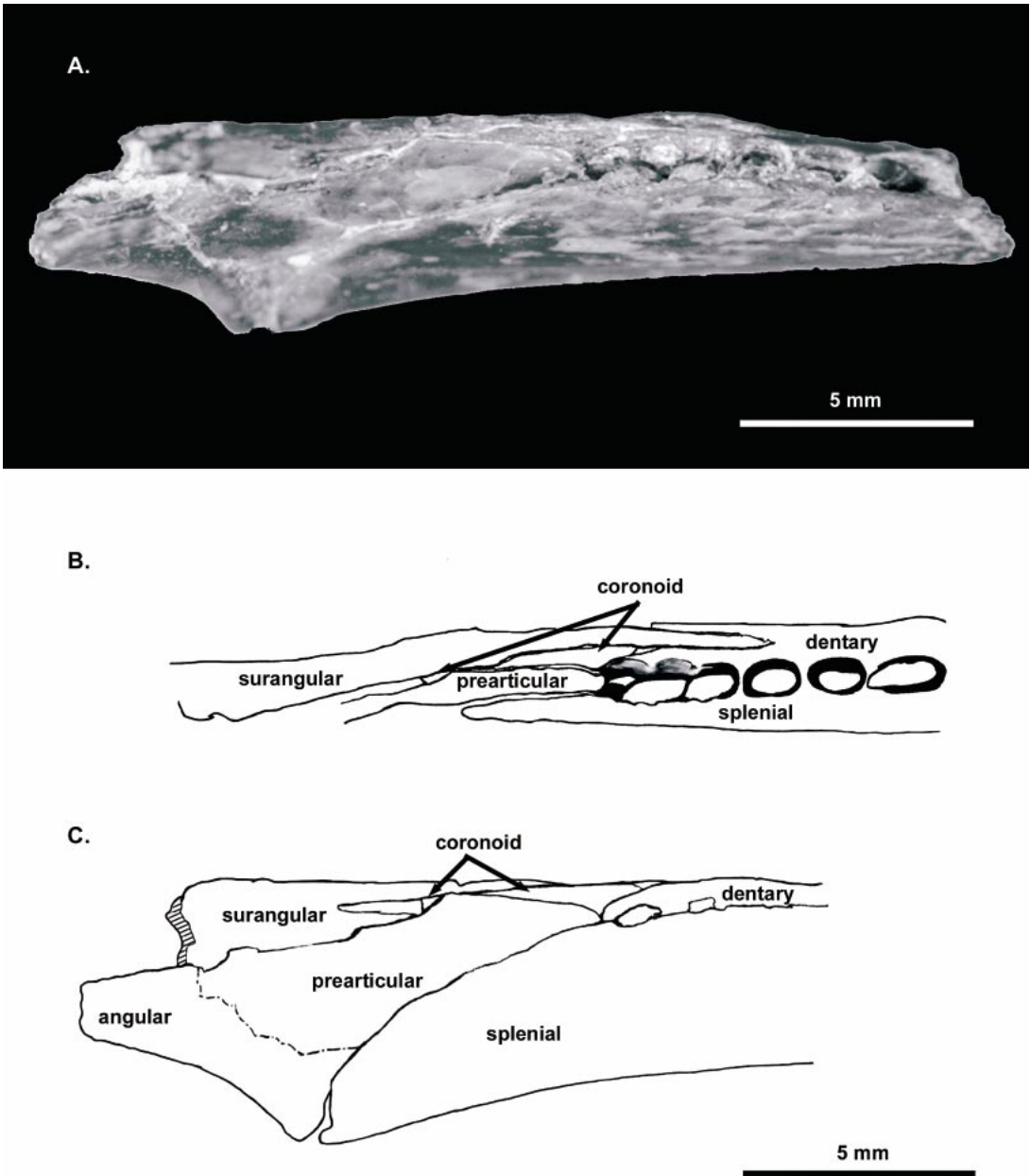


Fig. 30. The posterior portion of the left mandible of the *Ichthyornis dispar* holotype (YPM 1450) in (A, B) oblique mediodorsal and (C) medial views.

ich (1972) and Witmer (1990). The form of this feature can also be seen, undistorted, in YPM 1450; it is ovate and sits in a triangular depression. In YPM 1761, the morphology of the fossa is distorted by crushing (fig. 28A), which accounts for the interpretation

of it as “oblong” in Elzanowski et al. (2000: 718).

Medial to this foramen and directly posterior to the edge of the medial cotyla in YPM 6264, the entrance and exit of the n. corda tympani (Oelrich, 1956) are visible in

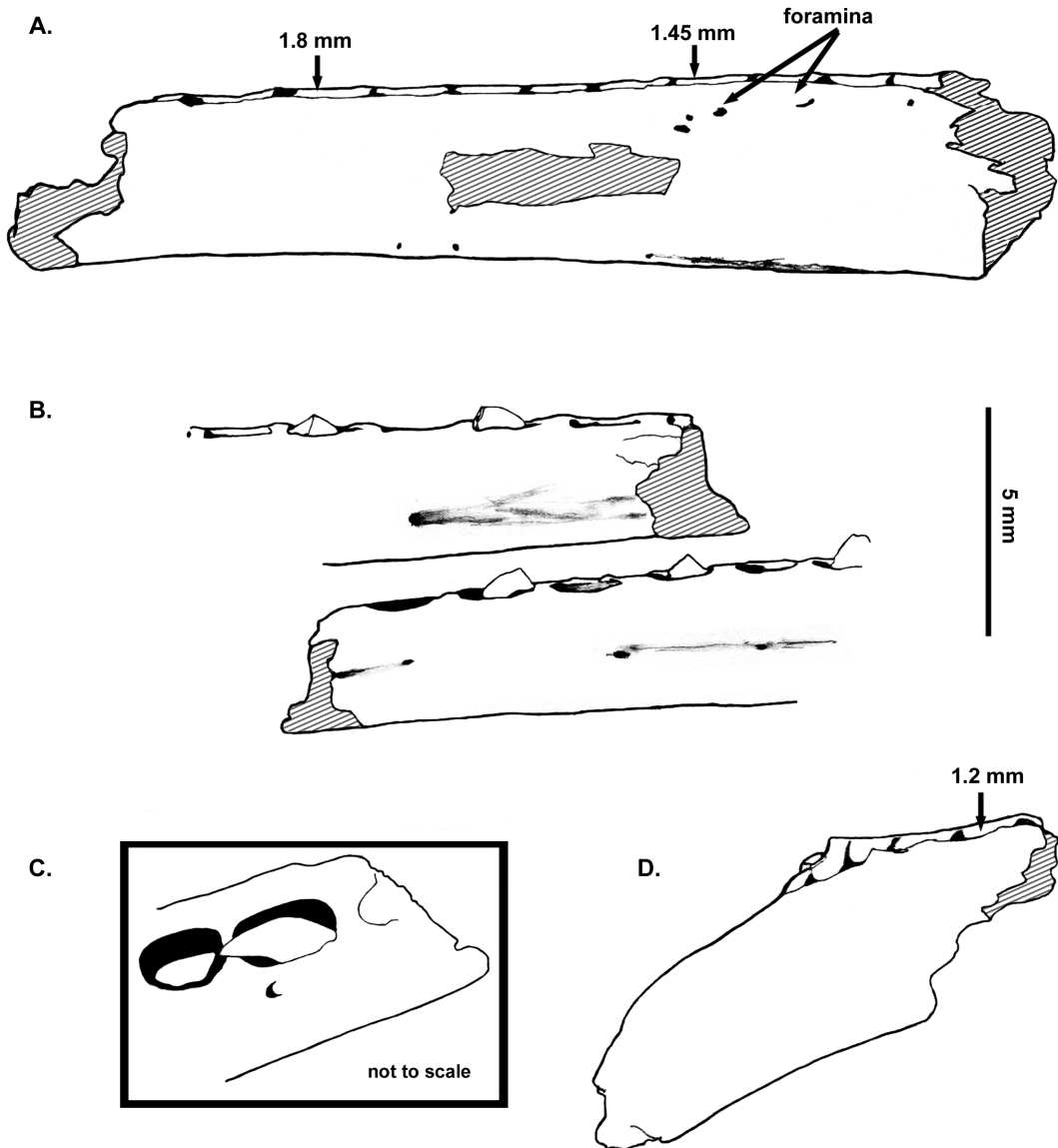


Fig. 31. The teeth and alveoli of *Ichthyornis dispar*: (A) the right mandible of YPM 1735 in medial view with measurements of the length of alveoli in anterior (left) and posterior (right) parts of the jaw fragment; (B) a mid tooth-row portion of the left mandible of YPM 1450 in medial (top) and lateral (bottom) views; (C) a developing tooth in the sixth alveolus from the posterior end of the dentary (YPM 1450; the tooth appears foreshortened as a result of the oblique dorsal view); (D) the posterior portion of the tooth row in YPM 1749 with the length of a representative alveolus.

what would be part of the prearticular, although sutures between this element and the articular are not visible. The entrance is located on a slight dorsal prominence medial to the foramen and the exit (anteroventral to it) is visible in medial view close to the pos-

terior edge of the cotyla. This feature is infrequently preserved and highly variable in Aves. While the passage of the n. corda tympani was demarcated in one specimen of *Chauna torquata* (Anhimidae), it was not visible in a specimen of the closely related

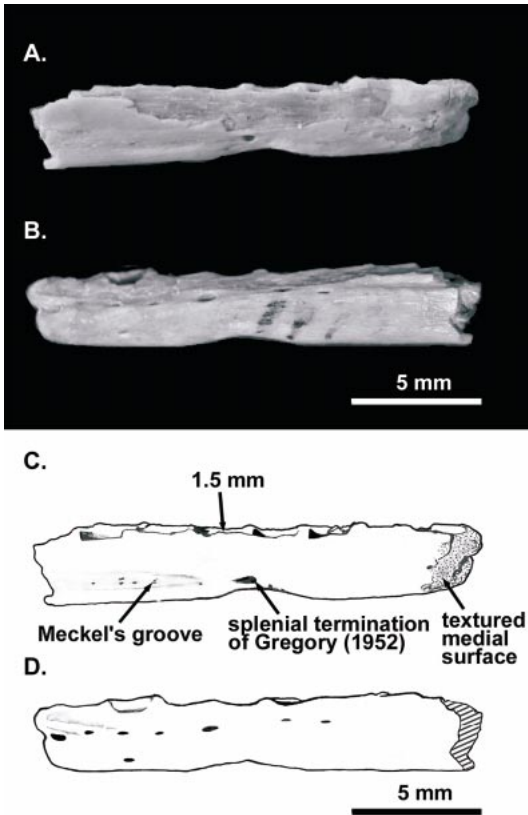


Fig. 32. The anterior end of the mandible in *Ichthyornis dispar* (YPM 1775) in (A, C) medial (internal) and (B, D) lateral (external) views. The length of a representative alveolus is indicated.

Anhima cornuta (also Anhimidae). It is much more conspicuous in *Gavia stellata*, where the anterior passage of the nerve could be traced for much of the length of the posterior mandible. By contrast, it was not demarcated in the exemplars of palaeognaths and galliforms surveyed (see Comparative Materials and Methods). The groove demarcating the passage for the nerve does not appear developed in the holotype of *Ichthyornis dispar* (YPM 1450) or in YPM 1761. In YPM 1450, however, the relevant area of the posterior mandible is not well preserved.

The morphology of the lateral cotyla is partially obscured by crushing in all three specimens. This cotyla is best preserved in YPM 6264 (fig. 28B), where its depth and medial extent are visible. Both of these dimensions of the lateral cotyla in *Ichthyornis*

dispar are greater than previously illustrated. YPM 1761 was illustrated (Elzanowski et al., 2000) as virtually uncrushed; it is, however, strongly crushed dorsoventrally (fig. 28A). The lateral cotyla is depicted as a shallow, round facet restricted to the lateral edge; however, there is a fracture that runs anteroposteriorly through the specimen from the posterolateral edge toward the midline (fig. 28A). It is this fracture and crushed bone that form the artifactual medial terminus of the cotyla illustrated in Elzanowski et al. (2000). The area of the anterior edge of the medial cotyla and what is visibly part of the lateral cotyla is also obliterated by damage, explaining the illustration of YPM 1761 in Elzanowski et al. (2000) in which the medial condyle appears smaller and shallower than in the condition visible in YPM 6264 (fig. 28B) and to some degree in YPM 1450.

A posterior prominence at the lateral terminus of the medial cotyla has been dubbed the articulation of a third condyle of the quadrate (Elzanowski et al., 2000). As discussed above with reference to the morphology of the quadrate, *Ichthyornis dispar* lacks a distinct third or “caudal” condyle, as is plesiomorphic for Avialae. There is a slight, posteriorly facing extension of the medial condyle, and it would have articulated with this prominence. However, as discussed above, to consider this feature the articulation of a distinct “caudal condyle” seems unjustified. This feature is considered simply the posterolateral edge of the medial cotyla. The posterior mandibular midline is broken in YPM 1450 and YPM 6264. In both of these specimens crushing was mediolateral, creating a central break and/or ridge.

As previously noted (Marsh, 1880; Gregory, 1952; Gingerich, 1972), *Ichthyornis dispar*, unlike *Hesperornis regalis*, lacks a retroarticular process. A short medial projection, or medial process (processus medialis mandibulae, Baumel and Witmer, 1993), is developed on the posterior end of the articular (Gingerich, 1972; fig. 28). The posterior surface of the mandible is slightly concave (fig. 28; shallow fossa caudalis, Baumel and Witmer, 1993).

Most of the contacts between the elements of the posterior mandible (i.e., posterior to the last alveoli) are best represented in YPM

1450 (figs. 29, 30) and YPM 6264, with a portion of the angular/surangular and angular/prearticular contacts also visible in YPM 1775. Portions of the angular, surangular, and prearticular are preserved in YPM 1761, but the sutures are all but completely closed. YPM 1775 preserved the contour of the posterodorsal margin of the dentary. YPM 1761 is larger than YPM 1450, YPM 1775, and YPM 6264. In YPM 1450, the morphology of both the right and left jaws is comparable; the left jaw, however, was depressed by crushing, especially at the posterior terminus of the preserved fragment (figs. 29, 30). Similarly, compression slightly exaggerated the height of the right jaw.

Gingerich (1972) noted that the angular forms the ventral edge of the mandible posterior to the angular/splenic contact (intra-mandibular joint). Gingerich (1972) further described that at this contact, the angular has an articular facet for the splenic; the surangular forms more than one-half the height of the lateral mandibular surface posterior to its splenic contact; the prearticular extends between the splenic and the dentary on the dorsal edge of the jaw. These morphologies were confirmed in YPM 6264 and observed in the holotype of *Ichthyornis dispar* (YPM 1450; figs. 29, 30).

The posterodorsal splenic margin forms a smooth arc from close to the last tooth to the intramandibular joint (figs. 29, 30). Just anterior to this joint, the splenic passes laterally, making up the ventral margin of the jaw. On the lateral surface of the left jaw, 1 mm from the ventral edge, approximately 3 mm of the splenic/dentary suture is visible passing anteriorly, roughly subparallel to this ventral margin. The anterior angular margin is slightly cupped ventrally to receive the splenic (fig. 30).

The posterior contacts of the dentary are best preserved on the right jaw of YPM 1450. In lateral view, the dorsal surface of the dentary arcs from its ventral contact with the splenic to the tooth row. Just ventrolateral to the alveolar margin, the dentary receives a short, narrow tongue of the surangular (fig. 30). In Aves, this process of the surangular can be much more extensive, often extending anteriorly for approximately one-half of the rostrum (see Sanz et al., 1997,

for a discussion of the distribution of this condition). On the left jaw, the anterior process of the surangular appears slightly longer than on the right jaw; however, this appears artifactual. A portion of this contact is more visible in YPM 1775; in medial view, the dorsal edge of the dentary in both jaws visibly curves posteroventrally. The exposed medial surface of this portion of the dentary bears the impressions of several incompletely formed alveoli: Two faint ridges separate three indentations that are approximately the dimensions of the alveoli that are completely formed in the anterior part of the tooth row (fig. 30C). The more posterior of these is most weakly developed. In the left jaw (that is not compressed significantly mediolaterally) two ridges are also visible with three alveolar impressions, and three corresponding teeth are preserved. The most posterior of these teeth is least erupted, and the posterior terminus of its incompletely formed alveolus and the apparent terminus of the dentary itself do not appear artifactual. Gregory (1952) considered the dentary to extend significantly posterior to the preserved portion of the prearticular; however, the dentary terminates anterior to the splenic/angular contact as described below.

A large coronoid was described for the holotype of *Ichthyornis dispar* (YPM 1450) by Gregory (1952). Gingerich (1972), however, saw no sign of a coronoid bone in the holotype (YPM 1450). This analysis confirms the presence of a coronoid in *Ichthyornis dispar* (e.g., YPM 1450), although it differs considerably from Gregory's (1952) illustrations (compare fig. 19C with figs. 29 and 30). In the left mandible of YPM 1450, a suture is visible between the posterior end of the dentary and part of element dorsal/posterodorsal to it (fig. 30C). Between this element, identified as the coronoid, and the surangular laterally, another suture is visible (in dorsal view; fig. 30B). The posterodorsal contact between the dentary and the coronoid is curved dorsoventrally. The shape of this contact can also be seen in both the right mandible of YPM 1450 and in YPM 1749. Posterior to the end of the dentary, the coronoid has an open sutural contact with the prearticular ventrally and the continuation of its contact with the surangular laterally (fig. 30).

The coronoid is also visible continuing just posterior to a contact between the prearticular and the surangular, which is an artifact of the compression of this mandible.

The position and contacts of the coronoid in the right jaw of YPM 1450 are the same as those preserved in the left. In the right jaw, a small, dorsoventrally flat facet that would have been occupied by the coronoid is preserved just dorsal to the posterior end of the dentary (fig. 29). The facet lies in the same position occupied by the anterior part of the coronoid in the left jaw and is formed of an artifactually exposed surface of the surangular contact. This exposed surface is continued posteriorly as an open suture (visible in dorsal view) between the surangular and coronoid, which is exposed as a diminutive tongue of bone (fig. 29B). A brief, tapering continuation of the coronoid is faintly visible continuing on the other side of a conspicuous fracture crossing the mandible (fig. 29). The coronoid/prearticular suture appears closed at the coronoid's posterior terminus.

Gregory (1952) described a massive coronoid with some of the same contacts described above. He described a large fragment of bone supposed to lie on the medial surface of the right jaw of YPM 1450 and considered this to be a part of the coronoid (fig. 19C). No such large fragment of bone was observed in the specimen removed from the mount, and it seems that what was represented was merely a portion of the prearticular anterior to the shallow mandibular fossa (fig. 29).

Ventral to the posterior end of the coronoid in YPM 1450, the surangular/prearticular contact is visible. Just posterior to this contact is the anterodorsal margin of a mandibular fossa (i.e., fossa aditus canalis mandibulae; Baumel and Witmer, 1993; fig. 29). A portion of the anteroventral margin of this fossa can be discerned in YPM 1761, YPM 1775, and YPM 6264. It appears to be formed of the prearticular (compare YPM 1775, where some of the prearticular/angular/surangular contacts remain open, and YPM 1761 in which the sutures appear closed; YPM 1761 is also the largest mandible of the YPM specimens). The lateral and dorsal edges of this fossa appear to have been formed of the surangular.

In YPM 6264, a large foramen is visible in medial view near the ventral edge of the preserved portion of the surangular and at close to the midpoint of the mandibular fossa. This foramen was not described by Gingerich (1972); it is directed posteriorly with no visible exit on the preserved portion of the lateral surface. A somewhat similar configuration was noted in *Crypturellus undulatus*, where foramina in the surangular are directed both anteriorly and posteriorly, and only the anterior of which appears to penetrate to the lateral surface. The feature probably represents a branch of fifth cranial nerve (trigeminal), possibly the n. intramandibularis (Dubbeldam et al., 1993). This foramen could not be seen in YPM 1450, where there is considerable breakage in this region. It is also possible that the prearticular could have covered the foramen medially, as it is posterodorsally incomplete in all specimens.

The posterior extent and contacts of the surangular, prearticular, angular, and articular are not well preserved in any of the specimens. However, the sutures between the angular/surangular, angular/prearticular, and angular/articular appear closed posteriorly (YPM 1450, YPM 1761, YPM 1775, YPM 6264). The anterior portion of the angular/surangular contact appears to be open in YPM 1775, and it may also be open in the smaller holotype of *Ichthyornis dispar* (YPM 1450). The angular extended dorsally approximately a third of the height of the posterior mandible in lateral view. Medially, the prearticular angles toward the ventral margin. There may be a slight indication of this contact in the right jaw of YPM 1450, anterior to the medial cotyla close to the ventral margin of the jaw (fig. 29). No suture between the prearticular and angular was discernable in YPM 6264, though Gingerich (1972) described the angular tapering to a point ventral to the articular cotylae for the quadrate.

The dorsal surface of the surangular is unbroken in YPM 1450, and it suggests that no coronoid process (processus coronoideus; Baumel and Witmer, 1993) was developed. The dorsal edge of the posterior mandible rises slowly from the level of the articular fossa and is highest just posterior to the level of the angular/splenic contact. No pseudo-

temporal tubercle (tuberculum pseudotemporale; Baumel and Witmer, 1993) is visible.

The dentigerous portions of both dentaries are well preserved in YPM 1450. Both right and left are complete with the exception of the anteriormost tip of the left, which is slightly abraded. The total length of the right jaw in YPM 1450 is 67 mm. The socketed tooth row extends 41 mm of this length (from posterior edge of last tooth to tip of dentary) confirming Marsh's measurements (Marsh, 1880: 125). Portions of the anterior jaw are additionally represented in YPM 1735 (fig. 31A), YPM 1749, and YPM 1775 (fig. 32). Anterior to the intramandibular joint, the dentary and splenial are completely fused in all specimens except for the short open suture on the lateral surface of left jaw of YPM 1450.

The splenial in *Ichthyornis* was described as making up the medial margin of the last four alveoli and then angling ventrally (Martin and Stewart, 1977; SMM "13520" = SMM 2503, YPM 1450). However, the location of the dorsal dentary/splenial contact is not conspicuous in any YPM material. A series of small foramina on the left jaw of YPM 1450 (approximately one per alveoli) lie close to the posteriormost complete socket and move slightly ventrally relative to the alveoli for each of the three anteriorly adjacent sockets. These foramina could demarcate the dorsal edge of the splenial in this area. In YPM 1735, five small foramina are aligned subparallel to the posterodorsal margin of the preserved fragment (which does not include the posterior terminus of the dentary; fig. 31A). The anterior two are positioned slightly ventral to the other three (fig. 31A). The line of foramina does not appear to extend further forward. It is also possible that these foramina are the same as those in YPM 1450, and demarcate a portion the dorsal splenial/dentary contact. That they are only developed posteriorly, and not along the entire tooth row, suggests that they may not be related to dental succession or replacement. Martin and Stewart (1977) reported that in a large specimen of *Ichthyornis* they referred to as SMM "13520" (which is here found to be SMM 2503 and referred to as such in this document; see Taxonomic Revision), the ventral splenial suture was oblit-

erated but marked by microscopic foramina. No such foramina were observed in the YPM material. Further, there is no apparent reason that the splenial/dentary contact should be indicated by foramina, as this is not its typical development in Aves, or elsewhere.

The position of the anterior terminus of the splenial is unclear. Norell and Clarke (2001) considered the splenial to extend to the tip of the mandible and to be involved in the symphysis. The smooth anteromedial surface of the jaw and the absence of a conspicuous Meckel's groove (fig. 32A,C) suggested this scoring for *Ichthyornis*. Gregory (1952) inferred that Meckel's groove was manifest as a short groove passing from a large foramen close to the tip of the jaw in YPM 1450 (fig. 19C) and what he interpreted as the "symphyseal area" (Gregory, 1952: 78). He inferred that the splenial terminated at this foramen, though he could discriminate no suture (Gregory, 1952). Martin and Stewart (1977) also considered the splenial to end at a large foramen, which they described as 19 mm from the tip of the mandible (fig. 32A,C). Meckel's groove was interpreted as terminating only a few millimeters anterior to the foramen (Martin and Stewart, 1977). However, the interpretation of the position of the large anterior foramen as demarcating the anterior tip of the splenial seems unjustified because in Aves (e.g., *Struthio camelus*, *Gavia stellata*), the splenial often continues along the ventral margin anterior to the opening of Meckel's canal (where it ceases to cover the cartilage) to extend into the symphysis.

A large, anteriorly opening foramen approximately 19 mm from the tip of the jaw and a shallow groove anterior to it (fig. 31B) are visible on the left mandible of the *Ichthyornis dispar* holotype (YPM 1450). These features appear to correspond with the groove and posterior foramen previously discussed (Gregory, 1952; Martin and Stewart, 1977). In the right jaw of YPM 1450, a foramen that may correspond with the anterior foramen lies 8.4 mm from the preserved end of the mandible, but no groove is discernable posterior to it.

The anterior portion of the groove and its termination at a second foramen are better preserved in YPM 1775, where this second

foramen lies dorsal to a notch in the ventral margin of the mandible, 7.1 mm from its tip (fig. 32A,C). In YPM 1775, this anterior foramen appears to enter the medial surface of the mandible at a high angle to the axis of the groove (fig. 32A,C). It is possible that this feature is better construed as the canal for the internal mandibular artery rather than related to the passage of Meckel's cartilage, which does not curve abruptly at any point.

In sum, the posterior medial foramen that opens anteriorly may represent the anterior opening of Meckel's groove, consistent with Gregory (1952) and Martin and Stewart (1977). If so, it then seems that this groove was very shallow and that Meckel's cartilage ran superficially along the medial surface of the jaw anteriorly. This superficial development was observed in a cleared and stained juvenile chicken (*Gallus gallus*, YPM 14517). However, is not clear that the anterior foramen represents the cartilage's exposure in the "symphyseal area", as suggested by Gregory (1952); the foramen perforates the jaw at a high angle relative to the axis of the groove. Finally, even if the posterior foramen represents the anterior opening of Meckel's canal, there is no necessary relationship between this opening and the termination of the splenial; as noted in Aves, a ventral tongue of the splenial often continues anterior to the opening of Meckel's canal.

Martin and Stewart (1977) described seven mental foramina on the lateral surface of the right dentary (YPM 1450), which were not indicated by Marsh (1880). A series of six large foramina was indicated by Gregory (1952) for the left jaw. On the right jaw of YPM 1450, six large and two small foramina are visible. On the anteriormost tip of the jaw (YPM 1450, YPM 1775), a large terminal foramen is developed (fig. 32B,D). The most posterior of the mental foramina was described as giving rise to a broad canal that widens posteriorly (Martin and Stewart, 1977). Gregory (1952) considered this feature artifactual, while the current analysis agrees with Martin and Stewart (1977) in considering this depression to be real. The lateral groove associated with the mental foramina seen on both the right and left mandibles of YPM 1450 is less pronounced in YPM 1775. The mental groove lies at the

apex of the dorsoventrally convex lateral surface. In YPM 1775, another foramen is located ventral to the second mental foramen, just dorsal and anterior to the notch in the ventral margin.

A prementary bone, or an intersymphysial ossification, lying between the anterior tips of the dentaries (Martin, 1987), was reported for *Hesperornis regalis* (KUV 71012) and *Parahesperornis alexi* (KUV 2287), and inferred, from the shape of the mesial termination of the dentary, to be present in *Ichthyornis* (Martin, 1987). There is no evidence in any YPM *Ichthyornis* specimen of a prementary bone, nor of terminal facets on the dentaries Martin (1987) described as articulating with the prementary bone in *Hesperornithes*.

In *Ichthyornis*, a discrete area of textured bone lies on the medial surface of the tip of the mandible in YPM 1775 (fig. 32A,C). It is interpreted as the limited area of fibrous attachment to the corresponding tip of the opposing mandibular ramus. The rami would have met at a very low angle with their symphysis developed as a restricted, primarily dorsoventral, strip of contact between the rami. The conformation of the attachment is not unreasonably compared to the small contact in *Sterna maxima* (ossified as in all Aves) in which the area of contact at the mandibular tips is also very limited and primarily dorsoventral with almost no ventral floor. Thus, it does not appear necessary to hypothesize a prementary bone to explain the shape of the distal terminus of the preserved mandibles in *Ichthyornis*.

Just posterior to the textured medial symphysis (YPM 1450, YPM 1775), a small foramen is visible (fig. 32A,C). A second small foramen lies in this area of textured bone in YPM 1775 that is not visible in YPM 1450 (fig. 32A,C).

DENTITION

Neither the illustration of a tooth from YPM 1450, the holotype of *Ichthyornis dispar*, in Marsh (1880: pl. XXI) nor the reconstruction of a tooth of *Ichthyornis* in Martin and Stewart (1977: fig. 2) closely approximate the actual shape of the teeth in *Ichthyornis*. The illustration in Marsh (1880) ap-

proximates only the tip rather than the complete tooth crown. Only portions of the roots and cementum are preserved in YPM 1749, and no teeth are preserved in YPM 1735, where only the shape of the empty alveoli can be observed.

Marsh commented (1880: 124) that *Ichthyornis* had socketed teeth with pointed, strongly recurved, compressed crowns that lacked serrations. Gregory (1952) noted that the tooth crowns were compressed, with recurved tips with sharp anterior and posterior cutting edges. Martin and Stewart (1977) reiterated Gregory's (1952) observation that the crowns were compressed and recurved posteriorly. Martin and Stewart (1977) further describe the tooth crowns as both medially and laterally convex, and that anterior edges of the teeth had a distinct shoulder that exaggerates the teeth's posteriorly recurved appearance. The teeth were supposed to rapidly expand as they entered the jaw and radiograms are cited as suggesting that the bases of the teeth may have inclined posteriorly in the tooth row to further exaggerate their recurved appearance (Martin and Stewart, 1977). Evaluation of the morphologies of YPM 1450 (fig. 31B,C) and YPM 1775 is compatible with the teeth indeed being pointed, posteriorly recurved, lacking serrations, and mediolaterally compressed with trenchant anterior and posterior edges.

In the six posteriormost teeth of the left mandible of YPM 1450, most aspects of dental morphology can be observed, although all aspects are not preserved in any single tooth portion. The first and sixth tooth portions (fig. 31C) preserve the tip of a striated and recurved tooth crown. The posterior margin of the crown is smoothly arched, rather than having the relatively straight posterior margin illustrated in Martin and Stewart (1977). The crown of the sixth exposed tooth is visibly more elongate and narrower (fig. 31C) than the stumpy morphology these authors illustrate (Martin and Stewart, 1977: fig. 2d).

In YPM 1775, a carina and a slight indentation at the anterior base of a tooth crown are visible. The teeth of *Ichthyornis* (crown and root) are much more compressed than illustrated in Martin and Stewart (1977: fig. 2) and lack the shoulder at the base of the crown seen in crocodilians that these authors

illustrate. The root is ovoid and slightly wider than the base of the crown. The expansion interpreted by Martin and Stewart (1977) could be a result of accreted cementum. They also interpret the one exposed tooth in *Hesperornis regalis* (YPM 1206) as having an enormously expanded root and this also appears to be cementum.

In a more recent publication (Martin and Stewart, 1999) addressing tooth implantation in avialans, complete nonavian theropod morphologies are compared with broken teeth from *Paraesperornis alexi* and *Alligator* (Martin and Stewart, 1999: fig. 2). In fact, consideration of the YPM material suggests that the shape of the tooth crown in *Ichthyornis* (e.g., YPM 1450) is much closer to nonavian theropod morphologies than is suggested by Martin and Stewart (1999: fig. 2). Crocodilian teeth lack the strong mediolateral compression present in *Ichthyornis* and other toothed theropods. There is also a distinct shoulder present, or a constriction ringing the tooth crown at its base, developed in crocodilians, that is not developed in *Ichthyornis* (e.g., YPM 1450).

SIZE AND NUMBER: Marsh (1880) estimated the position of the preserved maxillary fragment in YPM 1450 and then inferred that the opposing teeth in the posterior third of the dentary were smaller. This hypothesis is dependent on the position estimated for the portion of the maxilla relative to the mandibular tooth row. As Marsh (1880) noted, the largest tooth sockets in the mandible lie just posterior to the midpoint of dentary and then decrease in size slightly posteriorly; they do not decrease in size to the degree illustrated in *Odontornithes* (Marsh, 1880). Indeed, if the maxillary fragment was not posteriorly placed, there would not seem to be a notable difference in the size of the alveoli opposing them. However, to have larger upper tooth row sockets (and teeth) compared to the lower is an archosauriform synapomorphy (Gauthier et al., 1988), which could be plesiomorphically retained in *Ichthyornis*.

Marsh (1880: 124, 125) described 21 distinct tooth sockets in the right jaw of YPM 1450. Subsequent authors confirmed this number (Gregory, 1952; Martin and Stewart, 1977) for the right jaw. Twenty-one complete sockets in the left jaw and 17 alveoli are well

preserved in the right, with the septae between the four posteriormost teeth being obscured by parts of these teeth. However, in YPM 1450, three additional incompletely formed alveoli lacking septa are present in both dentaries for a total tooth-position count of 24. Posterior to the last preserved tooth in the right jaw (YPM 1450), the medial surface of the dentary preserves three alveolus-sized indentations (fig. 29B), also seen in the left jaw, where three teeth are preserved associated with these indentations (fig. 30B).

Marsh (1880) described the portion of the mandible belonging to YPM 1749 as more slender than YPM 1450, and containing a greater number of teeth. YPM 1749 was referred to *Ichthyornis anceps*, but cannot be compared to the holotype of *Ichthyornis anceps* (a junior synonym of *Ichthyornis dispar*; see also the Taxonomic Revision). The anterior mandible in YPM 1749 is quite poorly preserved and broken in two places, with the bases of several alveoli exposed on the medial surface. It may be slightly more delicate than YPM 1450, but it is estimated to have contained 23 and possibly 24 teeth, as in YPM 1450. Marsh considered YPM 1735 to be from a larger individual with a “stouter” mandible containing the same number of teeth as YPM 1450 (Marsh, 1880: 125). While YPM 1735 is from a larger individual, the number of teeth cannot be estimated as the dentary is anteriorly and posteriorly incomplete (fig. 31A). Martin and Stewart (1977) described a large *Ichthyornis*, SMM “13520” (= SMM 2503; see Taxonomic Revision). This specimen does not appear to represent an individual larger than YPM 1735 and it was reported to have 26 alveoli in each of the preserved dentaries (Martin and Stewart, 1977).

The septae separating the alveoli are comprised of a pocked and punky bone, as is best seen in the anterior portions of the left and right dentary of the holotype (YPM 1450). Counterintuitively, the septae in the smallest mandible (YPM 1450) appear thick and fully formed while those in the slightly larger YPM 1749 and in the still larger YPM 1735 appear thinner. Martin and Stewart (1977) described their large *Ichthyornis* (estimated as approximately the size of YPM 1735) as lacking sockets and having only slight con-

strictions of the dentary. From this description and figure 1 of that paper, the condition in SMM “13520” (= SMM 2503) appears the same as in YPM 1735. Martin and Stewart (1977) also noted that in YPM 1450, all but last two teeth are set in sockets. Indeed, the posteriormost teeth in YPM 1450 and YPM 1749 lie in a groove with slight ridges visible in the dentary where the septa would be developed. In YPM 1450, YPM 1735, and YPM 1749, the septae separating many of the posterior alveoli generally do not appear as well developed as those in the anterior part of the jaw.

Martin and Stewart (1977) concluded that the teeth appeared ontogenetically earlier in a groove, with septae between the individual alveoli developed later, and that the formation of septae appeared to proceed anterior to posterior in the jaw; both of these conclusions are agreed with here. However, rather contradictorily, Martin and Stewart (1977) also considered YPM 1735 to be an adult based on the closure of sutures in the jaw, although no septae were developed, suggesting, by their own criterion, that it would be a subadult. That the septae appear more completely developed in the significantly smaller YPM 1450 and less completely formed in larger individuals could suggest that these larger specimens are part of a distinct species of *Ichthyornis*. However, as discussed in the Taxonomic Revision, YPM 1450 and these larger specimens cannot be assumed to be even closely contemporaneous individuals. Further, even if they could be assumed to be contemporaneous, sexual dimorphism in the age at which the septa are completely formed cannot be ruled out (e.g., by sex difference in growth duration, or onset/offset of septae formation; see Taxonomic Revision).

TOOTH IMPLANTATION: Marsh (1880) inferred the pulp cavity to extend into the base of the crown. This is supported by teeth in YPM 1450, YPM 1749, and YPM 1775, which are broken close to the base of the crown, exposing parts of developing teeth within. He further commented that the teeth were set in deep sockets that they almost completely filled, and that dental succession appeared to have been vertical (Marsh, 1880). The former observation is borne out in YPM 1450 and YPM 1749. And, regard-

ing succession, developing teeth do appear to have entered the pulp cavity basally, and tooth succession appears to have been vertical (Marsh, 1880; Martin and Stewart, 1977). The medial surface of the root of the third tooth in the left jaw of YPM 1450 is exposed, but no resorption features are present. Further, in this tooth, which appears to have been nearly if not completely developed, part of a developing tooth is visible in the cross section that passes directly beneath the crown.

Marsh (1880) noted that young teeth were inclined when they appear above the jaw. Gregory (1952) reiterated Marsh's (1880) observation of alternating tooth succession. This inference, and that of ontogenetically earlier inclined teeth, is supported by the alternating inclined and completely everted (and vertically oriented) teeth in the middle of the right jaw in YPM 1450 (tooth positions 9–13).

VERTEBRAL COLUMN

Cervical vertebrae are known from the holotype of *Ichthyornis dispar* (YPM 1450) as well as from YPM 1733 and YPM 1775. Thoracic as well as sacral vertebrae are represented in YPM 1450, YPM 1732, YPM 1733, and YPM 1775. Caudal vertebrae are known in YPM 1732 and possibly in YPM 1775. All of these specimens except for YPM 1732 are referred on the basis of the presence of preserved apomorphies to *Ichthyornis dispar* (see table 1).

The vertebrae of *Ichthyornis* were extensively figured and discussed in *Odontornithes* (Marsh, 1880). Individual vertebrae will be described where the illustrations and/or commentary in *Odontornithes* do not appear to reflect either the morphology or current state of preservation of the material. Marsh (1880) illustrated four (two cervical and two thoracic) vertebrae from the holotype of *Ichthyornis dispar* (YPM 1450). These vertebrae are much less complete than they were originally illustrated by Marsh (1880).

Three vertebrae are represented in YPM 1775, only one of which (the axis) was discussed in *Odontornithes* (Marsh, 1880: 128) and none of which were figured. The axis in YPM 1775 (fig. 33A) is mentioned (Marsh,

1880: 128), while a poorly preserved posterior cervical, or anterior thoracic, and a possible portion of a pygostyle were not discussed. Ten presacral vertebrae are represented in YPM 1733. Six of these were figured (Marsh, 1880: pl. XXVII) and all 10 were discussed in *Odontornithes*. Two fragments of the sacrum were also preserved but were not mentioned.

All but one of the presacral vertebrae and the sacral fragments from YPM 1733 were included in the composite *Ichthyornis victor* panel mount (fig. 4). Additionally, the three thoracic vertebrae, a sacrum, and caudal vertebrae that are preserved in YPM 1732 were all incorporated into the mount (fig. 4). Nearly all of the vertebrae from YPM 1732 were figured in *Odontornithes*. The two thoracic vertebrae are mentioned as found in articulation with the sacrum, with the third lying close to these two (Marsh, 1880: 138).

For clarity in discussing the presacral vertebrae from each of the specimens considered, they will be referred to with the specimen number and a letter to indicate their relative (not absolute) position in the column. For example, the most anterior vertebrae preserved in YPM 1733 is here discussed as “1733A”. A posterior cervical vertebrae from the same specimen will be referred to as “1733D”. The exact position of this vertebra in the series is unknown; however, it is the fourth and most posterior presacral vertebrae preserved from YPM 1733. This method was considered preferable to referring to the vertebrae by the hypothesis of their position (e.g., the “third presacral”) because these hypotheses are based upon an inference of the total number of presacrals in *Ichthyornis*, a value that cannot be currently established. As is discussed below, Marsh (1880) referred to a vertebra as the “tenth”, but here it may be considered a posterior cervical, probably the 9th or 10th. No further resolution of its position is currently possible. The use of these tags in the text (e.g., “1733D”) does not imply that the association of any of these vertebrae with the specimens to which they were originally identified (e.g., YPM 1733) is in question.

A total of 18 presacral vertebrae are preserved in the YPM specimens (from 1450, 1732, 1733, and 1775). Marsh (1880) con-

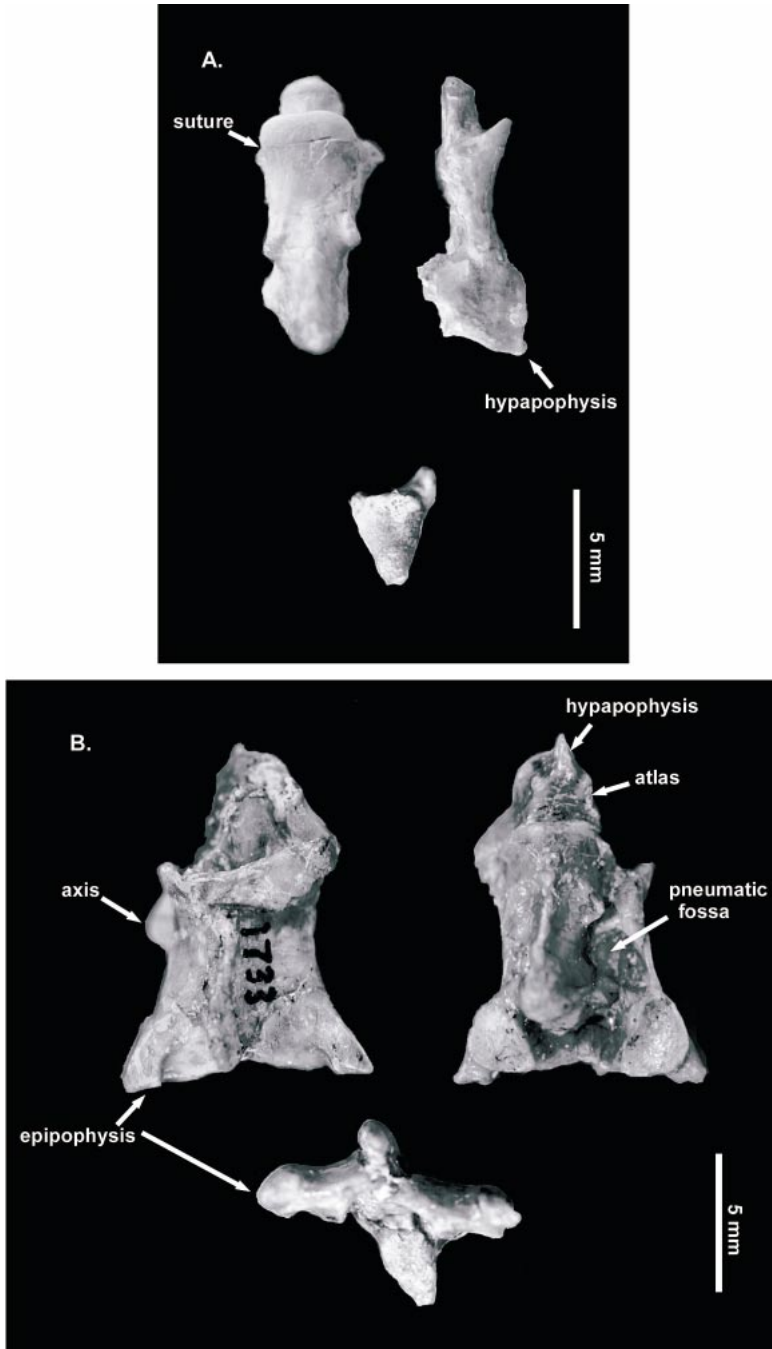


Fig. 33. The atlas and axis of *Ichthyornis dispar*: (A) the axis of YPM 1775 in (clockwise from top left) ventral, lateral, and posterior views and (B) the atlas and axis of YPM 1733 in (clockwise from top left) dorsal, ventral, and posterior views.

sidered there to be 21 presacral vertebrae in *Ichthyornis*, of which 14 were supposed to be cervicals. He based this estimate on comparisons made with the vertebrae of terns, writing, "Among existing birds, the Terns appear to bear the nearest general resemblance to *Ichthyornis*, and hence their vertebrae are used for comparison with those of that genus" (Marsh, 1880: 127). Estimates of the position of distinct vertebrae in *Ichthyornis* made (Marsh, 1880: e.g., 127) direct references to how the vertebra compares with that in the royal tern "*Sterna regia*" (junior synonym of *Sterna maxima*; see Comparative Materials and Methods). An ankylosed vertebra attached to the anterior end of sacrum in YPM 1732 (with a still visible suture between it and the succeeding vertebra) was considered to be a thoracic and the 21st presacral (Marsh, 1880: 140).

In *Hesperornis regalis*, Marsh (1880) estimated there to be 16 cervicals of 23 presacral vertebrae. While across the surveyed Aves the presacral number is 21 with relative consistency, the number of vertebrae of certain distinct morphologies is more variable. Given that only three thoracic vertebra morphologies are repeated in a second specimen (see discussion of YPM 1732 below), there must be minimally five thoracic vertebrae in *Ichthyornis*.

CERVICAL VERTEBRAE

Atlas: YPM 1733

The atlas is preserved only in YPM 1733 (fig. 33B) and discussed here as "1733A". It is not currently as complete as its illustration in *Odontornithes* (Marsh, 1880: pl. XXXVII, fig. 1). The ventral portion (corpus atlantis; Baumel and Witmer, 1993) is preserved only on the right side. The dorsal portion (arcus atlantis; Baumel and Witmer, 1993) is currently incomplete (fig. 33B). It is unclear if the right and left laminae of the neural arch were fused on the dorsal midline as depicted. A portion of a left postzygapophysis was preserved in a separate vial and was not included in the *Ichthyornis victor* panel mount. This process, if it belongs to the atlas (as labeled), is considerably more robust than in the Aves surveyed.

The atlas preserves a strikingly well-de-

veloped epipophysis that projects dorsal to the postzygapophysial articular surface (processus articularis caudalis; Baumel and Witmer, 1993) and extends as far as the posterior edge of this surface (Marsh, 1880: pl. XXXVII, figs. 1, 1a). A large atlantal hypapophysis is developed between two ventral tubercles (Marsh, 1880: 128, fig. 33B). Neither well-developed epiphyses or hypapophysis was observed in tinamous (e.g., *Nothura darwinii* or *Crypturellus noctivagus*) or in *Gallus gallus* or *Anas platyrhynchos*. In *Apteryx australis*, comparatively well-developed epiphyses are present but no robust hypapophysis. By contrast, in *Struthio camelus*, a moderately well-developed hypapophysis is present but there is no dorsal projection of the epipophysis. Both pronounced epiphyses and a hypapophysis were observed, for example, in *Gavia stellata*, although these are less well developed than those of *Ichthyornis dispar* (Marsh, 1880: 128).

Axis: YPM 1733

A nearly complete axis is represented in YPM 1733 (fig. 33B) and referred to here as "1733B". An incomplete axis is preserved in YPM 1775 (fig. 33A) identical in morphology with that preserved in YPM 1733 (Marsh, 1880). However, in YPM 1775, the suture between the first (atlantal) centrum and the second (axial) centrum is incompletely closed (fig. 33A). This suture is closed in the slightly smaller YPM 1733 (fig. 33B). Both of these specimens are larger than the holotype of *Ichthyornis dispar* (see further discussion of this suture as a possible sign of the relative immaturity of YPM 1733 in the Taxonomic Revision).

The description provided in *Odontornithes* (Marsh, 1880) accurately represented the morphology of this element in these specimens. However, the illustration of this element (Marsh, 1880: pl. XXVII, fig. 1) is not accurate in its depiction of the bone as uncrushed. The neural arch is crushed (fig. 33B) to close the neural canal (foramen vertebrale; Baumel and Witmer, 1993). Matrix between the collapsed neural arch and the centrum indicates that this breakage is original to the specimen. Thus, the dimensions

of the neural canal figured by Marsh (1880) were estimated, not observed.

The tip of the prominent hypapophysis is missing in both specimens. The anterior articular surface is exposed in YPM 1775 (fig. 33A) but covered by the atlas (fig. 33B) in YPM 1733 (Marsh, 1880). It matches its description in *Odontornithes* (Marsh, 1880: 128, 129). The paired pneumatic foramina noted (Marsh, 1880) are striking in their size (fig. 33B). These are not present in the axis of *Hesperornis regalis*; however, many pneumatic features are suppressed in diving taxa (Britt et al., 1998). They are located in the lateral surface of the neural arch laminae posterodorsal to paired protuberances on the centrum. These protuberances represent the capitula of fused cervical ribs in Aves (processus costalis; Zweers et al., 1987).

As illustrated in *Odontornithes* (Marsh, 1880), the epipophyses (YPM 1733) just surpass the postzygapophyses in distal extent and do not project significantly dorsally but rather are curved slightly ventrally (fig. 33B). They taper to a narrow ridge dorsally. Marsh (1880) correctly noted that they are unlike those of *Sterna maxima*. In that taxon, blunt processes project posterodorsally approximately the height of the posterior articular surface. Such a morphology (short, slightly ventrally projected epipophyses) is approached, for example, in *Nothura darwini* (Tinamidae).

The posterior articular surface the axis centrum is strongly compressed and extends slightly around the posterolateral centrum edges (YPM 1733 and YPM 1775; fig. 33A,B). Marsh (1880) considered the axis to show a kind of incipient heterocoely, and, of all preserved cervicals, it approaches this condition most closely. The lateral extension of the surface appears to approach the mediolateral convexity seen in heterocoelous vertebrae (see definition in appendix 1, character 52). However, the center of the surface is slightly depressed rather than broadly convex (fig. 33A). In *Hesperornis regalis* and Aves, by contrast, a distinct ventral lip forms the edge of a conspicuously dorsoventrally concave surface. Also, in the heterocoelous vertebrae of *Hesperornis regalis* and Aves, this conformation gives the posterior articular surface the appearance of broadening lat-

erally. This condition is not developed in the axis (fig. 33), third cervical vertebra (fig. 34), or in more posterior cervicals. Further comments on "heterocoely" are made below, as well as in appendix 1 (character 52).

Third Cervical Vertebra

YPM 1733: A vertebra identified by Marsh (1880) as the third is represented in *Odontornithes* (Marsh, 1880: pl. XXVII, fig. 2) and will be referred to as "1733C". This vertebra appears, consistent with Marsh (1880), to be the third cervical, as inferred from the shape of the centrum (compressed), the diminutive posterior-central articular surface, and the inclined anterior central articular surface (fig. 34). This vertebra (from YPM 1733) differs from its illustration in that the neural arch is partially crushed, distorting the profile of the neural canal, and because the right prezygapophysis and left postzygapophysis are missing (fig. 34). Fused cervical ribs enclose small transverse foramina. The anterior articular surface (figs. 34A,C, 35A, 36A) is angled to face ventrally at approximately a 60° angle (Marsh, 1880). There is a depression just posterior to this articular surface (fovea cranialis ventralis; Zweers et al., 1987; figs. 34C, 25A).

Unlike the condition in all Aves surveyed and *Hesperornis regalis* (Marsh, 1880), the anterior edge of the centrum articular surface, in ventral view, is anteriorly projected relative to the edge of the anterior openings of the transverse foramina. As a result, this surface appears as a curved notch in ventral view (figs. 35B,C, 36B,C). In *Ichthyornis dispar* (figs. 34A, 36A), the profile of the surface's anterior edge in ventral view is straight to slightly convex whereas in *Hesperornis regalis* and Aves, it is broadly concave (fig. 36B,C). Also, in ventral view, the surface is developed as two anteroventrally facing lobes with a deep depression between them. This morphology in *Ichthyornis* is unlike the development of a heterocoelous condition seen in any of the surveyed Aves and *Hesperornis regalis*, although it is also modified relative to the amphicoelous condition, where developed, in more basal theropods (e.g., *Deinonychus antirrhopus*; Ostrom, 1969). The development of a midline de-

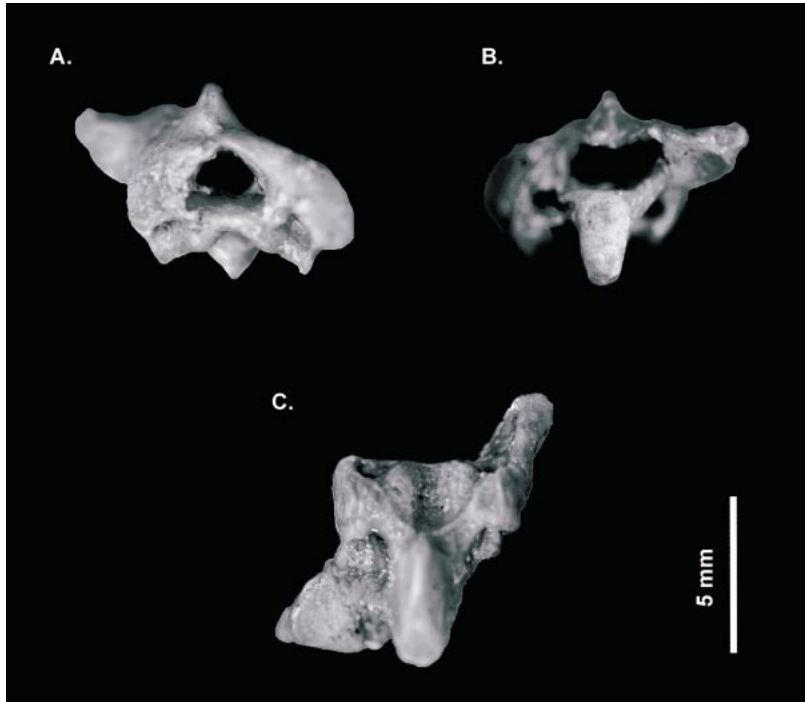


Fig. 34. The third cervical vertebra of *Ichthyornis dispar* (YPM 1733) in (A) anterior, (B) posterior, and (C) ventral views.

pression may represent an approach to the anterior concavity in Aves. However, in *Ichthyornis*, this concavity is developed only on the *ventrally facing* portion of the surface (figs. 34C, 35A, 36A).

As in the case of the axis, the posterior articular surface of the third cervical (1733C) is slightly compressed (figs. 34B, 37A), a condition which appears plesiomorphic, to at least Avialae (J. Gauthier, personal obs.). This surface is slightly concave and the lateral edges of the surface are less produced than the dorsal and ventral edges. This gives the surface a weakly developed concave profile in lateral view, which appears to be a derived condition shared with Aves. The medial depression (figs. 34B, 37A) is a plesiomorphic condition developed in platycoelic articulations. In Aves and *Hesperornis regalis* (Marsh, 1880), this posterior articular surface of the centrum is broadly convex mediolaterally.

A hypapophysis is developed on the posterior half of the ventral surface of the centrum (YPM 1733; figs. 34C, 35A). The pre-

zygapophyses are extremely long relative to the postzygapophyses and relative to the condition observed in all surveyed Aves (compare fig. 26A with fig. 26B,C). Marsh (1880) noted that they were longer than in *Sterna maxima*. There are shallow pneumatic fossae directly posterior to the transverse processes; however, these are slight depressions, and not the prominent feature depicted in Marsh (1880: pl. XXVIII, fig. 2). The ventral surfaces of the postzygapophyses do not appear pneumatic as they are in more posterior cervicals. However, this area is not well exposed.

Posterior Cervical Vertebrae

1733D: A vertebra identified as the 10th cervical (Marsh, 1880: 131, pl. XXVII, fig. 3) belongs to YPM 1733 (figs. 38, 39A). It will be referred to as "1733D". The postzygapophyses and centrum are well preserved; the left prezygapophysis is detached, and the right is missing. The diapophyses are also missing and only their base and the projected portion of the fused rib allow the

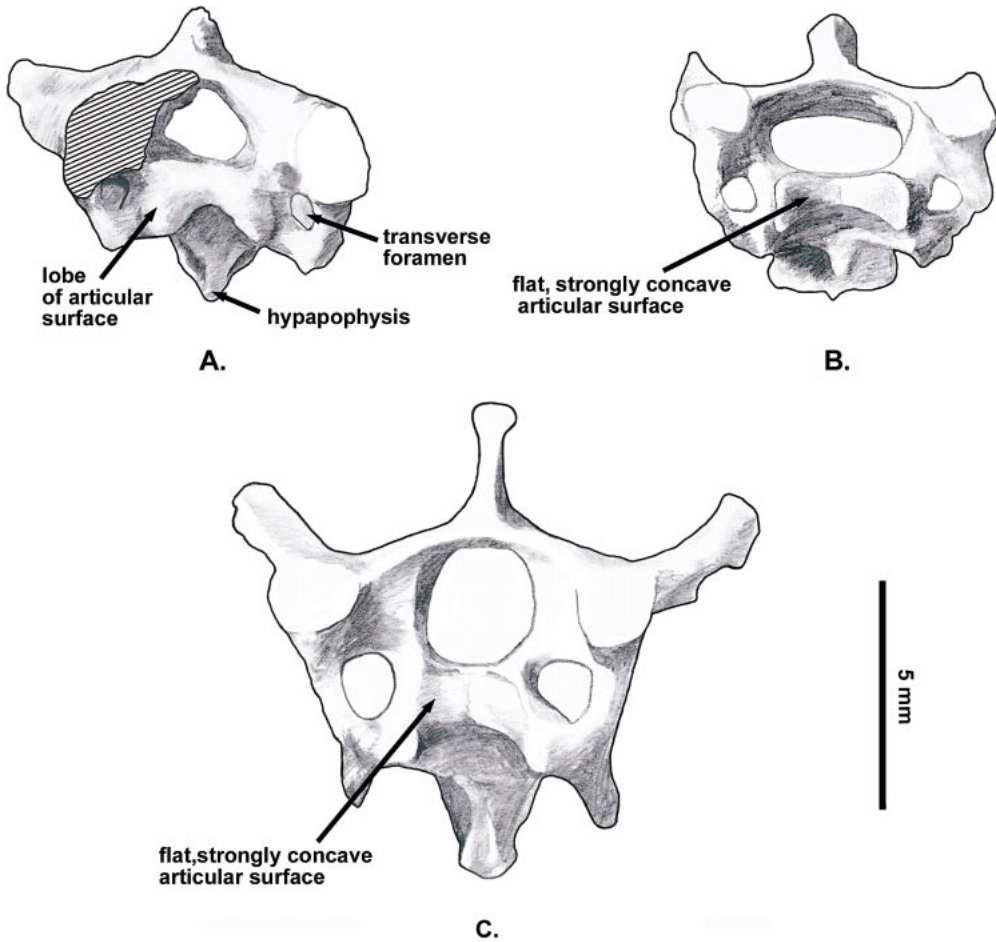


Fig. 35. The third cervical vertebra of (A) *Ichthyornis dispar* (YPM 1733), (B) *Crypturellus noctivagus*, and (C) *Sterna maxima* in anterior view.

shape of the transverse foramina to be partially inferred. The depicted diameter of the neural canal in Marsh (1880) is probably an underestimate for this vertebra, as the neural arch is clearly pressed toward the centrum. The pre- and postzygapophyses and the diapophyses were depicted as complete in *Odontornithes* (Marsh, 1880).

The anterior articular surface of 1733D is somewhat crushed dorsoventrally. The ventral margin of the centrum is strongly arched with prominent carotid processes that lie close to the midline (fig. 38). These processes project directly ventrally rather than ventromedially. Ventromedial projection is common in anterior cervicals in Aves, while directly ventrally projected processes are de-

veloped in more posterior cervicals. Marsh (1880) considered this vertebra to match best the 9th of *Sterna maxima*, although estimating it to represent the 10th cervical vertebra of *Ichthyornis*. While it cannot be positively identified as either the 9th or 10th cervical, the morphology of the carotid processes and the lack of a hypapophysis suggest this vertebra preceded the posterior cervicals that have well-developed hypapophyses. In Aves, the most posterior cervical with paired processes has these processes situated close to the midline and projected directly ventrally. However, the exact position and number of vertebrae with this morphology can vary. In *Sterna maxima*, as Marsh (1880) noted, this morphology is approached by the 9th cervi-

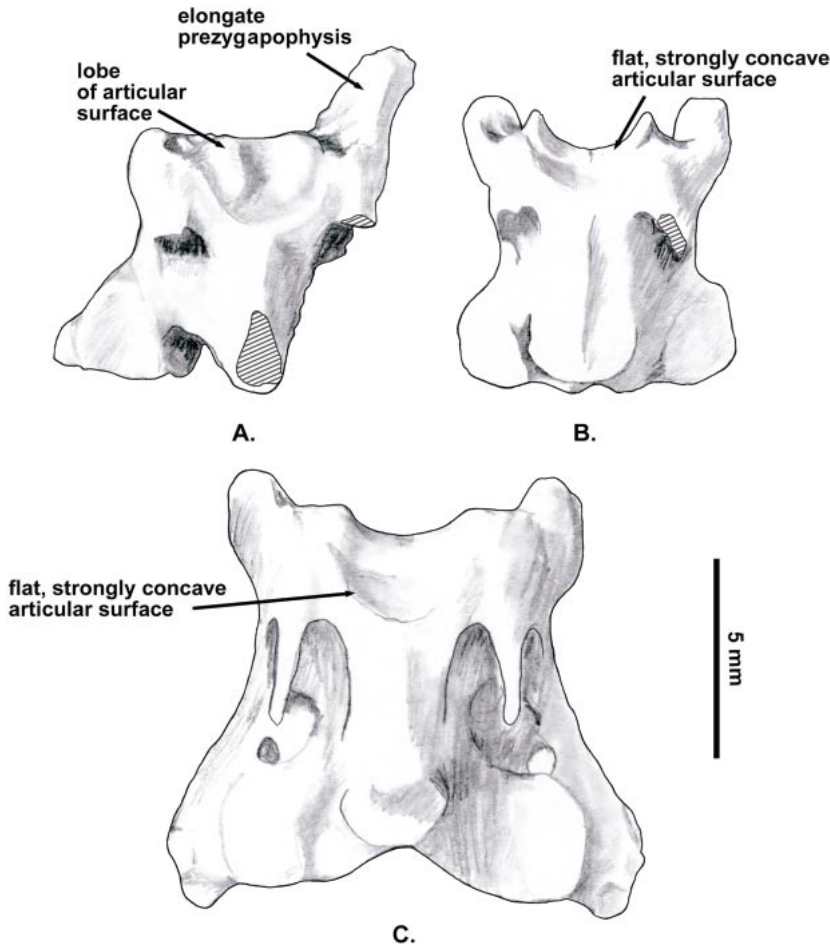


Fig. 36. The third cervical vertebra of (A) *Ichthyornis dispar* (YPM 1733), (B) *Crypturellus noctivagus*, and (C) *Sterna maxima* in ventral view.

cal. In *Nothura darwinii* (Tinamidae), it is approached by the 11th cervical while, in a second tinamou (*Crypturellus noctivagus*), it is approached best by the 12th and 13th cervicals. In *Columba livia*, these salient, ventrally projected, carotid processes occur on the 10th cervical, while in *Anas platyrhynchos* they appear on the 12th cervical.

Posterior cervical vertebra 1733D has fused cervical ribs and large transverse foramina. Marsh (1880: 131) discussed the anterior articular surface of the centrum as "sub-quadrate" in shape. However, the shape of this articular surface cannot be inferred with confidence, as it is crushed. That this surface is damaged was noted in *Odontornithes* (Marsh, 1880: 131), although it was

depicted as unbroken (Marsh, 1880: pl. XXVIII, fig. 3). The surface appears slightly more depressed than the posterior articular surface of the centrum.

This anterior articular surface in vertebra 1733D has a slightly concave center and may have angles somewhat dorsally. The posterior surface is completely preserved, subcircular, with a central depression (fig. 38B). Because only the anterior tip of the left prezygapophysis is preserved, most of the representation of the prezygapophyses in *Odontornithes* (Marsh, 1880: pl. XXVIII, fig. 3) could not be confirmed except that they were short. The anterior edge of the neural arch immediately dorsal to the neural canal is excavated, and a midline pit lies on the dorsal

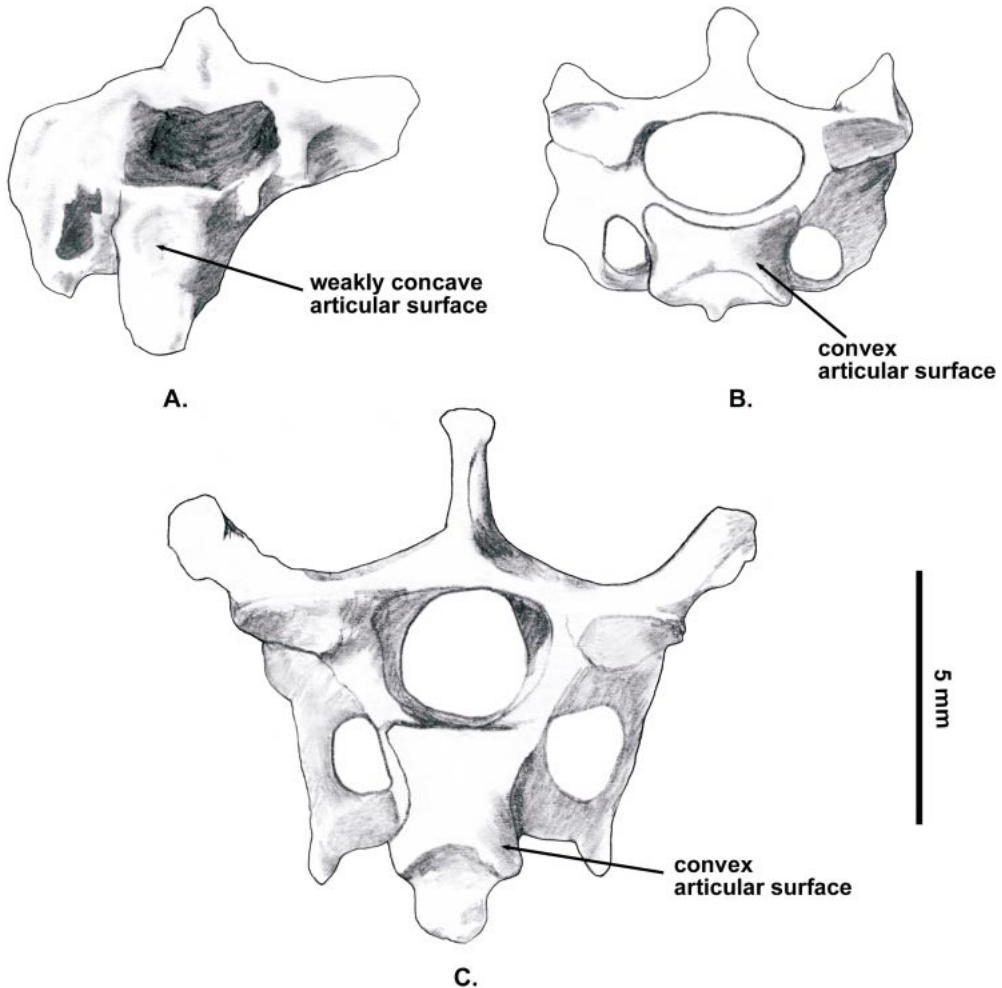


Fig. 37. The third cervical vertebra of (A) *Ichthyornis dispar* (YPM 1733), (B) *Crypturellus noctivagus*, and (C) *Sterna maxima* in posterior view.

surface of the neural arch (Marsh, 1880). Deep fossae are also developed in the neural arch lamina posterodorsal to the remains of the transverse processes.

The postzygapophyses 1733D and one posterior cervical (1450A; see below) from the holotype of *Ichthyornis dispar* (YPM 1450) have distinctive pneumatic fossae in the ventromedial surface of the postzygapophyses (figs. 38, 39A). The pneumatic cavities are somewhat asymmetrically developed in 1733D, but on both sides they excavate the ventral surface of the postzygapophysis, leaving the dorsal surface of the processes a

thin sheet of bone (figs. 38, 39A). As will be further discussed in reference to cervical 1450A, a pneumatic fossa entering the ventral surface of the postzygapophyses may be a synapomorphy of *Ichthyornis* + Aves.

1450A: One cervical vertebra illustrated in *Odontornithes* (Marsh, 1880: pl. XXII, fig. 2) was considered to be possibly the 14th and last cervical (Marsh, 1880). It will be discussed here as “1450A”. This vertebra (fig. 40A) is assessed herein to likely lie directly posterior to 1733D (considered the 10th cervical by Marsh, 1880), and anterior to that which he considered to be the 12th (here re-

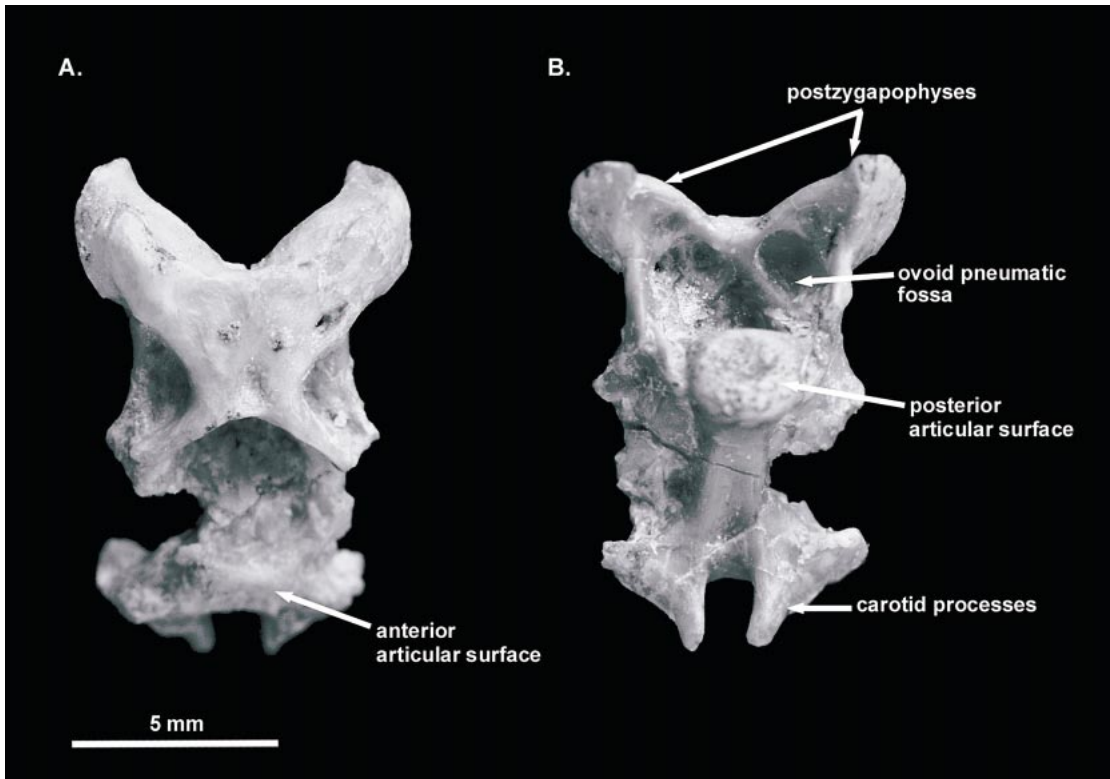


Fig. 38. A posterior cervical vertebra (“tenth” cervical of Marsh, 1880) of *Ichthyornis dispar* (YPM 1733) in (A) dorsal and (B) posteroventral views.

ferred to as “1450B”; see below). 1450A is currently much more incomplete than its representation in *Odontornithes* (Marsh, 1880). Its neural arch is poorly preserved; only the right postzygapophysis is preserved, connected by a narrow strip of the neural arch lamina to the incomplete left transverse foramen. The transverse foramina have a smaller diameter in 1450A compared to those in 1450B.

The hypapophysis in 1450A is rodlike (fig. 40A) and preserves one of the paired lateral projections at its tip depicted by Marsh (1880, pl. XXII, fig. 2d). By contrast, in 1450B (Marsh, 1880: pl. XXII, fig. 1d), the hypapophysis is bladelike and lacks these projections (fig. 40B). These projections of the hypapophysis appear related to the passage of the carotid arteries in Aves and have been suggested to be serial homologues of carotid processes (Zweers et al., 1987). No

vertebrae in *Gallus gallus*, *Anas platyrhynchos*, *Sterna maxima*, or *Columba livia* match this morphology closely. However, in *Sterna maxima*, the 10th cervical has an almost bifid hypapophysis (or midline, fused carotid processes), which should be further investigated as a potential homologue with the structure developed in 1450A.

A hypapophysis with lateral projections at its tip is also approached on the 10th vertebrae of *Burhinus capensis*, and to a lesser degree the 12th in *Nothura darwinii*. In both of these species and in *Hesperornis regalis* (Marsh, 1880: pl. IV, fig. 6), a rodlike hypapophysis with lateral projections at its tip is observed on the vertebrae just anterior to the first with a bladelike hypapophysis. Thus, it is suggested that vertebra 1450A, with a rodlike hypapophysis, is similarly anterior to that with a bladelike hypapophysis, 1450B,

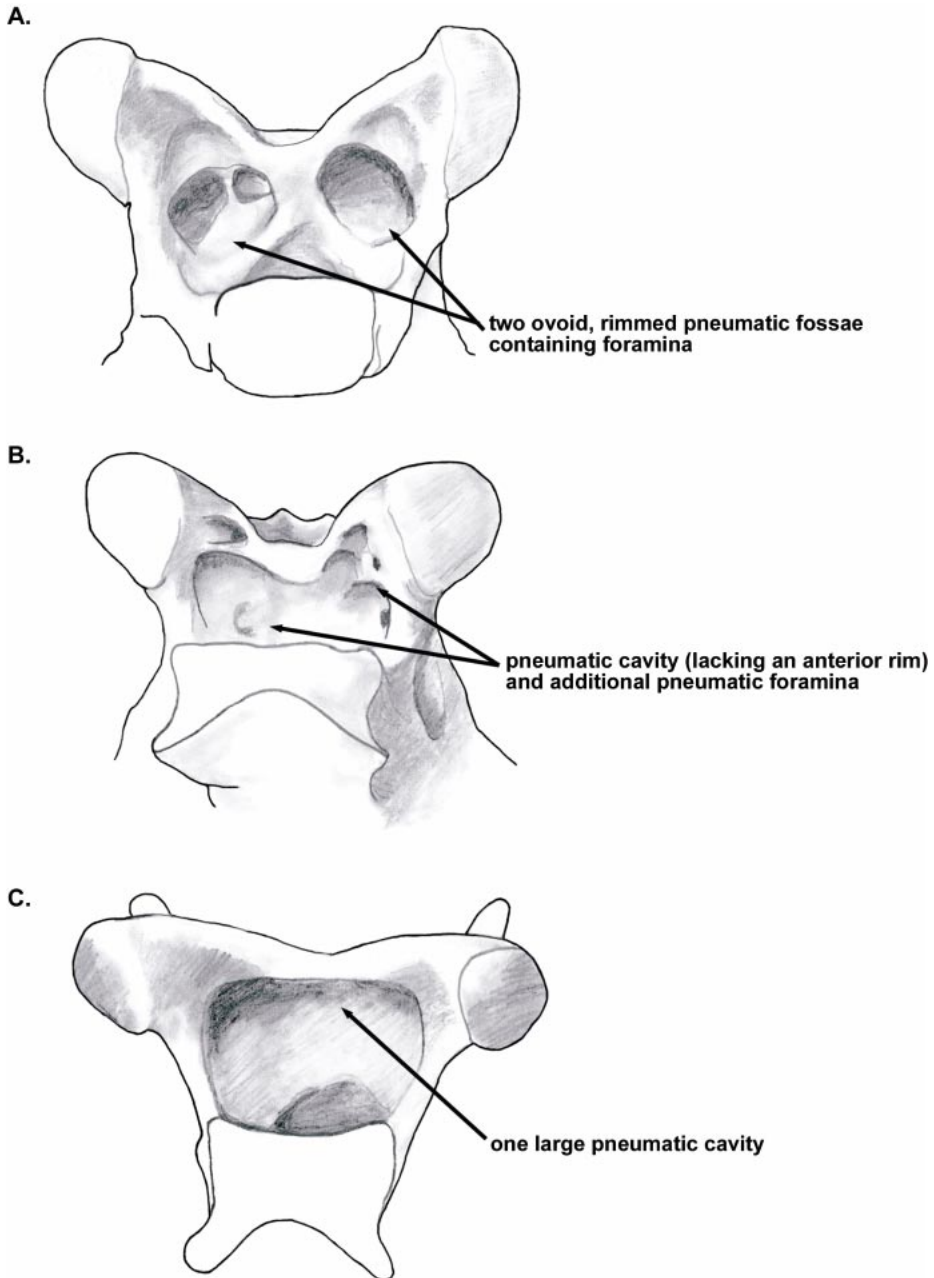


Fig. 39. The pneumatization of postzygapophyses of a posterior cervical vertebra in (A) *Ichthyornis dispar* (YPM 1733; "tenth" cervical of Marsh, 1880), (B) *Crypturellus noctivagus* (14th cervical vertebra), and (C) *Sterna maxima* (10th cervical vertebra).

rather than posterior to it as suggested by Marsh (1880).

A deep pneumatic fossa is seen on the lateral surface of the neural arch lamina in cer-

vical 1450A just anterior to the right postzygapophysis, between it and the transverse process (fig. 40A). A deep fossa in this position is developed in the 5th to 19th verte-

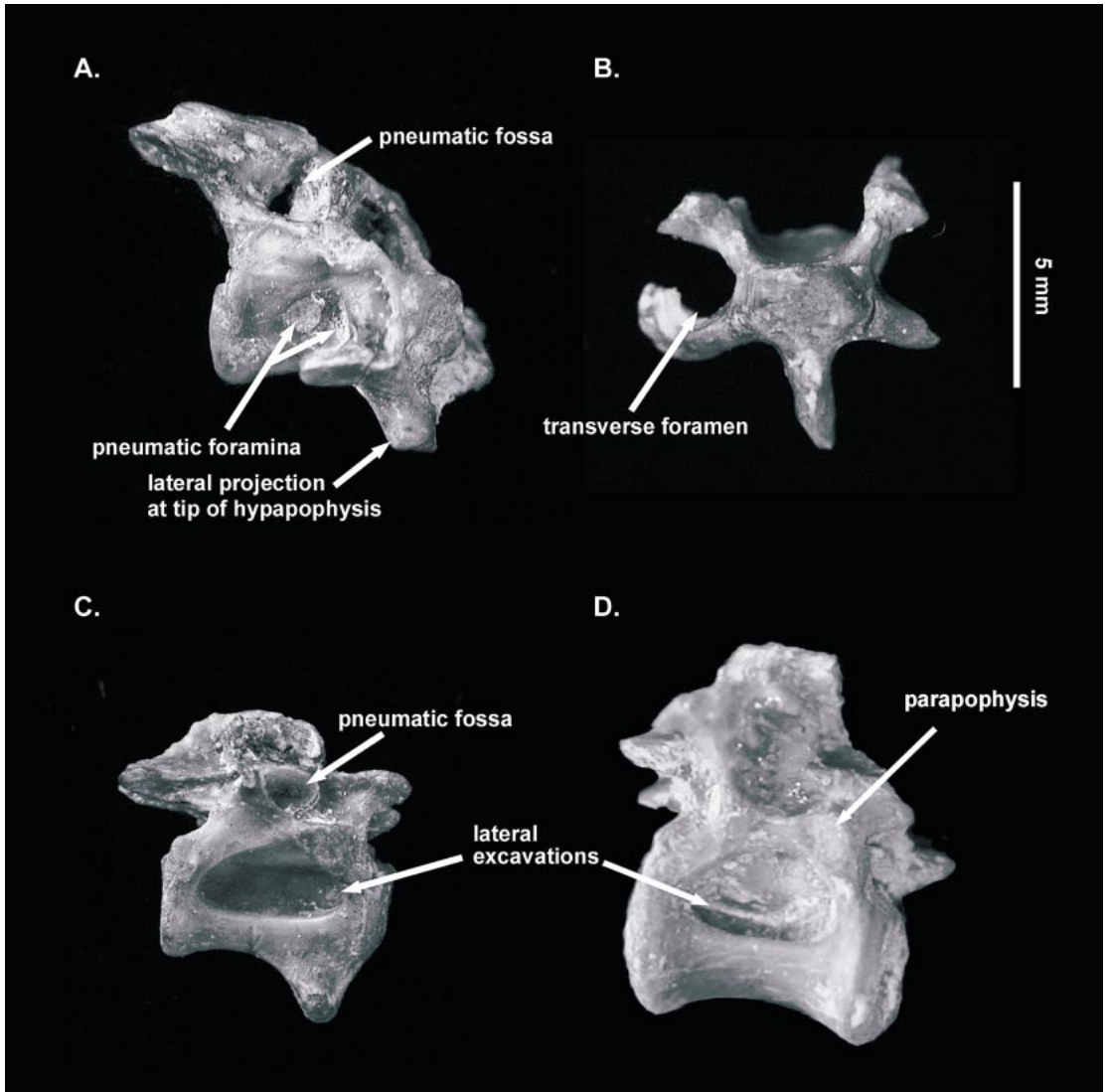


Fig. 40. Presacral vertebrae of *Ichthyornis dispar*. Two posterior cervical vertebrae from the holotype specimen (YPM 1450) referred to in the text as (A) 1450A and (B) 1450B are shown in right lateral and anterior views, respectively. An anterior thoracic from YPM 1450 (C) referred to as 1450C and (D) the posteriormost thoracic of YPM 1732 (1732C) are also shown in right lateral view. The identification of 1732C as the last presacral is based on notes (Marsh, 1880) indicating that it was discovered in articulation with the sacrum.

brae of *Hesperornis regalis*. Of the posterior cervicals in *Crypturellus noctivagus* and *Nothura darwinii*, small foramina are developed in the 11th to 13th vertebrae, while in *Gallus gallus* and *Anas platyrhynchos*, these are developed in the 13th and 14th. The 12th vertebra of *Nothura darwinii* has both a pneumatic foramen in the lateral surface of the

neural arch as well as the morphology of the hypapophysis seen in 1450A. Small pneumatic foramina perforating the lateral surface of the neural arch are present in the 12th and 13th vertebrae of *Sterna maxima*, with a fossa developed in the 14th. No such foramina or fossae appear present in *Columba livia* or *Burhinus capensis*.

Three pneumatic foramina are visible perforating the middle of the right side of the centrum (fig. 40A). The corresponding area on the left side of the centrum is not well preserved. These foramina lie in a shallow lateral depression. No pneumatic foramina perforate the middle of the centrum in any of the posterior cervicals of *Nothura darwinii*, *Crypturellus noctivagus* or *Gallus gallus*, while in *Alectura lathami*, one perforates the 14th, but is not as broad as those in *Ichthyornis dispar*. The centrum of all but the first cervical in *Anas platyrhynchos* bear pneumatic fossae that appear often to contain one or several small perforating foramina. Large foramina, more closely approximating the condition in *Ichthyornis*, are developed in the 13th–15th vertebrae in *Anas platyrhynchos*. In *Sterna maxima*, these are developed in the 11th–12th cervicals, with a large pneumatic fossa developed in the 10th. Thus, neither the presence nor the morphology of this pneumatic feature presents a clear signal of what position in the posterior cervicals 1450A might have had or what number within the presacrals it represents.

The ventral surface of the postzygapophysis in cervical 1450A is excavated by a large, rimmed pneumatic fossa, possibly with foramina developed within it. This fossa corresponds to one of the paired cavities just mentioned for cervical 1733D (fig. 38A). It excavates the ventral surface of postzygapophysis anterior to the process' articular facet. The postzygapophysis is broken to expose the dorsal extent of the fossa.

Small pneumatic foramina enter the ventral surface of the neural arch near the bases of the postzygapophyses in some posterior cervicals of tinamous (*Nothura darwinii* and *Crypturellus noctivagus*; fig. 39B). *Gallus gallus* (Galliformes) also has such small foramina in some posterior cervicals, but they lie farther from the tip of the postzygapophyses. In *Anas platyrhynchos* (Anseriformes), more foramina are present and lie closer to the tip of the postzygapophyses; by contrast, the neoavian, *Sterna maxima* (Charadriiformes), has a single large cavity in approximately the same position as *Ichthyornis dispar* (fig. 39C). No pneumatic foramina or fossae in this position are visible in *Burhinus capensis* (Charadriiformes).

Suffice it to say, there is significant variation in the development of pneumatic features in the postzygapophyses within Aves, and their distribution should be further investigated. However, it is hypothesized that these conditions are potential homologues of that in *Ichthyornis*. The anatomical details of this pneumatic feature (i.e., development as large, paired, and distinctly rimmed fossae) may be locally autapomorphic for *Ichthyornis* or may represent the primitive condition of pneumatic ventral surfaces of the postzygapophyses. The postzygapophyses are apneumatic, possibly apomorphically, in the diving *Hesperornis regalis* and unknown in more basal taxa. With further scrutiny, however, pneumatic postzygapophyses may be discovered to be a synapomorphy of *Ichthyornis* + Aves or of a more inclusive avialan clade.

1450B: Although illustrated as complete (Marsh, 1880: pl. XXII, fig. 1), only the ventral half of what Marsh (1880) considered the “twelfth” cervical vertebra is currently preserved (fig. 40B). This vertebra and that just discussed from the holotype of *Ichthyornis dispar* (YPM 1450) were included in the *Ichthyornis dispar* panel mount. It preserves the centrum and portions of attached cervical ribs (ventral margin of the transverse foramina; fig. 40B). The diameter of the transverse foramina in vertebra 1450B is significantly greater than that of the 1450A transverse foramina.

The details of the preserved portion of the vertebra match Marsh's description (Marsh, 1880: 132–133): A large pneumatic foramen pierces the centrum; a prominent, well-projected hypapophysis is developed (fig. 40B); and the anterior articular surface is “subquadrate” inclined to face slightly ventrally (fig. 40B), while the posterior surface is subround (Marsh, 1880: 132–133). The centers of the articular surfaces of the centrum are depressed. As in more anterior vertebrae, the anterior surface is not anteriorly saddle shaped; there is no indication of the dorsoventral convexity or of mediolateral concavity of the surface (fig. 40B) seen in anterior heterocoelous articular surfaces in *Hesperornis regalis* (Marsh, 1880) or Aves.

On the lateral surface of the centrum, just posterior to the anterior articular surface, are

paired, small, oblate fossae. No carotid processes are developed. Muscle scars on the lateral surfaces of the tip of the hypapophysis may be for the paired, ventral longus coli muscles (Baumel and Witmer, 1993). The presence of a pneumatic fossa in the neural arch lamina in the same location as that in vertebra 1450A is indicated by the morphology of a small portion of the neural arch. No further aspects of previously described (Marsh, 1880) neural arch morphologies could be confirmed for 1450B, as this part of the vertebra is evidently lost.

1450B was described as from “behind the middle of the [cervical] series” (Marsh, 1880: pl. XXII, fig. 1, caption) or, alternatively, as the 12th cervical (Marsh, 1880: 132). However, Marsh (1880) also considered the vertebra most similar to the 11th cervical of a tern (comparisons with “a tern” were made with *Sterna maxima*; see Vertebral Column above). In *Sterna maxima*, a prominent bladelike hypapophysis, like that in 1450B, occurs on the 10th and 11th posterior cervicals and to a lesser extent the 12th, and last, cervical. However, neither the hypapophysis on the 10th nor 11th cervical is as bladelike or as elongate as it is in *Ichthyornis*. The hypapophysis in *Sterna maxima* has a strongly concave anterior edge, with the tip projected anteriorly, features not developed in *Ichthyornis*.

In all avians surveyed, bladelike hypapophyses occur on the posteriormost cervical vertebrae. In *Crypturellus noctivagus* (Tinamidae), they are on the 13th–15th cervical vertebrae while in *Nothura darwinii* (Tinamidae), they occur on the 14th–16th cervicals. In *Gallus gallus* and *Alectura lathami* (Galliformes), these occur on the 12th–14th cervicals and in *Anas platyrhynchos* (Anseriformes), they occur on the 13th–15th, and are best developed on the 12th and 13th vertebrae, respectively. In the neoavian *Burhinus capensis*, these hypapophyses occur on the 11th–13th. Further, in another neoavian, *Columba livia* (Columbiformes), they are developed in the 11th and 12th vertebrae. In *Hesperornis regalis* (YPM 1207), a hypapophysis approaching that in 1450B would occur on approximately the 17th vertebrae, which would not be here categorized as a cervical but as a thoracic, as it lacks fused

ribs. However, Marsh (1880) considered this vertebra in *Hesperornis regalis* as the last cervical.

It may be that having bladelike hypapophyses developed more anteriorly (i.e., on the 11th as in the three neoavians surveyed: *Columba livia*, *Sterna maxima*, and *Burhinus capensis*, but not in the galloanserines, tinamous, or *Hesperornis regalis*) and having less cervicals are secondarily derived within Aves. These changes may be related to modifications of the number of vertebrae (e.g., total presacral number, cervical number) as well as in positional development of certain identities or characteristic morphologies occurring within Aves.

The complete cervical count is unknown for *Ichthyornis*, and varies from 12 to 16 in the small sample of avian exemplars surveyed. The number of vertebrae with blade-like hypapophyses also varies within Aves. Thus, rather than considering 1450B “the twelfth” (Marsh, 1880: 132), it is best considered as simply one of the two or three posteriormost cervicals. It may have been as posterior as the 15th or 16th cervical.

THORACIC VERTEBRAE

1775A: The crushed centrum of a short vertebra, to be referred to as “1775A”, is neither discussed nor figured in *Odontornithes* (Marsh, 1880). 1775A is considered to be one of the anteriormost thoracic vertebrae known for *Ichthyornis*, and to have come from a position posterior to that represented by 1450A. There is no indication of fused ribs in 1775A. The base of a large hypapophysis is visible. There is no evidence of paired ventrolateral tubercles (or carotid processes). The anterolateral edge of the centrum is damaged and parapophyses are not preserved. Small lateral excavations appear to have been present, represented on the left by an edge of the excavation’s ventral margin. The anterior articular surface is oriented slightly anteroventrally and is centrally depressed, with two vaguely lobate lateral surfaces in anterior view. The posterior is sub-circular, with a depression in its center, and curved edges.

The morphology of 1775A suggests that it is best regarded as an anterior thoracic be-

cause of evidence of large hypapophysis, the short length of the preserved vertebra, and the absence of fused ribs. However, it should be considered that there is some indication that YPM 1775 is a subadult individual (see Taxonomic Revision); thus, it is conceivable that this vertebra might be one of the posteriormost cervical vertebrae of a subadult YPM 1775.

1733E: A thoracic vertebra from YPM 1733, referred to here as "1733E", was considered by Marsh (1880) to be possibly the 15th in the series. It was illustrated in *Odontornithes* (Marsh, 1880: pl. XXVII, fig. 4) and is considered to follow the vertebra just described (1775A). The neural arch in 1733E is crushed toward the centrum, incompletely closing the neural canal. Matrix preserved between the broken pieces of the neural arch suggests that this breakage was present at the specimen's recovery and that the representation of this vertebra in Marsh (1880: pl. XXVII, fig. 4) involved substantial reconstruction.

The centrum of 1733E has an ovoid lateral excavation and stalked, anteriorly located parapophyses and a short hypapophysis with paired tubercles close its base (tuberculum laterale corporis; Zweers et al., 1987). In the surveyed Aves, vertebrae approaching this morphology were only observed posterior to those with well-developed and bladelike hypapophyses. However, also among the surveyed Aves (including *Sterna maxima*), the tubercles were not observed as close to the hypapophysis as they are in 1733E. Further, the ventral surface of the centrum in these avians is flat and broad in these vertebrae, while in *Ichthyornis*, none of the posterior cervicals or thoracic vertebrae exhibit a flattened and broad centrum (contra Marsh, 1880).

In vertebra 1733E, the centrum is narrow and slightly keeled. Both of the intervertebral articular surfaces are subcircular, with a straight dorsal edge and a shallow medial depression. The anterior surface is inclined to face slightly ventrally and its ventral edge is poorly defined. As Marsh (1880) observed, the neural spine is broken off. Both the prezygapophyses and the left postzygapophysis are missing. The right postzygapophysis is short, projected posteriorly, rather than pos-

terolaterally, with a ventrolaterally facing articular surface.

In the surveyed tinamous (e.g., *Crypturellus noctivagus* and *Nothura darwini*), no vertebrae with paired tubercles and a hypapophysis are present. In *Anas platyrhynchos*, *Alectura lathamii*, *Gallus gallus*, *Burhinus capensis*, and *Columba livia*, at least one vertebra with this morphology was present. In *Hesperornis regalis*, no vertebra with this morphology has been described (e.g., in Marsh, 1880). It is possible that the presence of vertebrae with these structures in the posterior cervicals/anteriormost thoracics is a synapomorphy of *Ichthyornis* + Aves. However, the distribution of this character in non-crown clade avialans needs to be further assessed.

1733F: A second vertebra with both a short hypapophysis and paired tubercles on the anteroventral surface of the centrum is represented in YPM 1733. Referred to here as "1733F", it was not figured, but was discussed in *Odontornithes* (Marsh, 1880: 136). This vertebra was described as posterior to 1733E and 1733E was regarded as the 15th in the series (Marsh, 1880: 136). 1733F is longer than 1733E. Only the centrum and part of the ventral-most portion of the neural arch are preserved. The articular surfaces of the centrum are approximately ovoid, with a flat dorsal margin. The centers of these surfaces bear a central depression and the ventral margin of the anterior central articular surface is weakly defined. The hypapophysis is developed as a midline tubercle on the anterior edge of the ventral surface. It is projected ventrally approximately the same distance as the paired tubercles (tuberculi laterale corporis; Zweers et al., 1987). These tubercles are developed more laterally than those in 1733E. This vertebra was broken at about its midpoint and subsequently glued such that its ventral surface is artifactually arched. Elongate and deep lateral excavations are present on the lateral surfaces of the centrum. The right parapophysis is visible and slightly projected. As in all of the thoracics, the parapophyses are anteriorly located.

1450C: The vertebra identified as the 16th (Marsh, 1880: 136) has a rodlike hypapophysis and a prominent lateral excavation of

the centrum (fig. 40C). It is referred to as "1450C". The posterior central articular surface is notably more concave than the anterior, as noted by Marsh (1880). By contrast to most other vertebrae, its present state of preservation approximates its illustration in *Odontornithes* (Marsh, 1880: pl. XXII, fig. 3). Two minor exceptions are the representation of the hypapophysis and a fossa in the neural arch. The tip of the hypapophysis is not as terminally bilobate as depicted (Marsh, 1880: pl. XXII, fig. 3), but rather bears two very slightly produced muscle scars on its lateral surfaces. A feature that appears in Marsh (1880: pl. XXII, fig. 3) as an irregular depression in the middle of the lateral surface of the neural arch is a deep, ovoid, lateral excavation of the neural arch (fig. 40C).

The morphologies of this vertebra suggests that it was not necessarily the first thoracic vertebrae, or that it immediately followed 1450A, as is reconstructed in plate XXVI (Marsh, 1880). In the surveyed tinamous (*Nothura darwinii* and *Crypturellus noctivagus*), a midline hypapophysis is developed in the anterior thoracics, including the first. No paired ventrolateral tubercles are developed in these vertebrae. However, in *Gallus gallus*, *Anas platyrhynchos*, *Burhinus capensis*, and *Columba livia*, at least the first and sometimes several of the anteriormost thoracics have both lateral tubercles and hypapophyses. They also lack pre- and postzygapophyses on these vertebrae that are as subparallel and close to midline as they are in 1450C (fig. 40C).

That this vertebra may represent a more posterior thoracic in the series is further supported by the presence in YPM 1733 of two vertebra (1733E, 1733F), as discussed above, with the paired tubercles (tuberculi laterale corporis; Zweers et al., 1987), along with comparatively short hypapophysis that often characterizes the anteriormost thoracic vertebrae in Aves. It is suggested that 1450C was in a position posterior to those of these two vertebrae.

1733G: Another thoracic vertebra figured in *Odontornithes* (Marsh, 1880: pl. XXVII, fig. 5), "1733G", was considered to be the 17th vertebra of *Ichthyornis*. It is nearly complete, lacking only the dorsal portion of the neural spine and transverse processes

(Marsh, 1880). However, this vertebra is depressed and compressed such that the neural canal is almost entirely closed and artifactually appears to have a diameter much less than that of the central articular surfaces. A portion of the dorsal edge of the anterior articular surface is broken. In these respects, the illustration in *Odontornithes* (Marsh, 1880: pl. XXVII, fig. 5) is misleading. Otherwise, however, this illustration faithfully depicts two asymmetrically developed tubercles, for example, on the anteroventral surface of the centrum. These tubercles lie close to the midline, with the one on the right being slightly more protuberant. No hypapophysis is developed. The pre- and postzygapophyses project, respectively, directly anteriorly and posteriorly. There are deep fossae between the prezygapophyses and diapophyses in the neural arch and large, oblong, lateral excavations of the centrum. The anterior and posterior articular surfaces of the centrum are like those in the preceding vertebra; they are ovoid, flattened dorsally, and have a midline depression. Marsh (1880) considered the articular surfaces to be compressed mediolaterally. This appearance is partially artifactual, being somewhat aggravated by deformation.

In *Sterna maxima*, the 17th vertebra has a small midline tubercle as well as a pair of strongly developed, ventrolaterally projected tubercles (tuberculi laterale corporis; Zweers et al., 1987). The right of the paired tubercles protrudes slightly more laterally than does the left. However, the morphology of this vertebra in *Sterna maxima* is otherwise quite different from that in 1733G; the tubercles do not lie close to the midline, project more laterally, and a small hypapophysis is present. However, a morphology more closely approximating that in *Ichthyornis* was not located among the avian exemplars surveyed or in *Hesperornis regalis* (Marsh, 1880). That this vertebra is part of the anterior thoracic series and only posterior to 1733E and 1733F is a reasonable inference from the orientations of the pre- and postzygapophyses and the lack of a hypapophysis; however, that this vertebrae was the 17th cannot be determined (contra Marsh, 1880).

Posterior Thoracic Vertebrae

Three posterior thoracics lacking hypapophyses and lateral tubercles (tuberculi laterale corporis; Zweers et al., 1987) with deep, oblong lateral excavations are part of YPM 1733. A second specimen, YPM 1732, also includes three such vertebrae as well as an additional vertebra incompletely fused to the anterior end of the sacrum, which Marsh (1880) considered a thoracic. The morphology of the vertebrae from these specimens corresponds well to each other and to their description in *Odontornithes* (Marsh, 1880). All but one of these vertebrae (YPM 1732, YPM 1733) were incorporated into the *Ichthyornis victor* panel mount; they are depicted schematically in the reconstruction of *Ichthyornis victor* (Marsh, 1880: pl. XXXIV). This illustration gives the misleading impression that all the thoracic vertebrae lacked hypapophyses. However, as discussed, several anterior thoracic vertebrae have hypapophyses. *Ichthyornis dispar* and *Hesperornis regalis*, like Aves, have hypapophyses on vertebrae of several of the anteriormost thoracics vertebrae (in addition to the posterior cervicals). To have hypapophyses on these vertebrae may be synapomorphic of at least *Hesperornis regalis* + Aves, and perhaps for a more inclusive avialan clade (see appendix 1).

Two of the three posterior thoracic vertebrae from YPM 1732, as well as of those from YPM 1733, are approximately the same length as 1733G; their centra are longer than wide. However, one thoracic vertebra from each specimen is shorter than these other two posterior thoracics. Marsh (1880) identified these short vertebra as the 20th in the series, with the 21st, and last, presacral vertebra incompletely incorporated into the sacrum of YPM 1732, which was preserved with the last two thoracics in articulation with the sacrum (Marsh, 1880).

In YPM 1732, the last thoracic as well as the first (but incompletely ankylosed) sacral are shorter and broader than those lying anterior to them (fig. 40D). In *Sterna maxima* and *Vanellus melanopterus*, a single vertebra, shorter than those immediately anterior to it, is incorporated into the sacrum. Thus, only one short vertebra with the morphology of a

thoracic is incompletely ankylosed to the sacrum in these charadriiforms. In *Ichthyornis*, however, one incompletely ankylosed vertebra, with the morphology of a thoracic, and one free thoracic are short (YPM 1732). The lateral excavations of these shorter vertebrae in *Ichthyornis* are ovoid (fig. 40).

1733H, 1733I, 1733J: In YPM 1733, one of the two comparatively long posterior vertebrae is represented by the centrum and neural arch with an incomplete neural spine, exclusive of the pre- and postzygapophyses (Marsh, 1880). This was considered to be the 18th vertebra (Marsh, 1880), and it is referred to as "1733H". The second vertebra, which Marsh (1880) considered immediately posterior to 1733H, is represented only by the anterior half of a centrum. This vertebra will be referred to as "1733I" and shows no differences from 1733H.

The short, broad vertebra from YPM 1733 mentioned above, and referred to here as "1733J", is crushed and lacks all but the ventral-most portion of the neural arch. The articular surfaces of its centrum, like those in the other thoracics, are subcircular with central depressions.

1732A: The anteriormost vertebra preserved in YPM 1732 (as identified by Marsh, 1880, from the semi-articulated specimen of YPM 1732; see above) includes the centrum, prezygapophyses, right postzygapophysis, and a portion of the neural spine. Two deep pneumatic fossae are visible in the lateral surface of the neural arch. Deep, oblong, lateral excavations are also developed. Crushing obscures the right side of this vertebra; however, in all preserved structures it matches posterior thoracics 1733H and 1733I.

1732B: The next vertebra, referred to here as "1732B", preserves most of the neural arch and centrum. Deep, oblong, lateral excavations and excavations in the posterolateral surface of the neural arch are developed. The portion of the transverse process preserved projects laterodorsally. The neural arch has been crushed mediolaterally to all but close the neural canal. However, even taking into account the distortion of the specimen, it appears that the diameter of this canal may have been small compared to the condition in Aves.

1732C: The final, short, thoracic vertebra

from YPM 1732, here called “1732C”, has already been commented upon. All of its preserved structures are the same as those in 1733J, and it is much more complete than that vertebra (fig. 40D). The centrum and most of the neural arch, including portions of the right transverse process, and a complete neural spine are preserved. The right prezygapophysis and most of the left transverse process are missing, and the left side is generally crushed. The dorsal edge of the neural spine is slightly projected laterally such that it appears slightly T-shaped in anterior or posterior view. The neural canal has been crushed mediolaterally, but again, the diameter of the neural canal appears relatively small. The shapes of the parapophyses and articular surfaces are the same as those seen in the other posterior thoracics.

1450D: The thoracic identified (Marsh, 1880: 140) as the 21st, and last, presacral vertebra is from the holotype of *Ichthyornis dispar* (YPM 1450). It was figured (Marsh, 1880: pl. XXII, fig. 4) as uncrushed, and comparatively short dorsoventrally, compared to 1450C. However, unlike its representation, this vertebra, here referred to as “1450D”, has the neural arch pressed into the dorsal surface of the centrum to completely close the neural canal. The centrum is also crushed dorsoventrally, partially closing the prominent lateral excavations and deforming its anterior articular surface. Matrix between the broken parts of this vertebra suggests that this deformation is the vertebra’s original state of preservation. Marsh’s (1880) illustration cannot but be considered a misleading reconstruction.

Marsh (1880: 140) noted that in this vertebra, the postzygapophyses face approximately laterally, and that the parapophyses are ovoid. Both of these morphologies are also seen in 1450C; however, the ventral edge of the centrum in lateral view was slightly more arched than 1450C. The width of the centrum of 1450D and the proportions of its articular surfaces are not notably greater than in 1450C (contra Marsh, 1880). There is no hypapophysis (Marsh, 1880). The edge of a deep pneumatic fossa in the lateral surface of the neural arch is preserved. The stumps of the transverse processes indicate that they would have angled dorsally.

The position of this element, 1450D, within the thoracic series should be considered uncertain. There is no reason to believe that it is the 21st and terminal vertebra of the series, or even to believe that there are necessarily 21 presacral vertebrae in *Ichthyornis*. Indeed, it is best considered a posterior thoracic other than the most posterior one or two. YPM 1450, the holotype of *Ichthyornis dispar*, represents a significantly smaller individual than YPM 1732; thus, the last thoracic of YPM 1450 should be smaller than the corresponding vertebrae in YPM 1732. However, 1450D is longer than both 1732C, the last “free” thoracic, and the vertebra fused on the sacrum in YPM 1732 (considered the last thoracic by Marsh, 1880). 1450D is approximately the same length as the midthoracic vertebra, 1450C, not shorter than it, while both the last thoracic or first sacral are shorter than the more anterior thoracics in YPM 1732. Marsh (1880) gave no taphonomic reason for the identification of this vertebra as the most posterior thoracic (e.g., that they were in articulation). Therefore, 1450D is considered a posterior thoracic vertebra (based on the lack of a hypapophysis and projection of the zygapophyses) other than the last or penultimate vertebra (based on its proportions).

SACRAL VERTEBRAE

The sacrum of *Ichthyornis* is represented in three YPM specimens: the holotype of *Ichthyornis dispar* (YPM 1450), YPM 1733, and YPM 1732. The sacra of the holotype of *Ichthyornis dispar* and YPM 1732 were figured in *Odontornithes* (Marsh, 1880). While the illustration of the *Ichthyornis dispar* sacrum is largely accurate (Marsh, 1880: pl. XXVII, figs. 5–7), that of YPM 1732 as representative of *Ichthyornis victor* (Marsh, 1880: pl. XXXII, figs. 2, 3) differs significantly from the actual material. The extremely poorly preserved partial sacrum in YPM 1733 was not figured or discussed, although many presacral vertebrae from that specimen were figured and incorporated into the *Ichthyornis victor* panel mount.

Ten fused vertebrae comprise the sacrum of the holotype of *Ichthyornis dispar* (YPM 1450; fig. 41A,C). As illustrated by Marsh

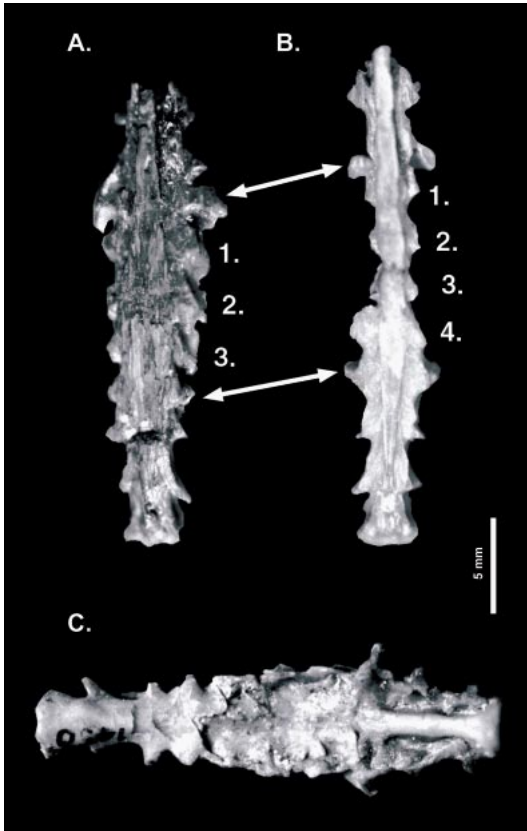


Fig. 41. The sacrum of the *Ichthyornis dispar* holotype (YPM 1450) in (A) dorsal and (C) ventral views. The number of midseries sacra with diminutive and dorsally projected transverse processes in (A) *Ichthyornis dispar* and (B) *Apatornis celer* (YPM 1451) are indicated.

(1880) it is strongly crushed dorsoventrally (fig. 41C). The description of the sacrum in *Odontornithes* (Marsh, 1880) is also largely accurate. The anterior articular surface is depressed (though not strongly concave) and subcircular. The centra of the first three vertebrae are narrow, with the anteriormost having shallow excavations. There do not appear to be parapophyses on the first sacral vertebra. The transverse processes of the first two vertebrae are narrow and rodlike (fig. 41A). Those on the third vertebra are broader than the transverse processes of the preceding two vertebrae (fig. 41A). The transverse processes of all three of these vertebrae are directed dorsolaterally and are not as well preserved as their illustration indicates.

The following three vertebrae have very short, broad, and directly dorsally projected transverse processes (fig. 41A). By contrast, the 7th vertebra has a narrow, laterally projected transverse process and appears to also have the stump of a fused rib (processus costalis; Baumel and Witmer, 1993). The following three vertebrae have narrow transverse processes, the first of which projects directly laterally, subparallel to that of the 7th vertebra. The transverse processes of the 9th and 10th sacra project posterolaterally, and those of the 10th sacral are located close to the posterior edge of the sacrum. Though crushed, the sacrum is visibly widest at about its midpoint. The last sacral is slightly shorter than the vertebra directly preceding it. There are well-developed prezygapophyses on the first sacral (fig. 41A) and postzygapophyses on the last sacral. The iliosynsacral grooves (sulci iliosynsacralis; Baumel and Witmer, 1993) were open dorsally (fig. 41A). The fused neural spines on the anterior vertebrae are broad at their dorsal tips, thickened by ossified tendons and forming a roughly T-shaped cross section.

The second sacrum (fig. 42) figured and discussed in *Odontornithes* as representative of *Ichthyornis victor* is from YPM 1732. Its reconstruction (Marsh, 1880: pl. XXXII, figs. 2, 3) differs from the actual material that was removed from the *Ichthyornis victor* panel mount and reprepared (fig. 42). At present, only the pelvic bones from the right side are preserved (fig. 42B,D). These include the preacetabular ilium, the anterior tip of the pubis, and an almost complete ischium. Complete pubes, ischia, and preacetabular ilia were originally depicted as present by Marsh (see fig. 42C).

The sacral series of YPM 1732 was figured (fig. 42C) as anteriorly incomplete or covered in matrix (Marsh, 1880: pl. XXXII, figs. 2, 3); however, removal from the panel mount and further preparation revealed that it is complete and well preserved (fig. 42B,D). Ten vertebrae were described as comprising the sacral series in YPM 1732 and the anteriormost attached vertebra considered by Marsh (1880) to be the last thoracic. This vertebra is here discussed as a sacral: While there is a conspicuous suture between this vertebra and the rest of the sacral

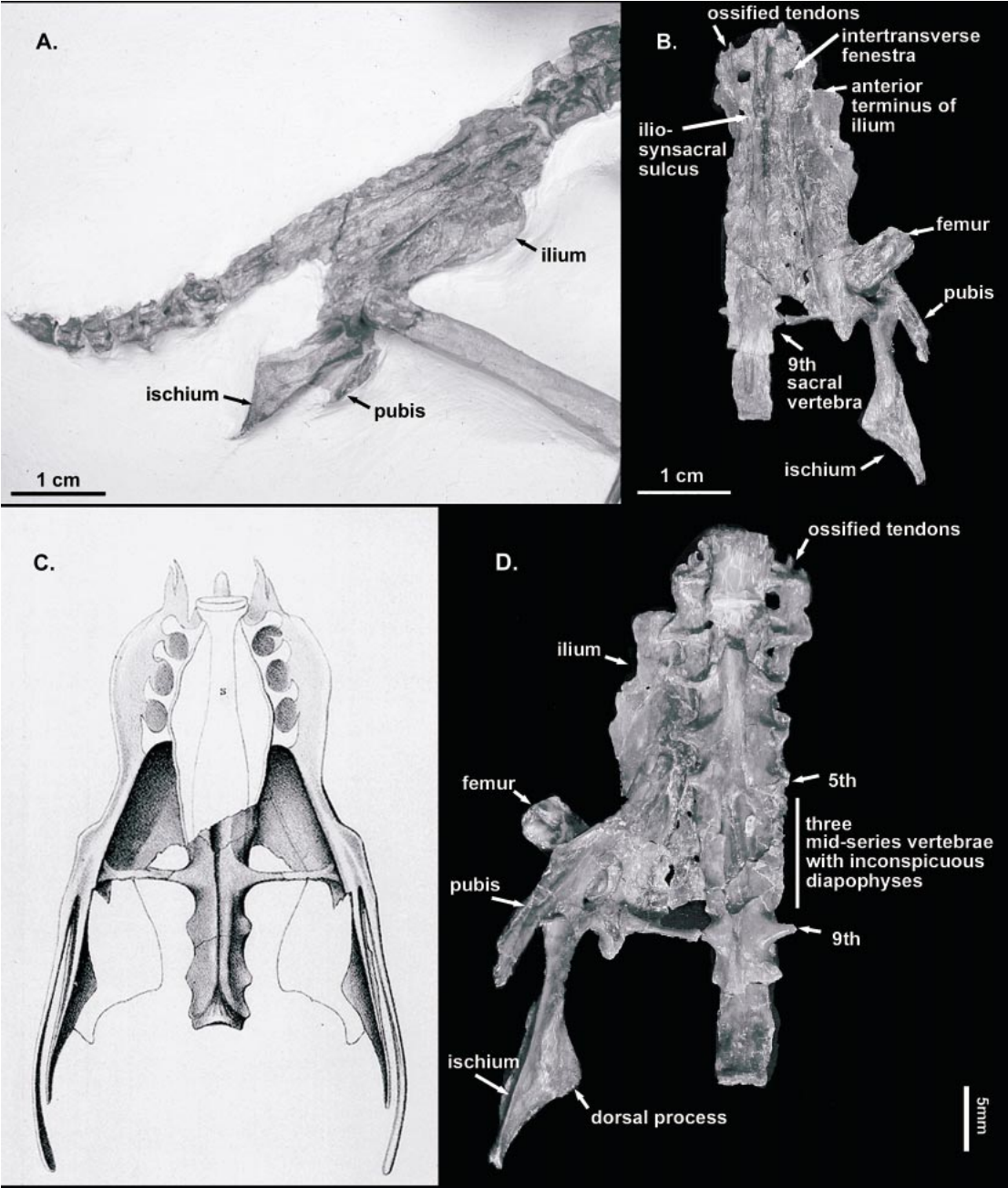


Fig. 42. The sacrum and pelvic bones of *Ichthyornis dispar* (YPM 1732) in dorsal view (A) as included in the "*Ichthyornis victor*" panel mount and (B) removed from the mount; in ventral view (C) as depicted in Marsh (1880) and (D) after their removal from the mount and further preparation. In "A" the thoracic and caudal vertebrae as well as the femur also belong to specimen YPM 1732.

series (fig. 42D), it is ankylosed to these vertebrae. Marsh considered this vertebra fused on the anterior end of the sacrum in YPM 1732 specifically to correspond to a thoracic vertebra of the *Ichthyornis dispar* holotype (i.e., vertebra 1450D). As discussed above, the vertebra in YPM 1450 and that on the anterior end of the sacrum in YPM 1732 differ in morphology, and this assumption is considered baseless.

Twelve vertebrae actually comprise the sacrum in YPM 1732 (or 11 if the most anterior is considered to be a thoracic). The anteriormost sacral (or last thoracic of Marsh, 1880) is a short vertebra with an incompletely closed suture between its centrum and that of the following sacral. Ossified tendons are fused to the transverse processes of this vertebra and pass posteriorly to also fuse with these processes of the second sacral (fig. 42B,D). On the left side of this vertebra, dorsal and anterior to the remains of what appears to be a small lateral excavation, a parapophysis is visible. This first sacral appears similar in morphology to the last thoracic which was found in association with it, 1732C (i.e., short compared to more anterior thoracics; fig. 40D). The apparent lack of parapophyses on the first sacral of the *Ichthyornis dispar* holotype and their presence in YPM 1732 may suggest that this character should be also be considered polymorphic for *Ichthyornis dispar*. The ilium overlapping one set of ribs (indicated by the presence of a parapophysis) has been considered a synapomorphy of Aves (appendix 1, character 161). However, the ilium in YPM 1732 is short, and while ribs did articulate with the first ankylosed vertebra, it does not appear to have been covered by the ilium (fig. 42B).

The centrum of the second sacral, which would appear to correspond morphologically to the first of the *Ichthyornis dispar* holotype (YPM 1450), is more compressed than that of the first sacral of YPM 1732. The transverse processes of this vertebra, as well as those of the first and third sacrals, are narrow, rodlike, and projected directly laterally. The transverse processes of the fourth sacral appear stouter than those of the preceding vertebrae; however, their shape appears somewhat distorted by crushing.

The transverse processes of the fifth sacral

are narrow, rodlike, and projected directly laterally (fig. 42D). By Marsh's count, this vertebra would correspond to the fourth sacral of the holotype of *Ichthyornis dispar* (YPM 1450); however, the transverse processes of the fourth sacral in YPM 1450 project dorsally and appear absent in lateral view. In YPM 1732, this morphology is developed on the following three sacral vertebrae, but not on that which would correspond to the fourth in YPM 1450.

The centra of the three vertebrae with this morphology are expanded laterally with dorsally directed transverse processes in the holotype of *Ichthyornis dispar* (YPM 1450; fig. 41A) and YPM 1732 (fig. 42D) while there are four in *Apatornis celer* (fig. 41B). The presence of midsacral vertebrae that appear to lack transverse processes or have them projected directly dorsally (such that only a line of spinal nerve foramina is visible close together on the edged of compressed vertebra) is only known with confidence for *Ichthyornis* and Aves (appendix 1, character 62). In YPM 1732, like the holotype of *Ichthyornis dispar*, the centra are the broadest in the middle of the series (fig. 42D).

The 9th sacral vertebra has a well-developed sacral rib that extends to contact the ilium just posterior and dorsal to the acetabulum. The 10th vertebra preserves the base of the transverse process projecting directly laterally, subparallel to that of the preceding vertebra (fig. 42D). The transverse processes of the 11th and 12th sacral vertebra are not preserved. The transverse processes of the 12th sacral appear to have arisen close to the posterior terminus of the sacrum as in *Ichthyornis dispar* (figs. 41C, 42D). Two faint tubercles are developed close to the anterior edge of this vertebra. These tubercles are also weakly developed in the holotype of *Ichthyornis dispar* (fig. 41C) and more conspicuous in that of *Apatornis celer* (fig. 14B). Marsh (1880) described and illustrated a pronounced groove on the ventral midline of the centra of the posterior portion of the sacrum (fig. 42C). There is a midline crack posteriorly and breakage in midseries that gives the centra this appearance. There may have been a slight groove on the 5th to 11th sacral vertebra, but it was clearly not as deep as figured.

The anterior and posterior articular surfaces of the 1st and 12th sacral vertebrae, respectively, are slightly concave as in *Ichthyornis dispar*. There are well-developed prezygapophyses on the first vertebrae while no postzygapophyses are preserved on the last. Between the transverse processes of the 1st and 2nd sacral vertebrae, as well as between the 7th and 8th vertebrae, openings to the dorsal surface of the sacrum are present (fenestrae intertransversariae; Baumel and Witmer, 1993).

YPM 1733 includes two fragments of the sacral series that are severely crushed dorsoventrally. The sacrum of YPM 1733 is from a smaller individual than that of YPM 1732 but larger than the *Ichthyornis dispar* holotype (YPM 1450). One fragment preserves what would correspond the 4th sacral of YPM 1732 and the 3rd sacral of the *Ichthyornis dispar* holotype. In dorsal view, the coossified neural spines are relatively broad mediolaterally from attached ossified tendons. The iliosynsacral sulci are broad. The second fragment of YPM 1733 includes what would correspond in YPM 1732 to the 7th sacral through a small part of the 10th sacral, or the sixth part of the 9th in the holotype of *Ichthyornis dispar* (YPM 1450). The base of the rodlike transverse processes on the 9th vertebra of YPM 1732 and the 7th vertebra in *Ichthyornis dispar* (YPM 1450) are visible. The centra in the portion preserving the 7th through 9th sacral vertebrae are broad, as in the midsacra of both YPM 1732 and YPM 1450.

Marsh (1880) noted that *Ichthyornis* differed from *Sterna maxima* in having only 10 sacra as opposed to 13 in *Sterna maxima*. Total sacral number increases toward Aves (appendix 1, character 61); however, this character may vary within *Ichthyornis*. In the *Ichthyornis dispar* holotype (YPM 1450), there are 10 fused sacra while in YPM 1732 there are 12. The number of vertebrae posterior to the strut at the acetabulum, the single vertebra with a costal strut, and the number of vertebra that appear to lack transverse processes is the same in both YPM 1450 and YPM 1732. However, the number of vertebrae anterior to the first appearing to lack transverse processes is different. In the holotype of *Ichthyornis dispar* there are three

anterior vertebrae with laterally projecting transverse processes while in YPM 1732 there are five. One appears to have been added to the anterior end and the second between the third and fourth of *Ichthyornis dispar*. While in YPM 1450 and YPM 1732 three midseries sacra lack conspicuous transverse processes, four lack them in the holotype of *Apatornis celer* (appendix 1, character 62). Thus, it is the *morphology* of the “additional” vertebra (relative to the *Ichthyornis dispar* holotype) that appears to differ between *Apatornis celer* and YPM 1732, while the position of this vertebra is the same; it is at the end of the series of vertebrae with the “anterior morphology” and the beginning of those with the “midseries morphology”.

Marsh (1880) noted two further differences between *Ichthyornis* and *Sterna maxima* in the numbers of vertebrae of certain morphologies in the sacrum. He noted that the strutlike costal process (i.e., “strong transverse bar”, Marsh, 1880: 162) in the area of the acetabulum occurs on the 7th sacral in *Ichthyornis* and on occurs on the 9th in *Sterna maxima* and that three vertebrae are posterior to this strut in *Ichthyornis* and four in *Sterna maxima*. However, he was referring to the holotype of *Ichthyornis dispar*: By contrast, YPM 1732 (referred to *Ichthyornis dispar*) has the costal strut on the 9th ankylosed vertebra (fig. 42D). In Aves, this strut typically occurred on the 9th or 10th sacral as mentioned by Marsh (1880) for *Sterna maxima*.

In *Ichthyornis* (YPM 1450, YPM 1732) and *Apatornis celer* (YPM 1734), there are only three vertebrae (figs. 41A, 42C) posterior to the strut at the acetabulum. By contrast, all Aves surveyed had more vertebrae posterior to this strut. In the tinamous and galloanserines considered, there were at least five and sometimes seven vertebrae (e.g., *Crypturellus noctivagus*). As the total vertebral count is unknown for *Ichthyornis* and cannot be compared to that in Aves, it is unclear whether additional elements were incorporated from the caudal series or whether additional new iterated elements were developed (i.e., that the total number of vertebrae increased by the addition of vertebrae with

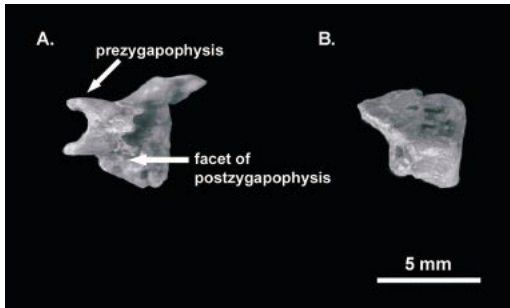


Fig. 43. The caudal vertebrae of *Ichthyornis dispar* (YPM 1732): (A) the third free caudal in dorsal view and the (B) incompletely preserved fused, distal caudals (pygostyle) in right lateral view. In A, the morphology of elongate prezygapophyses, and the absence of projected postzygapophyses (developed as facets) are indicated.

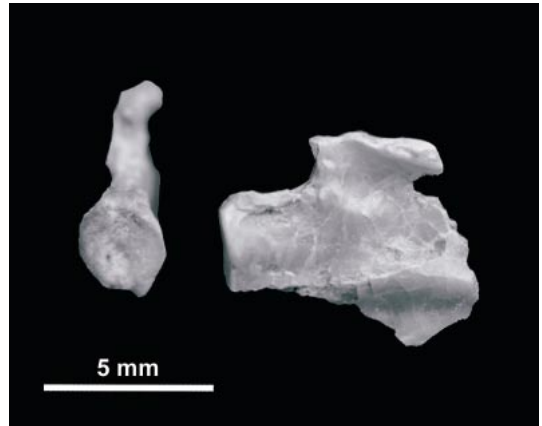


Fig. 44. An element from YPM 1775 that bears comparison to a pygostyle but which differs markedly from the morphology of that element in YPM 1732 (compare fig. 43).

this morphology phylogenetically after the loss of caudal vertebrae).

CAUDAL VERTEBRAE

Caudal vertebrae are only represented in YPM 1732 (fig. 43) and possibly by a part of a pygostyle from YPM 1775 (fig. 44). In YPM 1732, five free caudals and the base of the pygostyle are known. These vertebrae were figured in *Odontornithes* (Marsh, 1880: pl. XXVIII, figs. 2–7). Marsh (1880) refers to seven caudals as preserved in YPM 1732 and figured in plate XXVIII. Five free caudals and a pygostyle are figured. Marsh (1880) reasoned that the pygostyle was comprised of two vertebrae. The tip of the pygostyle is missing for YPM 1732 (Marsh, 1880). Detailed descriptions of the individual vertebrae are provided in the text of *Odontornithes* (Marsh, 1880) and were used in conjunction with plate XXVIII to identify vertebrae removed from the *Ichthyornis victor* panel mount (fig. 2). By contrast to their illustration, the last two free caudal vertebrae, when removed from the *Ichthyornis victor* panel mount, were joined by original matrix to each other and to the pygostyle. Apparently, the depiction of the anterior and posterior articular surfaces of the fifth, the posterior surface of the fourth, and the anterior surface of the sixth (Marsh, 1880: pl. XXVIII, fig. 6) were largely reconstructed. The transverse processes of the free caudal

vertebrae are significantly less complete than their illustration (Marsh, 1880). This is especially the case of the second and third caudals (Marsh, 1880: pl. XXVIII, figs. 3, 4).

As Marsh (1880: 166) noted, the prezygapophyses preserved on the two first caudals are extremely long and would have articulated on the dorsal surface of the preceding vertebra (fig. 43A). This is the opposite of the normal relation of pre- and postzygapophyses. Such a relationship is well developed in *Vanellus melanopterus* (Charadriiformes), while in many other avian taxa, the pre- and postzygapophyses on the caudals are weakly developed, nonarticulating tubercles (e.g., *Nothura darwinii*, *Crypturellus noctivagus*, *Anas platyrhynchos*, *Columba livia*). In *Sterna maxima*, *Alectura lathamii*, *Gallus gallus*, and *Meleagris gallopavo*, this relationship is present but slightly less developed than in *Ichthyornis* or *Vanellus melanopterus*. In *Sterna maxima*, this articulation appears more conspicuous on the posterior caudals, whereas in Galliformes it is more conspicuous on the anteriormost caudals. Development of this articulation appears to be synapomorphic of at least *Ichthyornis dispar* + Aves. It is not developed in *Hesperornis regalis*, although the inclination of the anterior margin of the neural spine in the first two caudals is reminiscent of the

condition in Aves where this articulation is weakly developed (e.g., *Columba livia*).

In YPM 1732, there is no preserved indication of articular facets for unfused chevrons. Chevrons also do not appear fused to any of the caudal vertebrae in YPM 1732. As remarked by Marsh (1880), the ventral surface of the centra bears a slight midline ridge with two shallow lateral depressions. In the fifth caudal, the last with transverse processes, this morphology is more pronounced. The complete neural arch illustrated for the fifth free caudal vertebrae is no longer present. The central articulations are all platycoelous. The central articular surfaces of the third caudal are crushed such that they appear strongly depressed (Marsh, 1880: pl. XXVII, fig. 4). The posterior articular surfaces of at least the last two free caudals are inclined to face slightly dorsally. This curvature indicated that the tail in *Ichthyornis* (YPM 1732) would have been curved somewhat dorsally as in most of Aves (Gauthier and de Queiroz, 2001).

As the neural spines are missing in all of the free caudals, it is unknown whether they were bifid as in many Aves (e.g., *Crypturellus noctivagus*, *Nothura darwinii*, *Gallus gallus*, *Anas platyrhynchos*). This condition is also present in *Hesperornis regalis*, and it is possible that having at least one caudal with bifid neural spines is a synapomorphy of that taxon + Aves. The condition in *Asaravis ukhaana* is unknown.

The centrum articular surfaces of the caudal vertebrae, where preserved, are ovoid and flat. There is an unusual tubercle at the midpoint of the dorsal edge of the anterior and posterior articular surfaces of the first, third, and fifth caudal vertebrae. On the fourth, it is only preserved on the posterior surface, while the anterior face is broken in this area. In what Marsh (1880) identified as the second caudal, this tubercle is not developed on the anterior surface, but it is developed on the posterior surface. Because a tubercle is also absent on the last vertebra of the sacrum, it is possible that this surface articulated with the anterior central surface of what Marsh (1880) considered to be the second caudal; thus, the vertebra Marsh (1880) considered the first and that which he considered the second may be misidentified (reversed).

However, at least the last two free caudals and the pygostyle were evidently found in articulation; it is possible that these anterior caudals were as well. Such tubercles were not observed in the surveyed Aves.

The two terminal caudal vertebrae are fused. The dorsal edge of the preserved portion of the fused terminal caudals is unbroken, while the base of this element is damaged and it lacks its distal end (fig. 43B). The element formed of fused terminal caudals was not long, and it appears to have some of the dorsally projected "plowshare" shape, as well as loss of transverse processes, consistent with the conformation of a pygostyle in Aves. The large ventral notch in this fragment is artifactual. The triangular neural canal is preserved above the slightly concave articular surface (fig. 43B). Paired foramina are developed near the dorsolateral surface of the preserved portion of the pygostyle in its lateral surface. These foramina were not illustrated in *Odontornithes* (Marsh, 1880). Foramina are in a similar location in *Vanelus melanopterus*. A feature apparently topologically congruent with the foramina, a notch, is developed in the dorsal edge of the pygostyle in *Nothura darwinii* between the neural spines of the first two partially fused vertebrae. Neither foramina nor a notch were observed in *Gallus gallus*, *Anas platyrhynchos*, or *Columba livia*. The shape of the distal end of the pygostyle, although broken, does not suggest additional vertebrae were incorporated.

A fragment that is part of YPM 1775 could be part of a pygostyle (fig. 44). If so, it appears to differ significantly from that in YPM 1732. It also does not correspond well with the pygostyles of the surveyed Aves. This fragment includes what is interpreted as an ovoid, slightly concave, articular surface and a flat lamina that, while broken close to the ovoid articulation, has a projected lip on one edge (ventral?; fig. 44). This element deserves further scrutiny. No neural canal is preserved, and the piece narrows abruptly distal to the ovoid articular surface unlike the condition in YPM 1732.

RIBS

The proximal portions of several ribs are preserved in the *Ichthyornis dispar* holotype

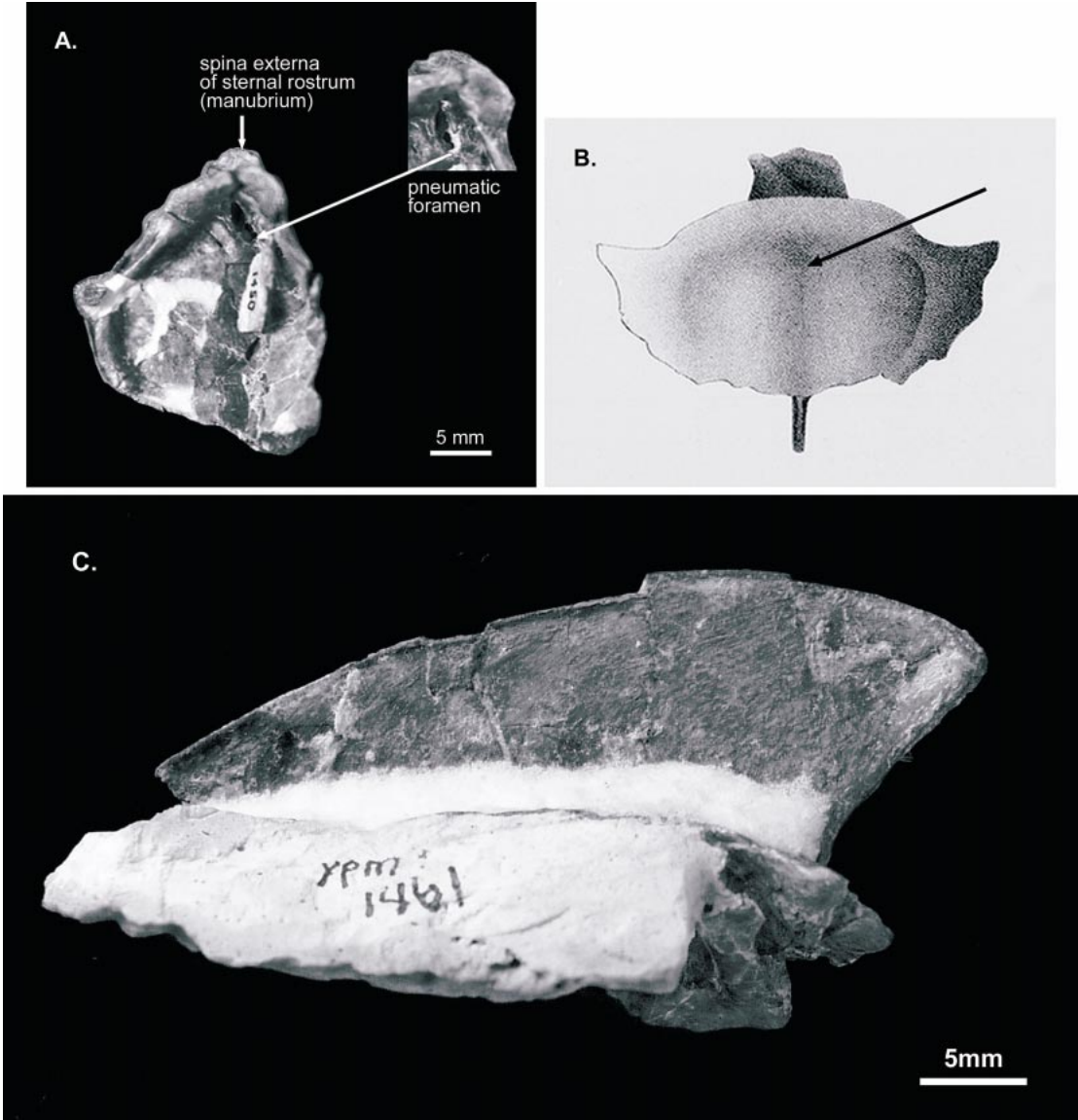


Fig. 45. The sternum of *Ichthyornis dispar*. The holotype specimen (YPM 1450) sternum in (A) dorsal view and (B) as represented by Marsh (1880) as well as two sterna from referred specimens (C) YPM 1461 and (D) BMNH A905 in left lateral view. The location of a large midline pneumatic foramen shown in “A” is indicated with an arrow in “B”.

(YPM 1450). No pneumatic fossae or foramina are visible in the preserved ribs, and there is no evidence of fused or unfused uncinate processes.

STERNUM

The sternum of *Ichthyornis* is represented in two YPM specimens, the holotype of *Ich-*

thyornis dispar (YPM 1450; fig. 45A,B) that was incorporated into the *Ichthyornis dispar* panel mount and YPM 1461 (fig. 45C), which was incorporated into the *Ichthyornis victor* panel mount. The sternum is also well preserved in a referred specimen (see Taxonomic Revision) from the BMNH (BMNH A905; fig 45D), which is commented on with

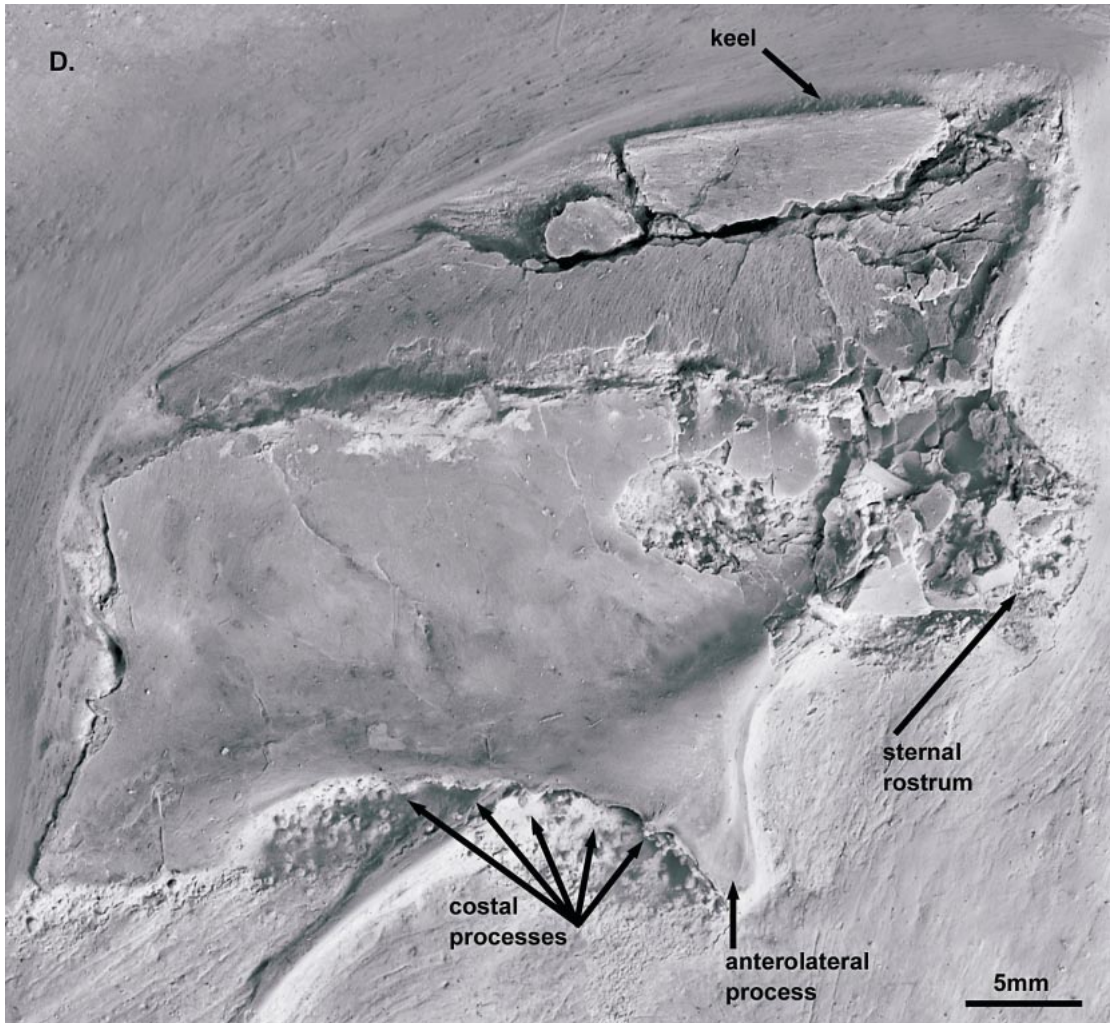


Fig. 45. The sternum of *Ichthyornis dispar* (continued).

respect to morphologies not preserved in the YPM material. The *Ichthyornis dispar* holotype (YPM 1450) sternum differs markedly from its illustration in *Odontornithes* (Marsh, 1880: pl. XXIII, figs. 1–4; compare fig. 45A and B). The sternum of YPM 1461 (fig. 45C) was figured only in the reconstruction of *Ichthyornis victor* (Marsh, 1880: pl. XXXIV).

The preserved portions of the *Ichthyornis dispar* holotype sternum consist of one large piece of its anterior end and a narrow strip of bone from the left sternal margin bearing the projected articular facets for sternal ribs (processuum costalis; Baumel and Witmer, 1993). The first fragment was figured as un-

crushed (fig. 45B); however, it is badly damaged. This damage is considered original to the specimen as discovered, as matrix lies between the crushed pieces of bone that comprise it. Marsh (1880) did not figure the second fragment.

As Marsh (1880) illustrated (pl. XXIII, fig. 1) and discussed, the right coracoidal sulcus lies ventral to the left where they cross on the midline in YPM 1450. The sulci in this specimen, as well as in YPM 1461, are crossed such that the edge of the right sulcus passes ventral of the left for several millimeters, a condition more extreme than in *Burhinus capensis*, for example, where the

sulci are less strongly crossed. The condition in *Ichthyornis dispar* in which the right coracoidal sulcus crosses ventral to the left is known in all Aves with crossed sulci (Ericson, 1997). In *Crypturellus noctivagus*, *Nothura darwinii*, *Gallus gallus*, *Alectura lathami*, *Anas platyrhynchos*, *Columba livia*, *Gavia stellata*, and *Sterna maxima*, the coracoidal grooves are uncrossed (for a more complete discussion of taxa with crossed facets, see Houde, 1988; Ericson, 1997). The ventral midline portion of the sternum is projected in a relatively broad external spine of the sternal rostrum (rostrum sterni: spina externa; Baumel and Witmer, 1993; fig. 45D). On its ventral surface, a prominent, low midline ridge extends from the anterior sternal margin posteriorly toward the remains of the keel.

The anterior portion of the sternal keel in the *Ichthyornis dispar* holotype specimen is broken and appressed to the remains of the right side of the sternum. The ventral edges of the coracoidal sulci do not project anteriorly as far as do the dorsal edges. No intermuscular lines are preserved. No portion of the ventral edge of the keel is preserved, although illustrated in *Odontornithes* (Marsh, 1880: pl. XXIII, fig. 2).

The anterodorsal surface of the sternum is depressed posterior to an anterior rim or bar (pila coracoidea; Baumel and Witmer, 1993; fig. 45A). In this depression (facies visceralis sterni, pars cardiaca; Baumel and Witmer, 1993) lies a large, ovoid, midline pneumatic foramen (fig. 45A). Pneumatization of the dorsal sternum is a synapomorphy of at least *Ichthyornis* + Aves (appendix 1, character 73:1 and Part II, Results).

A notch in the anterior edge of the sternum lies just dorsal to the external spine of the sternal rostrum (rostrum sterni: spina externa; Baumel and Witmer, 1993) even with the dorsal edges of the coracoidal sulci. The pneumatic foramen and notch were not figured or discussed in *Odontornithes*. In fact, the sternum was illustrated with a complete, well-preserved anterodorsal surface lacking a foramen (fig. 45B). Also illustrated for YPM 1450 were anterolateral processes that are not currently preserved.

Marsh (1880) did not comment on or figure the fragment of YPM 1450 with the pre-

served costal processes (processuum costalis; Baumel and Witmer, 1993) for sternal rib articulation. Five costal processes appear to have been present, although the anterior- and posteriormost processes are only indicated by a narrowing of the edge of the sternum. Five costal processes are also present in a well-preserved sternum referred to *Ichthyornis* from the Smoky Hill Chalk of Kansas (BMNH A905; fig. 45D). No pneumatic foramina between these processes are present in YPM 1450 or BMNH A905. And, pneumatization of this part of the sternum may be a synapomorphy of Aves relative to *Ichthyornis*.

YPM 1461 consists of the medial portion of the sternum lacking its posterior terminus (fig. 45C). Most of the lateral portions of the corpus of the sternum are missing. The keel is virtually complete. The structures preserved in the sternum are the same as those preserved in the holotype of *Ichthyornis dispar* and the London sternum (BMNH A905; fig. 45D), so far as they can be compared. YPM 1461 similarly has a large pneumatic foramen close to the anterior margin of the dorsal surface of the sternum. This foramen also lies in a depression bounded by a well-developed anterior rim. The coracoidal facets are crossed and the sternal rostrum is broad as it is in *Ichthyornis dispar* holotype (YPM 1450; fig. 45C).

The keel originated close to the anterior edge in *Ichthyornis dispar* (YPM 1450, YPM 1461, BMNH A905; fig. 45C,D). Its anterior face, best preserved in YPM 1461, is flat and relatively broad in anterior view. Its apex is pointed and would have extended anteriorly approximately as far as the tip of the sternal rostrum (fig. 45C,D). It appears to extend slightly past this point in YPM 1461, but the sternal rostrum has been crushed posteriorly as indicated by a crack at the anterior edge of the base of the keel. No intermuscular lines or ridges demarcating the attachments of the m. supracoracoideus and m. pectoralis are visible (fig. 45C,D). A slight ridge is developed along the ventral margin of the keel. The morphology of this posterior margin or that of the anterolateral processes (processi craniolateralis sterni; Baumel and Witmer, 1993) is not preserved in either YPM 1461 or YPM 1450. As preserved in BMNH

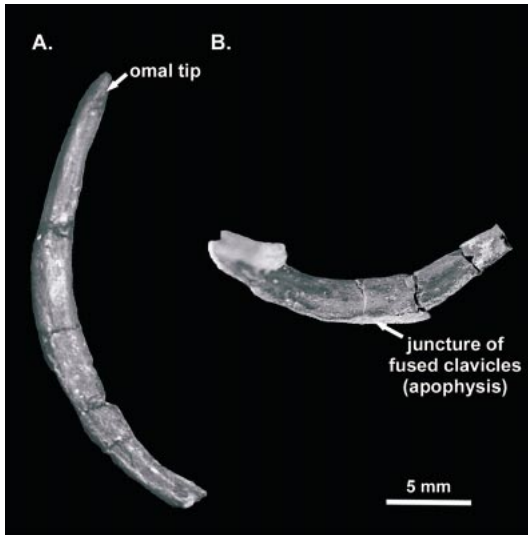


Fig. 46. Two fragments of the furcula of *Ichthyornis dispar*: (A) right(?) ramus in medial view including omal tip (SMM 2503) and (B) juncture of fused clavicles in posterior view (YPM 1755).

A905, the sternum was broad, the anterolateral processes were relatively elongate, the keel appears to have approached the posterior margin of the sternum, and no xiphoid processes (processi caudolateralis sterni; Baumel and Witmer, 1993) or processes projecting posterolaterally from directly posterior to the facets for the sternal ribs appear to have been developed (fig. 45D). Sternal incisures (incisurae sterni; Baumel and Witmer, 1993), were they developed, must have been restricted to indentations of the posterior margin; this margin is incompletely preserved in BMNH A905 (fig. 45D), but the lateral sternal edges are well preserved and show no indication of pronounced incisures (e.g., the deep, posterolateral incisures developed in tinamous and galliforms).

FURCULA

Marsh considered the furcula to be unrepresented in the YPM *Ichthyornis* material (Marsh, 1880: 144). However, a portion of what appears to be the area of juncture between the fused clavicles is preserved in YPM 1755 (fig. 46B). YPM 1755 is a specimen referred to *Ichthyornis dispar* on the basis of apomorphy (see table 1). The section

is a broad arch, delicate and nearly round in cross section, while appearing to flatten slightly at what is interpreted as the midpoint of the furcula (juncture between the fused clavicles; fig. 46B). A hypocleideum does not appear to be present. However, the surface where one would be developed (the ventral surface of the midpoint of the element) is not well exposed, and it is possible that one was present. A specimen from the Smoky Hill Chalk Member, Niobrara Formation of Kansas (SMM 2503) referred to *Ichthyornis dispar* by apomorphy (see Taxonomic Revision) also preserves a portion of the furcula that includes the narrow, blunt omal tip of the right (?) furcular ramus (fig. 46A).

CORACOID

The coracoid is represented by 24 YPM specimens (table 1) including the holotype of *Ichthyornis dispar* (YPM 1450). However, the distal coracoid from YPM 1458 and the proximal coracoid from YPM 1459 articulate perfectly. Because the YPM 1459 portion of the coracoid is identified in the YPM VP Catalogue notes as collected a year later than the rest of YPM 1459, it is suggested that this coracoid be removed from YPM 1459 and associated with YPM 1458 (table 1). Thus, although there are 24 YPM specimen numbers discussed, there are only 23 YPM *Ichthyornis* coracoids.

Of the 24 coracoids, then, from the YPM *Ichthyornis* material, 5 are nearly complete: right coracoids from YPM 1733 and YPM 1745 as well as left coracoids from YPM 1743, YPM 1757 and YPM 56577. These and 6 other right coracoids (i.e., YPM 1461, YPM 1727, YPM 1741, YPM 1746, YPM 1768, YPM 1776) and 8 further left coracoids (i.e., YPM 1450, YPM 1452, YPM 1458 + part of YPM 1459, YPM 1718, YPM 1719, YPM 1763, YPM 1767, YPM 1773) are referred to *Ichthyornis* based on apomorphies and/or detailed correspondence in morphology and the description given from referred specimens (see table 1). Four additional coracoids (YPM 1446, YPM 1765, YPM 1766, YPM 1774) and YPM 1745 (listed above) are referred to *Ichthyornis* but differ in some detail of their morphology. These

differences are listed in table 4. All but two coracoids (i.e., YPM 1765, YPM 1766) are notably larger than the holotype of *Ichthyornis dispar*. The coracoid from YPM 1446 is the largest individual represented, while YPM 1765 is one of the smallest specimens referred to *Ichthyornis*. A nearly complete coracoid (SMM 2503) is also discussed. As mentioned in the Taxonomic Revision, it is referred to *Ichthyornis dispar* on the basis of apomorphy.

The coracoid and scapula of YPM 1734 (named as the holotype of *Iaceornis marshi*), which is not referred to *Ichthyornis dispar*, were incorporated into the *Ichthyornis victor* panel mount. The proximal coracoid from YPM 1452 was the only portion (contra Marsh, 1880) of the *Ichthyornis victor* holotype illustrated in *Odontornithes* (Marsh, 1880: pl. XXIX, figs. 13–16). The illustrated coracoid was identified as YPM 1452 by its correspondence with (1) the length of the preserved portion of YPM 1452, and (2) a crack illustrated on the procoracoid process (that now marks the end of the preserved portion of the process in YPM 1452).

Only the sternal portion of the left coracoid is represented in the holotype of *Ichthyornis dispar* (YPM 1450). It is figured in *Odontornithes* (Marsh, 1880: pl. XXIII, figs. 5, 6) but is presently less complete than its illustration. It is figured with a prominent lateral process that was discovered to be missing when the coracoid was removed from the *Ichthyornis dispar* panel mount. None of the 23 YPM coracoids has a complete lateral margin. However, most of this region is preserved in a newly identified specimen, YPM 56577, which was in a drawer of uncataloged YPM material from the Smoky Hill Chalk (see also Historical Background). Further, in SMM 2503, a specimen discussed above with reference to the *Ichthyornis furcula* and referred on the basis of apomorphy (see Taxonomic Revision), a large lateral process is developed which corresponds well to its illustration in *Odontornithes* (Marsh, 1880: pl. XXIII, figs. 5, 6).

In the holotype of *Ichthyornis dispar* (YPM 1450), the ventral surface of the coracoid has a broad shallow depression close to its sternal articulation. An intermuscular line runs along the lateral edge of this de-

pression from close to the sternal edge of the ventral surface toward the omal end of the coracoid (fig. 47A). The muscular impression (fig. 47A), represented by the depression possibly is that of a belly of the m. supracoracoideus (Chamberlain, 1943; Hudson et al., 1972). This impression is particularly well developed in *Burhinus capensis*. An intermuscular line is visible in many Aves (e.g., *Gallus gallus*, *Crax pauxi*, *Chauna torquata*, *Vanellus melanopterus*). In some taxa, the intermuscular line (linea intermuscularis ventralis; Baumel and Witmer, 1993) appears more intimately related to the common edge of the laterally adjacent attachment of the m. coracobrachialis posterior as well as the m. supracoracoideus in Aves (Baumel and Witmer, 1993). This line is not pronounced in the tinamous surveyed or in *Anas platyrhynchos*. The contour of the facet for articulation with the sternum on the ventral surface is vaguely sigmoidal, rising from the medial edge of the coracoid, then sloping toward the sternal edge of the coracoid at the base of the muscular depression just noted (fig. 47A). Just lateral to the depression it again turns slightly proximally.

The dorsal and ventral sternal facets are continuous in the holotype of *Ichthyornis dispar* and the referred YPM coracoids where this section of the coracoid is preserved. In these coracoids, the facet on the dorsal surface is higher medially with a projected ridge marking its anterior apex. This crista (or edge of the facet) would have articulated with the dorsal edge of the coracoidal sulcus of the sternum. The edge of the dorsal articular surface is also slightly more omal than the comparable apex of the ventral surface. An intermuscular line is visibly developed on the lateral margin of the dorsal surface of the coracoid. It is interpreted as topologically equivalent with the edge of the surface of origin of the m. sternocoracoideus in Aves (fig. 47A; Chamberlain, 1943; impressio m. sternocoracoidei; Baumel and Witmer, 1993). In the middle of a slightly depressed region interpreted as the m. sternocoracoideus impression in the holotype of *Ichthyornis dispar* (YPM 1450), a small foramen opens anteroventrally into the bone (fig. 47A). This feature was also observed in all other referred YPM specimens that pre-

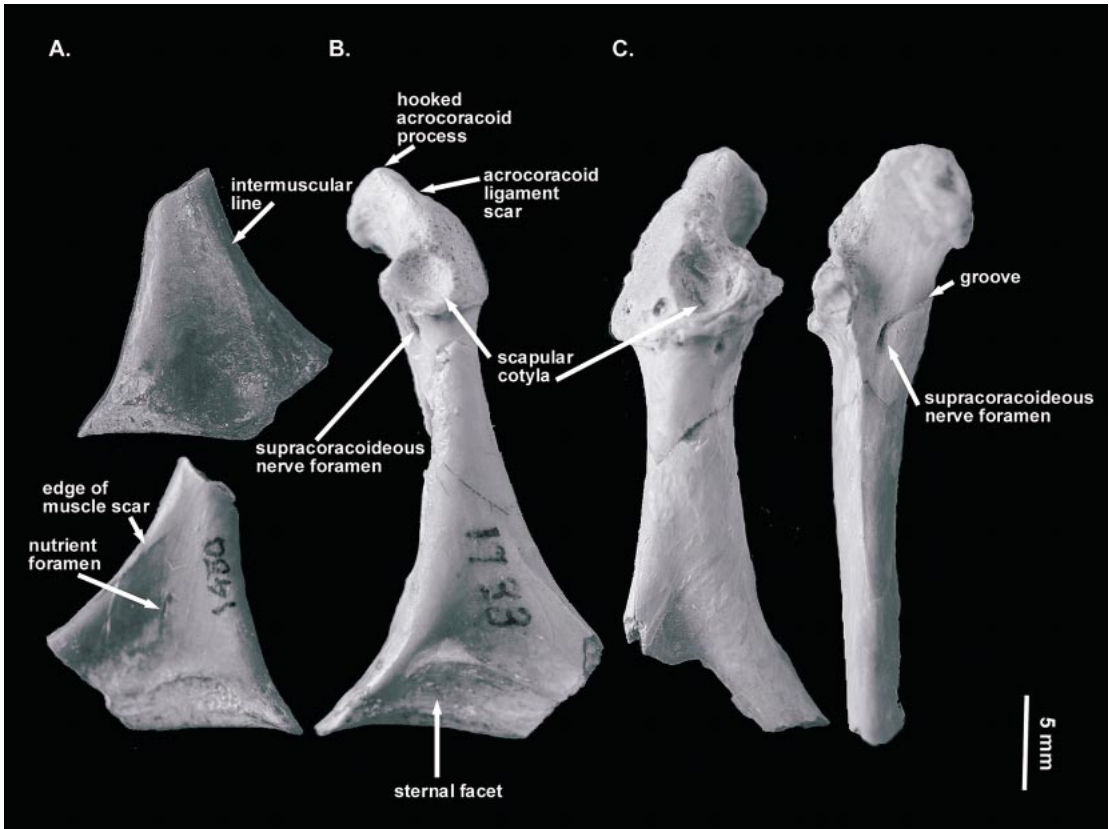


Fig. 47. The coracoid of *Ichthyornis dispar*: (A) distal left coracoid of the *Ichthyornis dispar* holotype (YPM 1450) in (top) ventral and (bottom) dorsal views; (B) right coracoid, YPM 1733, in dorsal view; and (C) proximal left coracoid, YPM 1446, referred to "*Ichthyornis validus*" in Marsh (1880) in (left) dorsal and (right) medial views.

serve this portion of the coracoid (e.g., YPM 1733, YPM 1765) with the exception of YPM 1745 (see table 4).

As Marsh (1880) noted, the scapular cotyla in *Ichthyornis* is subcircular and extremely deep (fig. 47B,C). These features are also present in *Lithornis* (Houde, 1988). The scapular cotylae of *Hesperornithes* (Marsh, 1880; Martin and Tate, 1976) and *Apsaravis ukhaana* (Norell and Clarke, 2001) are also subcircular, but are comparatively shallow concavities. The n. supracoracoideus foramen in *Ichthyornis dispar* (e.g., YPM 1452, YPM 1718, YPM 1733) is large and enters just distal and medial to the scapular cotyla (fig. 47B,C). This posterodorsal opening of the n. supracoracoideus foramen has the appearance of lying at the end a short groove

extending from close to the edge of the scapula cotyla to the foramen (fig. 47B).

The n. supracoracoideus foramen exits through the medial surface of the triossial canal (e.g., YPM 1452, YPM 1718, YPM 1733; fig. 47B,C). The sternal edge of the glenoid facet lies at the same level as the scapular cotyla (Marsh, 1880). The acrocoracoid ligament scar is prominent and elongate. The acrocoracoid process curves medially with the anteromedial extremity of the furcular articular surface (facies articularis clavicularis; Baumel and Witmer, 1993) slightly hooked in posterior view (fig. 47B). The brachial tubercle is bulbous, with a prominent anteroposteriorly elongate, muscular impression on its anterolateral surface. All that can be discerned about the procora-

coid process from YPM 1452 is that one was present. In YPM 1461, YPM 1743, and YPM 1773, the procoracoid process is preserved. It is an elongate, narrow flange with a pointed tip and a flat omal surface. This surface does not appear to have contacted much, if any, of the acromion process of the scapula in *Ichthyornis*; the extent of the acromion is minute in comparison with that of the process (see Scapula).

If the four nearly complete coracoids of similar size are compared (see list above) as well as YPM 1458 (+ part YPM 1459), which is also nearly complete, total length appears more variable than the dimensions of the proximal articular surfaces. All of these coracoids are from larger individuals than the *Ichthyornis dispar* holotype. There also appears to be some difference in the development of the ridge at the edge of the dorsal sternal facet. This ridge appears to be located more anteriorly and to be more curved on the right than on the left side.

Several specimens varying slightly in the morphology of the coracoid from the description just given are also listed in table 4 with their differences. Three of these, YPM 1446, YPM 1765, and YPM 1766, are described in more detail below. YPM 1446 is the proximal half of a large coracoid (fig. 47C). The scapular cotyla is just slightly larger than other large YPM specimens (the majority of the YPM specimens, e.g., YPM 1452), and the body of the coracoid appears more robust. It may represent a more mature individual. The dorsal entrance of the n. supracoracoideus does not appear to lie in the short groove visible in other specimens (compare fig. 47B,C). However, a groove unique to this specimen among the YPM material extends from the medial exit of the n. supracoracoideus in the triossial canal (fig. 47C). There is also possibly osteoarthritic (?) sculptured bone around the glenoid facet and scapular cotyla (fig. 47C).

YPM 1765 is a significantly smaller coracoid than the holotype of *Ichthyornis dispar*. It is nearly complete but lacks part of the lateral margin. The medial margin of the dorsal surface has a slightly more projected mark (interpreted as corresponding to an attachment of the sternocoracoclavicular membrane in Aves; Baumel and Raikow, 1993)

than that developed in the *Ichthyornis dispar* holotype. The coracoid is otherwise morphologically congruent with the holotype of *Ichthyornis dispar* and other referred specimens in the details of the following anatomical features: (1) the exits of the n. supracoracoideus foramen, (2) the facet for articulation with the sternum, and (3) the nutrient foramen in the area of the m. sternocoracoideus impression.

The corpus of the coracoid of YPM 1766 is deformed, being strongly compressed dorsoventrally. However, it appears approximately the same size as the holotype of *Ichthyornis dispar* (YPM 1450). The facet for articulation with the sternum in YPM 1766 is positioned somewhat more omal on the ventral surface and is slightly more curved than in the left coracoid *Ichthyornis dispar* holotype. However, these features of the facet are like those developed on other referred *right* coracoids. As discussed above, the facet is slightly differently developed on the right and left coracoids related to the asymmetry of the crossed coracoidal sulci on the sternum. The structure of the nearly complete procoracoid process and the scapula cotyla and the position of the glenoid fossa in YPM 1766 are the same as those in the other coracoids (e.g., YPM 1452).

SCAPULA

Portions of the scapula of *Ichthyornis* are represented in 11 YPM specimens (i.e., 1452, 1458, YPM 1718, 1727, 1733, 1741, 1753, 1763, 1772, 1773, 56577). The scapula of YPM 1734 (holotype of *Iaceornis marshi*, new taxon, previously referred to *Apatornis celer*) was used in the *Ichthyornis victor* panel mount.

The scapula of YPM 1718 is probably that illustrated in *Odontornithes* as *Ichthyornis victor* (Marsh, 1880: pl. XXIX, figs. 9–12). Two breaks on the proximal end of the figured scapula correspond well to those in YPM 1718. The scapula of YPM 1718 may have been partially reconstructed, as it is missing the distinct pointed tip of the acromion illustrated. This pointed tip is also missing in YPM 1772, but preserved in YPM 1452 (fig. 11B). Although Marsh (1880) appears to have figured the scapula of YPM

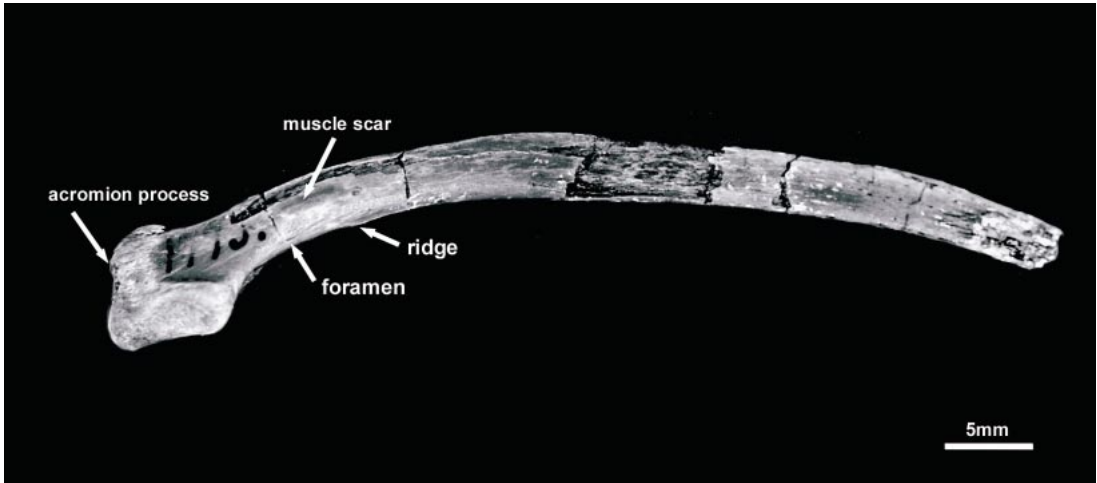


Fig. 48. The left scapula of *Ichthyornis dispar* (YPM 1773) in dorsolateral view.

1718 as *Ichthyornis victor*, he referred the specimen to *Ichthyornis dispar* (Marsh, 1880:143). The coracoid from YPM 1718 can be directly compared to the holotype of *Ichthyornis dispar* and is from a larger individual. Indeed, all known scapulae are larger than the holotype of *Ichthyornis dispar* and close in size to the *Ichthyornis victor* holotype. The poorly preserved portion of a scapula in YPM 1772 appears to be from the largest individual represented.

In *Ichthyornis dispar* (e.g., YPM 1452, YPM 1763), the acromion does not extend beyond the boss (tuberculum coracoideum; Baumel and Witmer, 1993) that is the articular surface for the coracoid (facies articularis coracoidea; Baumel and Witmer, 1993; figs. 48, 11B). The presence of an extremely short and pointed acromion process is optimized as autapomorphy of *Ichthyornis dispar* (see Diagnosis).

As Marsh (1880) noted and figured, the projected coracoid tubercle (tuberculum coracoidea; Baumel and Witmer, 1993) is large, hemispherical, and largely confluent with the glenoid facet (fig. 48). The glenoid facet is ovoid, set at an angle to the long axis of the proximal end, and is flat to slightly concave (fig. 48). No pneumatic foramina are developed (e.g., YPM 1452, YPM 1772, YPM 1773).

Only one YPM specimen preserves most of the scapular blade, YPM 1773 (fig. 48),

and it was discovered in the collection in four pieces. YPM preparator M. Fox repaired this scapula, which presently lacks a portion of its distal end and is heavily abraded (fig. 48). Marsh (1880) did not figure or discuss the anatomy of the scapular blade in *Ichthyornis*.

The *Ichthyornis* scapula (YPM 1773) has an elongate, recurved, and relatively broad blade (fig. 48), approximately the same width throughout its length. The distribution in Avialae of the presence of a relatively elongate blade (e.g., compared to coracoid height) may suggest that this morphology is ancestral for Aves: It is present in *Apsaravis ukhaana* (Norell and Clarke, 2001), in *Ambiortus dementjevi* (Kurochkin, 1985), and a taxon placed as a outgroup of crown clade galliforms (i.e., *Paraortygoides messelensis*; Mayr, 2000) as well as *Ichthyornis dispar*.

YPM 1773 also preserves muscle scars on the proximal surface of the scapula. Posterior to the glenoid facet, on the ventral edge of the scapula (e.g., by approximately 6.1 mm in YPM 1773; fig. 48), is a small foramen also observed in YPM 1718 and YPM 1741. This section of the shaft is not preserved in any other YPM specimens. Just distal to this foramen is the beginning of a narrow ridge that continues down the ventral edge of the scapular blade for at least its proximal third. On the lateral surface of the blade, dorsal to the proximal terminus of this ridge, is a

small, oblong, muscle scar (fig. 48). The ridge and muscle scar are also seen in YPM 1718 and YPM 1741.

The scar and ridge in *Ichthyornis dispar* may be topologically equivalent, with features in Aves related to the m. scapulohumeralis anterior and posterior, respectively (m. scapulohumeralis cranialis and caudalis; Vanden Berge and Zweers, 1993). Butendieck and Wissdorf (1981) describe the more dorsal scar in *Meleagris gallopavo* and refer to it as the tuberculum retinaculi. The equivalent of the ventral ridge distal to the glenoid in *Meleagris gallopavo* appears to be what these authors refer to as the tuberculum scapulae. In *Gallus gallus*, the ridge (tuberculum scapulae; Butendieck and Wissdorf, 1981) is produced as a tubercle, and the lateral muscle scar does not appear present. In *Anas platyrhynchos*, the lateral scar (tuberculum retinaculi?; Butendieck and Wissdorf, 1981) is produced as a tubercle. In tinamous (e.g., *Crypturellus noctivagus* and *Nothura darwinii*), a foramen and lateral scar are developed that appear topologically equivalent to those in *Ichthyornis dispar*. The ventral ridge in tinamous is shorter and more well projected than in *Ichthyornis dispar*.

A lateral scar is developed in *Paraortygoides messelensis* (Mayr, 2000), which has been placed as a sister taxa to Galliformes. It was considered to correspond with a "ventral tubercle" in crown clade Galliformes (Mayr, 2000). Here, this "ventral tubercle" of galliforms is considered to be the tuberculum scapulae described by Butendieck and Wissdorf (1981) for *Meleagris gallopavo*, which, as discussed above, is identified as corresponding to the relatively diminutive ventral ridge present, for example, in *Crypturellus noctivagus*, *Anas platyrhynchos*, and *Ichthyornis dispar*. By contrast, the lateral scar in *Paraortygoides messelensis* (Mayr, 2000) appears to correspond to the lateral scar in *Ichthyornis dispar* and the tuberculum retinaculi (Butendieck and Wissdorf, 1981) in some Aves.

A pneumatic foramen in the proximal end of the scapula is not developed in *Ichthyornis* or more basal avialans with this region preserved. A pneumatic foramen is developed in *Lithornis*, *Crax pauxi*, *Chauna torquata*, and *Anhima cornuta*. The distribution of this

character should be further investigated; it may be discovered to be synapomorphy of the avian crown clade relative to *Ichthyornis*.

HUMERUS

The humerus is represented in 31 YPM specimens: 29 referred to *Ichthyornis dispar* as well as the right and left humeri of the holotype specimen of *Ichthyornis dispar* (YPM 1450; figs. 49, 50). These 29 referred YPM specimens include: 1447, 1452, 1457, 1461, 1720, 1721, 1722, 1725, 1729, 1730, 1733, 1737, 1738, 1741, 1742, 1747, 1748, 1749, 1750, 1755, 1756, 1757, 1762, 1763, 1764, 1773, 1775, 9148, 9685. There is a near continuous range in the size of the individuals represented, and previous referral (Marsh, 1880) to distinct species of *Ichthyornis* appears to have been arbitrary (fig. 51). While this pattern is seen if the sizes of other elements are compared, it is most clearly observed in the humerus, as it is the most abundant element in the YPM *Ichthyornis* collection.

The left humerus from YPM 1450 is illustrated in *Odontornithes* (Marsh, 1880: pl. XXIV, figs. 1–4). A right humerus identified as *Ichthyornis victor* was illustrated only in posterior view (Marsh, 1880: pl. XXX, fig. 7). The specimen figured might be YPM 1447, which was incorporated into the *Ichthyornis victor* panel mount. YPM 1447 is the only right humerus preserving both ends mentioned as referred to *Ichthyornis victor* in *Odontornithes* (Marsh, 1880). It is also the best preserved large right humerus among the YPM material. Also figured (Marsh, 1880: pl. XXX, fig. 8) is a specimen referred to *Ichthyornis tener* (YPM 1738; see the Taxonomic Revision).

The left humerus of the holotype of *Ichthyornis dispar* (YPM 1450) is nearly complete (fig. 49). It currently lacks the proximal portion of the deltopectoral crest, but was figured as complete (Marsh, 1880: pl. XXIV, figs. 1–4). Marsh (1880) commented on only four aspects of the anatomy of the humerus: that the deltopectoral crest is large; that it projected directly dorsally rather than anteriorly as in Aves; that it, unlike *Sterna maxima*, was approximately the same length as the ulna, rather than being shorter; and that

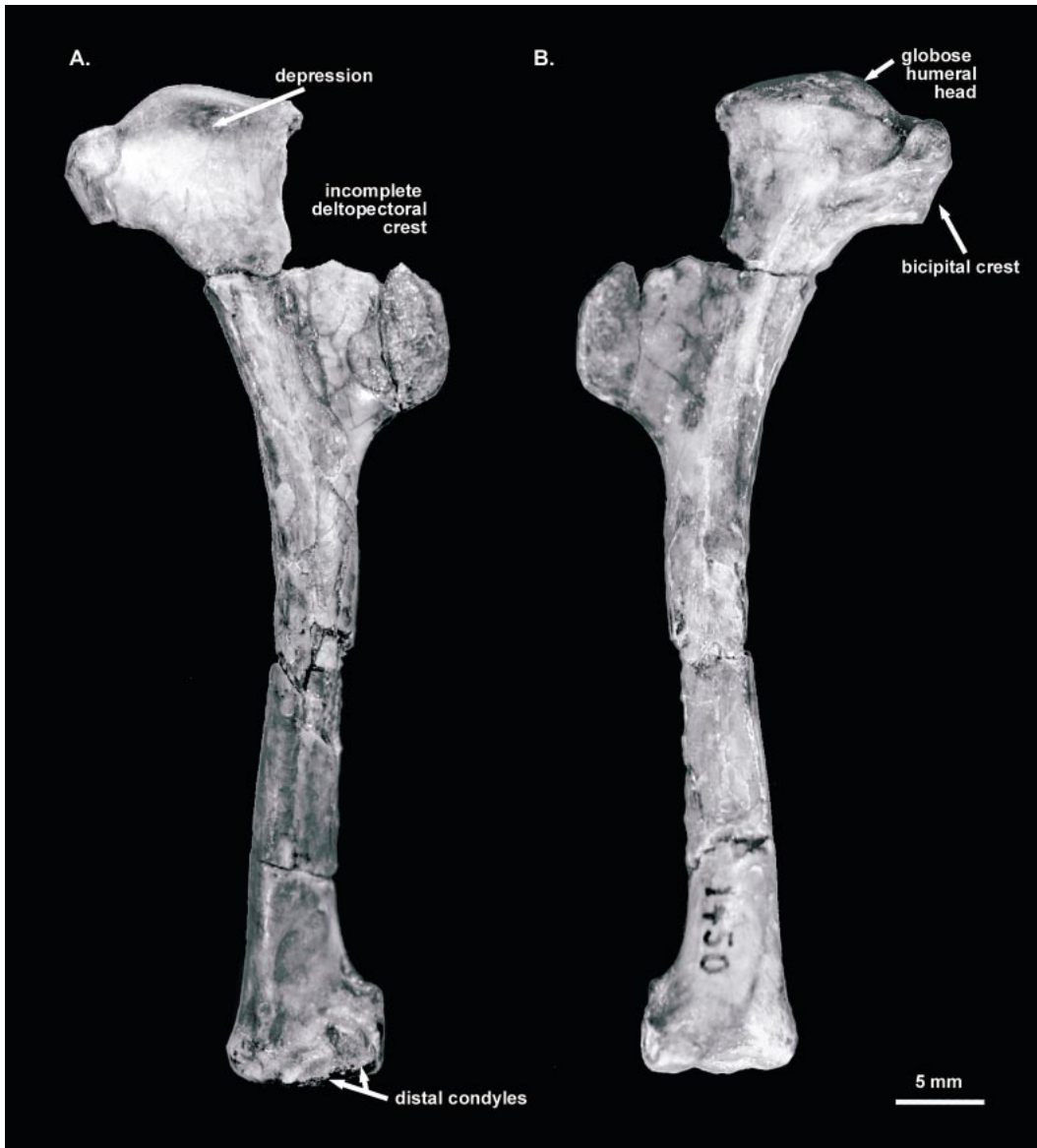


Fig. 49. The left humerus of the *Ichthyornis dispar* holotype (YPM 1450) in (A) anterior and (B) posterior views.

the humerus is apneumatic (figs. 49B, 50B). Though several humeri have additionally been referred to *Ichthyornis* (i.e., Olson, 1975; Lucas and Sullivan, 1982; Fox, 1984; Parris and Echols, 1992), only Olson included detailed comments on humeral anatomy in the process of describing the holotype of *Ichthyornis antecessor* (here synonymized with *Ichthyornis dispar*). Clarke and Chiappe

(2001) also provided discussion of the anatomy of the *Ichthyornis dispar* humerus and other forelimb elements in a comparative context.

The following aspects of the distal humerus noted by Olson (1975) are consistently present where preserved in the YPM humeri (figs. 39C, 40C): a prominent ectepicondylar process (i.e., dorsal supracondylar process)

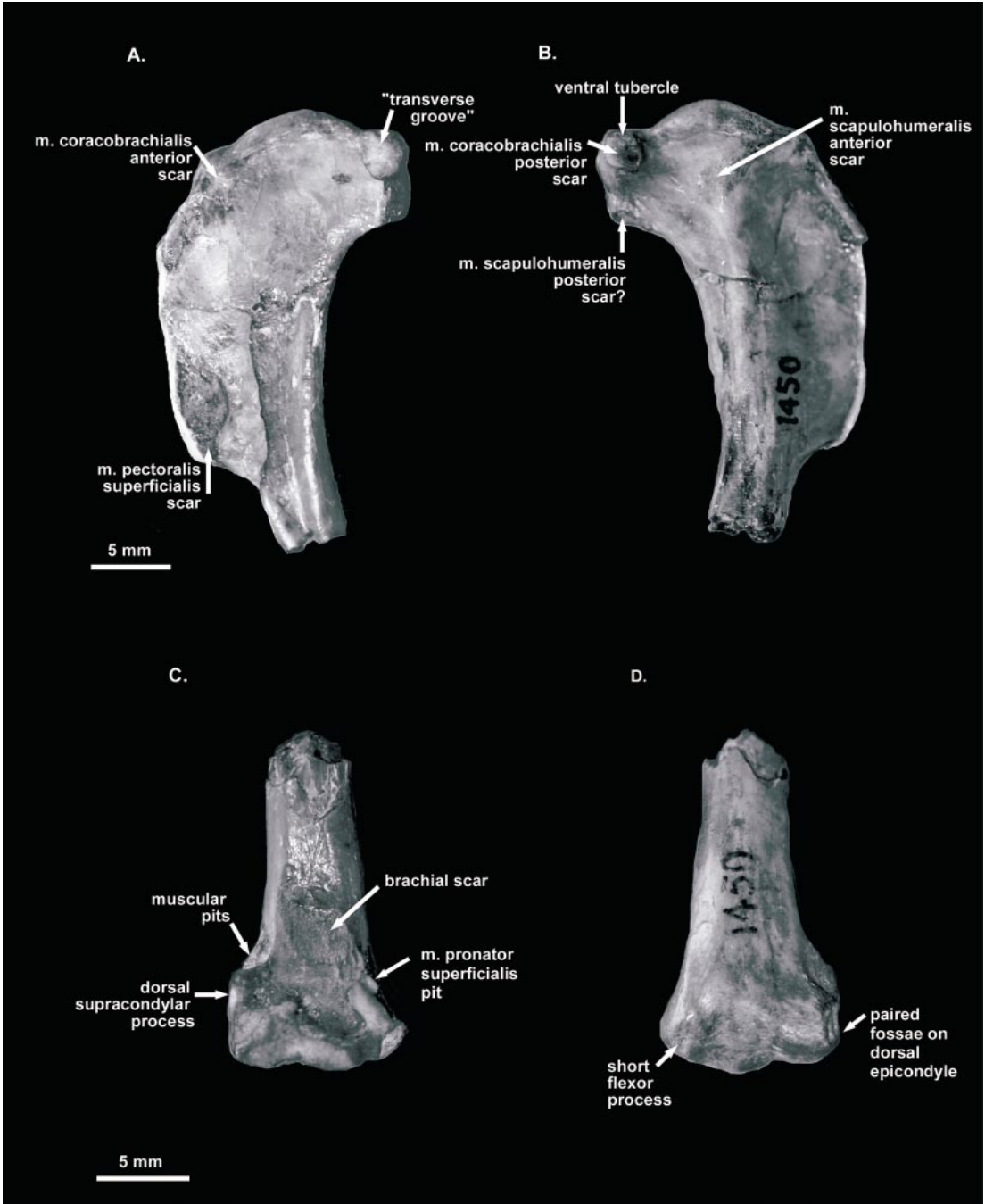


Fig. 50. The right humerus of the *Ichthyornis dispar* holotype (YPM 1450): proximal end in (A) anterior and (B) posterior views and distal end in (C) anterior and (D) posterior views.

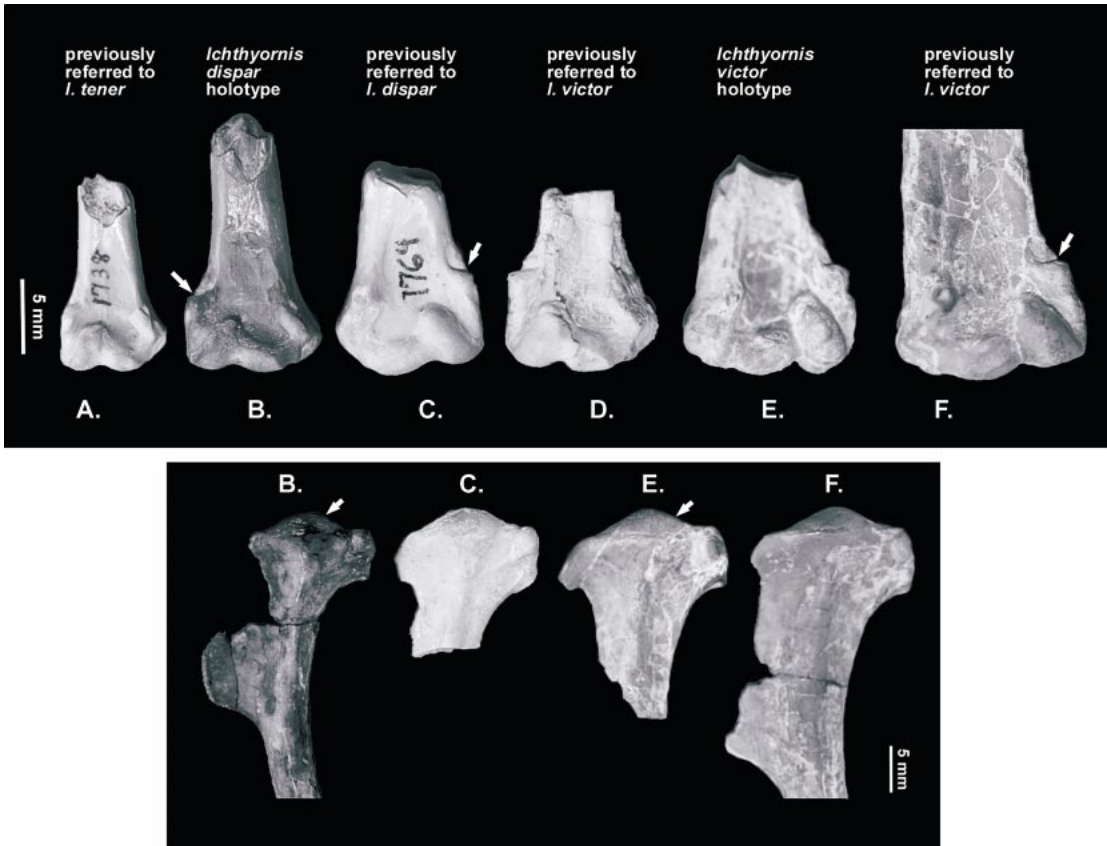


Fig. 51. Comparison of size and morphology of *Ichthyornis dispar* humeri: (top: distal humeri in anterior view; bottom: proximal humeri in posterior view): (A) YPM 1738, (B) YPM 1450, (C) YPM 1764, (D) YPM 1733, (E) YPM 1452, (F) YPM 1742. These specimens were previously identified as parts of three distinct species (see table 1) but are here referred to *Ichthyornis dispar*. The range in the height of the dorsal supracondylar process (top) and the size of the humeral head (bottom) appears to be continuous (see arrows).

situated relatively high on the shaft with a distinct pit on its proximal surface; a well-developed entepicondylar process (tuberculum supracondylare ventrale; Baumel and Witmer, 1993); brachial depression shallow; shaft not markedly curved; olecranon fossa ill defined; and the tricipital grooves on the posterodistal end indistinct. These morphologies are described for the YPM specimens in more detail below; however, none are found to diagnose *Ichthyornis* or *Ichthyornis dispar*.

As seen in the holotype of *Ichthyornis dispar* (YPM 1450), the deltopectoral crest is extremely thin and nearly translucent near its proximal midpoint. Its posterior surface is subtly concave with a slight rim along its

dorsal and distal edges (fig. 49B). An ovoid muscle scar lies near the distal edge of the anterior surface of the process that, although not marked in the holotype, is well developed in larger specimens referred by Marsh to *Ichthyornis victor* (e.g., YPM 1461, YPM 1720, YPM 1742). It (fig. 50A) possibly corresponds to the insertion of the m. pectoralis superficialis developed in Aves (Ashley, 1941; Fisher, 1946). It may only be developed at the distal end of the crest, as it becomes indistinct proximally. This scar is much less conspicuous in the smaller humeri (e.g., YPM 1756, YPM 1450). At about the midpoint of the anterior surface of the proximal end (facies bicipitalis; Baumel and Wit-

mer, 1993), a difference in texture appears to indicate another muscular scar.

There is a marked subtriangular depression on the anteroproximal surface of the bicipital crest that corresponds to the development of the transverse groove (sulcus lig. transversus; Baumel and Witmer, 1993) as a depression (a condition commented on in Clarke and Chiappe, 2001). As such, it would represent the attachment of the lig. acrocoracohumeral (Baumel and Witmer, 1993; fig. 50B). The anterior surface just distal to the humeral head is broadly depressed (fig. 50A). This surface in *Enantiornithes* (Chiappe, 1996) has a differently developed, discrete depression at approximately the midpoint of the humeral head. The bicipital crest is extremely short proximodistally, and its ventral edge is slightly projected anteriorly.

The distal end of the humeral bicipital crest bears a conspicuous oval pit that opens nearly directly distally (fig. 50B). This fossa is considered the topological equivalent of the insertion of the m. scapulohumeralis posterior in Aves (see appendix 1, character 115). The generally ovoid scar associated with the muscular attachment of the m. scapulohumeralis posterior in Aves is located on the distal end of the bicipital crest (Ashley, 1941; Ballmann, 1976; Vanden Berge and Zweers, 1993). However, whereas in Aves it is developed as a flat scar on the posterodistal surface of the crest, in *Ichthyornis* it is a pit-shaped fossa opening directly distally and located on the distal tip of the crest. The position of the fossa in *Ichthyornis* is currently an autapomorphy of that taxon with a pit-shaped fossa on the anterodistal surface of the crest developed in more basal avialans (see Diagnosis, character 5; appendix 1, character 116). It is possible, with the discovery of additional taxa close to but outside of Aves, that this morphology will be discovered to be plesiomorphic for a more inclusive clade.

There are two other discrete muscle insertions visible, but these are developed on the flat, ventral surface of the bicipital crest (Marsh, 1880: pl. XXIV, fig. 4). One of these is developed as a pit and lies at about the midpoint of that surface. This pit may represent the insertion of the m. biceps brachii (Shufeldt, 1890). The other is more proximal

and with less pronounced edges. As a suite of muscles inserted in this region, the identity of those muscles responsible for these scars is unclear. They may be related to the insertions of the m. subcoracoideus and the m. subscapularis (after Ashley, 1941). These insertions appear better developed in the holotype of *Ichthyornis dispar* than in any other YPM specimen surveyed (e.g., YPM 1447). On the proximodorsal edge of the anterior surface, a small flat scar is developed close to the dorsal terminus of the humeral head. It may be related to either the insertion of the m. supracoracoideus or, more likely, the insertion of m. coracobrachialis anterior (after Dilkes, 2000; fig. 50A). This scar is not visible in YPM 1764, a humerus slightly larger than the holotype of *Ichthyornis dispar* (YPM 1450), visible but not conspicuous in YPM 1450 and YPM 1749, and conspicuous in YPM 1742, a humerus larger than YPM 1450.

The humeral head is broadly convex, although neither as strongly arched nor globose as in most Aves (fig. 49B). It is axially narrow, anteroposteriorly and slightly more projected posteriorly than anteriorly. The proximodorsal tip of the ventral tubercle (tuberculum ventrale; Baumel and Witmer, 1993) bears a pitlike fossa for muscular insertion that may be related to m. coracobrachialis posterior (m. coracobrachialis caudalis; Vanden Berge and Zweers, 1993), which inserts on the ventral tubercle dorsal to the common insertions of m. subcoracoscapulares in Aves (Vanden Berge and Zweers, 1993; fig. 50B). A faint muscle insertion is also visible just distal to approximately the midpoint of the humeral head (fig. 50A). It may represent one insertion of a part of m. scapulohumeralis (m. scapulohumeralis cranialis; Dilkes, 2000). In a shallow depression between the tip of the ventral tubercle and the distal pit on the diminutive bicipital crest is an elongate muscle scar. It appears to extend down the corpus of the humerus for a short distance distal to the bicipital crest. It is conspicuous in YPM 1764 as well as in the *Ichthyornis dispar* holotype (YPM 1450). This depression ventrodorsal to the ventral tubercle is interpreted as a muscle origin, probably of m. humerotriceps (Baumel and Wit-

mer, 1993). There is no pneumatic fossa or foramina developed.

The anterior surface of the distal humerus bears two well-developed condyles and a well-projected dorsal supracondylar process compared to more basal avialans (fig. 50C). The ventral supracondylar tubercle is also projected, with an anterior pitlike fossa for m. pronator superficialis (Vanden Berge and Zweers, 1993) attachment (m. pronator brevis attachment; Howard, 1929). The brachial impression is developed as a medial, flat, textured band angling ventrodistally from proximal to the dorsal supracondylar process toward the proximal edge of what in Aves corresponds to the attachment of the lig. colaterale ventrale (Baumel and Witmer, 1993; fig. 49A). The shallow brachial scar and its position in the middle of the distal humerus is similar to that in the surveyed Tinamidae (see Comparative Materials and Methods), *Lithornis* (Houde, 1988), and the “graculavid” humeri from the Late Cretaceous Hornerstown Formation of New Jersey (Olson and Parris, 1987).

The proximal surface of the dorsal supracondylar process is the site of a conspicuous complex of at least three distinct muscle insertions that were discussed by Clarke and Chiappe (2001; fig. 50C). Loss of this complex morphology, less developed in *Limenavis patagonica* and *Lithornis*, appeared to be a synapomorphy of the crown clade (Clarke and Chiappe, 2001). Interestingly, the “graculavid” humeri from the Hornerstown Formation, including *Anatalavis rex*, a basal anseriform relative from the London clay (Olson, 1999), have a flat insertion and a dorsal one that is pit-shaped. These appear to be related to the origin of either one or two heads of m. extensor carpi radialis (Vanden Berge and Zweers, 1993) and possibly to the insertion of m. deltoideus major (Dilkes, 2000; m. deltoideus, pars propatagialis; Vanden Berge and Zweers, 1993) in Aves. Brodkorb (1963) identified a similar configuration of pits as related to m. tensor patagii brevis and m. extensor carpi radialis in *Torotix clemensi*.

The dorsal and ventral condyles are well developed and the intercondylar incisure is shallow, such that these condyles appear clustered together (figs. 49A, 50C). The long

axis of the dorsal condyle is only slightly longer than that of the ventral, and the dorsal condyle projects at a low angle to the axis of the humeral shaft. Clarke and Chiappe (2001) discussed the distribution of the former character and Chiappe (1996) and Clarke and Chiappe (2001) discussed the latter. *Confuciusornis sanctus*, *Ichthyornis dispar* (all specimens in which this morphology is preserved), and the surveyed Tinamidae, Galliformes, and Anseriforms all have such a proximally directed dorsal condyle. In Enantiornithes, the dorsal condyle projects at a high angle to the axis of the humeral shaft (Chiappe, 1996). In *Apsaravis ukhaana*, it also projects at a relatively high angle to the humeral shaft (Norell and Clarke, 2001).

The distal edge of the humerus in the holotype of *Ichthyornis dispar* is nearly straight, approximating a right angle to the axis of the humeral shaft (fig. 49). The flexor process is short (but slightly more projected than in the holotype of *Ichthyornis dispar*, YPM 1450, than in the other YPM humeri, e.g., YPM 1764; compare B and C in fig. 51). In *Apsaravis ukhaana* and Enantiornithes (Norell and Clarke, 2001), the whole distal margin of the humerus angles ventrally. In *Confuciusornis sanctus* (Chiappe et al., 1999) like *Ichthyornis dispar*, the flexor process is short and the distal margin of the humerus does not angle ventrally. The olecranon fossa is very weakly developed in all *Ichthyornis* humeri (fig. 50D).

Olson (1975) reported a nutrient foramen just proximal to the dorsal condyle in *Ichthyornis dispar* and *Ichthyornis antecessor*. It is also present in other YPM humeri (e.g., YPM 1764, YPM 1748) but may not be present in all (e.g., YPM 9685), and can vary slightly in position and size. Indeed, in the holotype of *Ichthyornis dispar*, the foramen is conspicuous on the right but not on the left humerus. Two depressions are variably distinguishable in the pit on the distal ventral epicondyle (fig. 50C, D), with an additional one on its proximoanterior edge between the ventral epicondyle and the pit-shaped attachment of m. pronator superficialis (m. pronator brevis; Howard, 1929) on the ventral supracondylar tubercle (fig. 50C). There is also an additional, slightly depressed muscular scar on the anterior surface of the dorsal mar-

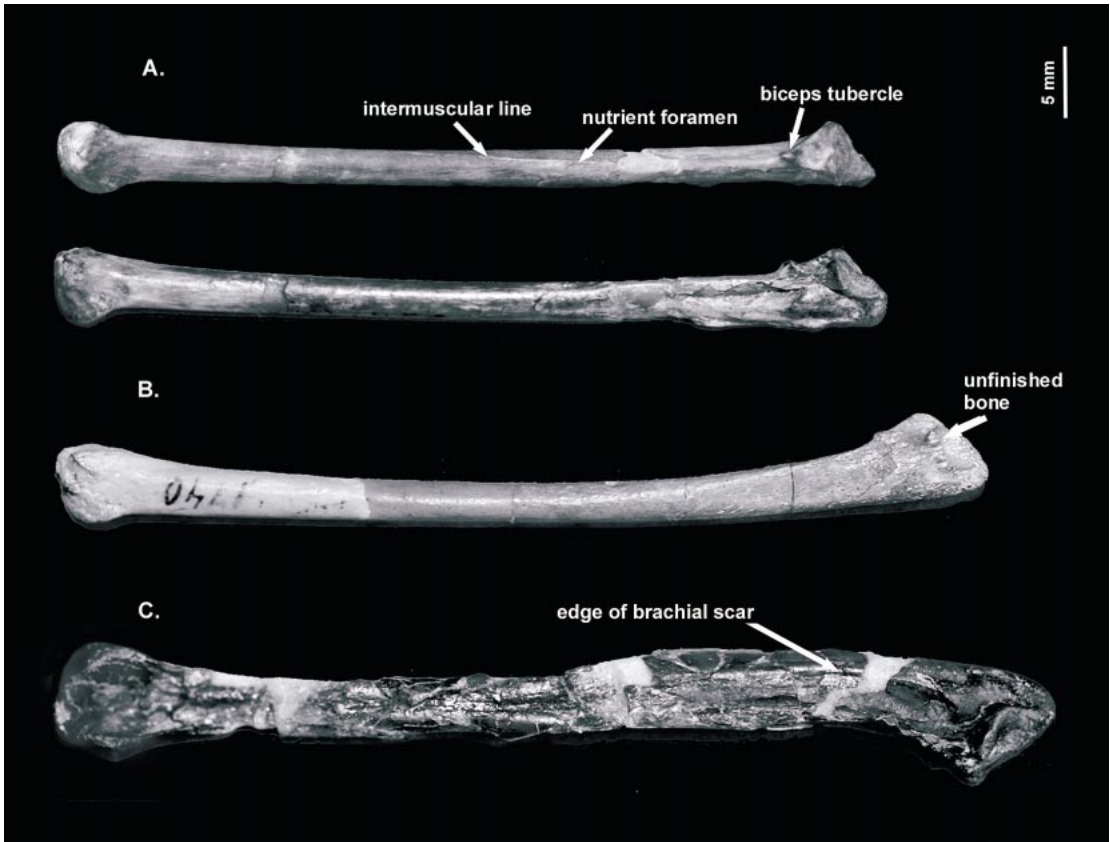


Fig. 52. The ulna of *Ichthyornis dispar*: (A) the right ulna of the *Ichthyornis dispar* holotype (YPM 1450), (B) the right ulna of the *Ichthyornis validus* holotype (YPM 1740), and (C) the left ulna of YPM 1453 (which was incorporated into the “*Ichthyornis victor*” panel mount) in ventral view.

gin just distal to the dorsal supracondylar tubercle. These scars are present in all YPM humeri in which this region is preserved.

The m. scapulotriceps groove is very weakly developed in the holotype of *Ichthyornis dispar*. It is inconspicuous in *Ichthyornis* specimens generally (Olson, 1975; Clarke and Chiappe, 2001); however, its development appears to vary slightly with size. The development of this impression is slightly more conspicuous in larger humeri, those approximating the size of the *Ichthyornis victor* holotype (e.g., YPM 9685). In addition, the passage of m. scapulohumeralis (Baumel and Witmer, 1993) is indicated only by a shallow depression, but one that is slightly more produced than that of m. scapulotriceps.

ULNA

The ulna is represented in 14 YPM specimens (i.e., left: 1453, 1454, 1460, 1757, 1764; right: 1457, 1462, 1731, 1740, 1744, 1755, 1758, 1775; and left and right of the *Ichthyornis dispar* holotype, 1450). The ulna included in the *Ichthyornis victor* panel mount was YPM 1453 (fig. 52C), based on Gibb's notes (fig. 3). The left ulna of the *Ichthyornis dispar* holotype is figured in *Odonotornithes*, but is described as the right ulna in the figure caption (Marsh, 1880: pl. XXIV, figs. 5–8). The right ulna from YPM 1450 (fig. 52A) is nearly complete. It was repaired, however, and its current length is probably just slightly longer than its original length due to the inserted glue. The left ulna is missing a section of the shaft. The nearly

complete right ulna figured in *Odontornithes* (Marsh, 1880: pl. XXX, figs. 11–14) is YPM 1740, and was named as the holotype of *Ichthyornis validus* (fig. 52B). One key aspect of its morphology is not figured: The bone surfaces at the ends of the element appear to have been porous and unfinished as opposed to the surface of the middle of the shaft (figs. 52B, 12), suggesting YPM 1740 could be part of a juvenile individual (see Taxonomic Revision).

Marsh (1880) describes the following features of the *Ichthyornis* ulna: a “strong, moderately curved bone” (p. 152); the articular surface for the humerus is larger and “obliquely placed” (p. 152) relative to the axis of the shaft; “approximately a dozen” faint quill impressions are developed (p. 153). The ulna is only slightly bowed and just slightly longer than the humerus.

Perhaps the most conspicuous feature of the *Ichthyornis dispar* (YPM 1450) ulna is its enormous bicipital tubercle (tuberculum bicipitale ulnaris; Baumel and Witmer, 1993; fig. 52A), which can be seen in the illustrations in *Odontornithes* (Marsh, 1880: pls. XXIV, XXX). A large bicipital tubercle is present in *Confuciusornis sanctus* (e.g., JM-Ukr-1997/1 in fig. 35, Chiappe et al., 1999), *Patagopteryx deferrariisi* (Chiappe, 1996), and *Apsaravis ukhaana* (Norell and Clarke, 2001). Loss of a conspicuous tubercle, which in Aves marks the insertion of the m. biceps brachii (tuberculum bicipitale ulnae; Baumel and Witmer, 1993), appears to be a synapomorphy of Aves relative to *Ichthyornis*. A well-projected tubercle is not present in the galloanserines and tinamous surveyed. In *Apsaravis ukhaana* (Norell and Clarke, 2001), the bicipital tubercle is located well distal to the radial depression, whereas in *Ichthyornis*, it lies on its edge. Because no discrete radial depression is visible in *Confuciusornis sanctus*, the polarity of this character is accordingly ambiguous.

The radial depression in the holotype of *Ichthyornis dispar* is a discrete triangular depression with a distinct edge (fig. 52A). This condition does not appear present in more basal avialans (e.g., *Confuciusornis sanctus*, *Enantiornis leali*, *Baptornis advenus*), but appears present in *Apsaravis ukhaana* (Norell and Clarke, 2001), galloanserines, and

tinamous. It has been described in *Patagopteryx deferrariisi* (Chiappe, 1996), but it appears more weakly developed in that taxon than in *Ichthyornis dispar*. Several muscle scars on the proximal ulna can be distinguished in positions corresponding to the attachments of the lig. collaterale ventrale, m. sacapulotriceps and m. brachialis in Aves (see Clarke and Chiappe, 2001, for more details concerning variation across Avialae in the attachments of the lig. collaterale ventrale and m. brachialis).

The olecranon process is of moderate size (fig. 52) and appears to have a scar on the ventral surface of its tip, which may correspond to the attachment of the m. humerotriceps in Aves (Baumel and Witmer, 1993). The dorsal and ventral cotylae are well developed and approximately the same size. The dorsal cotyla is very weakly convex, while the ventral is subtly concave. No distinct rim (crista intercotylaris; Baumel and Witmer, 1993) bordering the dorsal cotyla separates the cotylae (Clarke and Chiappe, 2001).

A raised intermuscular line extends distal to the bicipital tubercle for roughly the proximal third of the bone, at which point, although it continues, the ridge becomes noticeably less pronounced (fig. 52A). A nutrient foramen, present in Aves, perforates the shaft in line with the intermuscular line (fig. 52A). It is developed where this ridge becomes less conspicuous toward the proximal end of the ulna. No such nutrient foramen has been described for more basal avialans except that it is noted to be absent in *Baptornis advenus* (Martin and Tate, 1976). It is possible (but difficult to test given the preservation of most Mesozoic avialans) that the presence of this foramen is synapomorphic of *Ichthyornis* + Aves.

Eleven scars are visible on the right ulna of the *Ichthyornis dispar* holotype (YPM 1450), indicating the insertion of the follicular ligaments of the secondary flight feathers in Aves (Baumel and Witmer, 1993). Scars are additionally seen on the left ulna of YPM 1450, as well as in YPM 1454, YPM 1462, YPM 1731, and YPM 1740. The scars in YPM 1740 appear more weakly developed than in the holotype of *Ichthyornis dispar*, further evidence consistent with its

proposed younger, possibly subadult status (see Taxonomic Revision).

Several of these scars, especially the first six, appear as two coalesced scars, the more posterior being located proximal to the slightly more anterior. The five more distal scars are clearly distinct. Edington and Miller (1941) noted that two follicular ligaments are developed for each secondary feather and that a second line of “quill knobs”, or scars, was often present in the avian species they surveyed. All of the 11 lie on the dorsal surface of the ulna rather than its posteriormost edge. No scars of the follicular ligaments are known from *Confuciusornis sanctus* (Chiappe et al., 1999), *Patagopteryx deferrariisi* (Chiappe, 1996), *Hesperornithes* (Marsh, 1880; Martin and Tate, 1976), or *Apsaravis ukhaana* (Norell and Clarke, 2001). They have, however, been described for an avian enantiornithine (Hutchinson, 1993) and for *Rahonavis ostromi* (Forster et al., 1998). In *Sterna maxima*, these points of attachment are represented by approximately 17 distinct paired knobs, with one series on the posterior edge of the dorsal surface and a second series on the posteroventral surface. However, in tinamous (e.g., *Nothura darwini* and *Eudromia elegans*), the attachments are hardly more than raised scars and are not as conspicuously paired.

The distal ulna has a strongly curved (semilunate) dorsal condyle. The width of the trochlear surface of the dorsal condyle and its distal extent down the posterior edge of the shaft are approximately subequal (Clarke and Chiappe, 2001). The tendinal pit and a ridge demarcating the tendinal groove (Howard, 1929; incisura tendinosa; Baumel and Witmer, 1993) are visible near the anterior edge of the dorsal condyle. These two associated features are related to the passage of the m. extensor metacarpi ulnaris and m. extensor digitorum communis and the fibrous retinaculum through which they pass in Aves. The pit and groove are not known in *Archaeopteryx lithographica* or *Confuciusornis sanctus* but are known from several of the El Brete Enantiornithes, *Limenavis patagonica*, and all crown-clade avian taxa surveyed (Clarke and Chiappe, 2001). The condition in *Apsaravis ukhaana* (Norell and Clarke, 2001) is not discernable. A trans-

verse ligamental impression (Clarke and Chiappe, 2001: character 29) on the dorsal surface of the distal ulna is not visible in *Ichthyornis*. The intercondylar incisure in *Ichthyornis* is moderately deep. There is a conspicuous scar on the posterior surface of the carpal tubercle. It is, however, separated from the ventral condyle by a slight notch (incisura tuberculi carpalii; Baumel and Witmer, 1993). Clarke and Chiappe (2001) comment in further detail on the morphology of the distal ulna of *Ichthyornis* in a comparative context.

RADIUS

The radius is represented in 9, possibly 10, YPM specimens including the holotype of *Ichthyornis dispar* (1450) and 1457, 1733, 1741, 1755, 1758, 1770, 1773, 1775, and possibly by a fragment in 1763. All other radii are significantly larger than the holotype of *Ichthyornis dispar*. All but that of YPM 1733 are the size of the majority of YPM material (from individuals approximately the size of that represented in the *Ichthyornis victor* holotype): Several specimens can be compared directly to the *Ichthyornis victor* holotype (e.g., YPM 1773 and YPM 1775) to determine this.

The one complete YPM radius (fig. 53), which was included in the *Ichthyornis victor* composite panel mount, is identified as YPM 1741 by Gibb's notes. The distal end of the right radius from the holotype of *Ichthyornis dispar* (YPM 1450) is illustrated in *Odonotornithes* (Marsh, 1880: pl. XXIV, figs. 9 and 10). Proximal and distal portions of the radius identified as belonging to *Ichthyornis victor* were also illustrated (Marsh, 1880: pl. XXX, figs. 9 and 10). The illustration of the proximal portion (Marsh, 1880) matches only one specimen in the YPM material: YPM 1733. The detail of the conspicuous notchlike break at the distal end of the fragment and the edge of a ventral muscle scar opposite it matches YPM 1733. The illustration and the specimen are both of a right radius, rather than a left radius as indicated by Marsh (1880). The distal radius illustrated (Marsh, 1880: pl. XXX) appears to be the distal left radius of YPM 1733. Marsh (1880: 152) gives measurements for the radius of

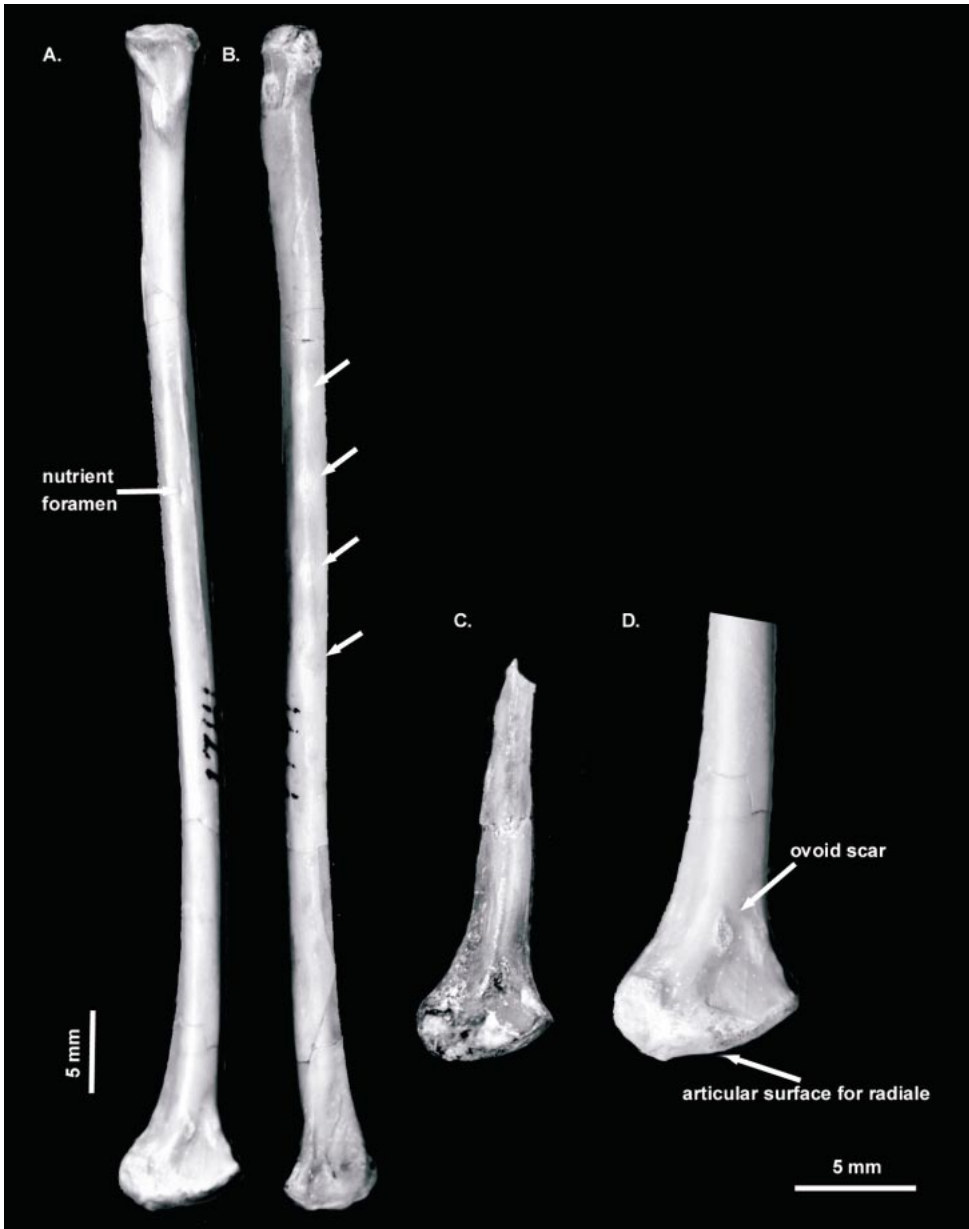


Fig. 53. The right radius of *Ichthyornis dispar*. (A, B, D) the radius incorporated into the “*Ichthyornis victor*” panel mount (YPM 1741; A, D: posteroventral view, B: posterior view); (C) the *Ichthyornis dispar* holotype (YPM 1450) in posteroventral view. In B, evenly spaced (follicular?) impressions along the posterior edge of the element are indicated with arrows.

YPM 1733 that are consistent with the illustrated specimen and consistent with YPM 1733 representing a smaller individual than *Ichthyornis victor*.

A single paragraph in *Odontornithes*

(Marsh, 1880) describes the morphology of the *Ichthyornis dispar* radius. Marsh (1880: 151) noted that it was “strong and robust” and proximally had a slightly concave, sub-elliptical humeral cotyla, a weakly developed

ulnar facet, and bore a tubercle opposite the ulnar facet close to the edge of the humeral cotyla. He also commented that the radius was nearly straight, except that a slightly protuberant oval facet just distal to the humeral cotyla gave the proximal part of the shaft the appearance of being bent (Marsh, 1880: 151). While these points were confirmed on restudy of the material, unmentioned features, including what might be peculiarities of *Ichthyornis*, were also observed.

The proximal end of the radius in YPM 1733, YPM 1741, and YPM 1773 has the notably shallow humeral cotyla and poorly demarcated ulnar facet noted by Marsh (1880). The outline of the humeral cotyla is ovoid and the robust tubercle Marsh mentioned (capital tuberosity; Howard, 1929) is visible on its dorsal edge. The tubercle may be related to features identified in Butendieck and Wissdorf (1981) and Baumel and Raikow (1993) as associated with the attachment of the meniscus radioulnaris and possibly also the dorsal collateral ligament in Aves (fig. 53A,B). Distal and slightly posterior to this tubercle two other scars are conspicuous: One is lineate (oriented proximodistally) and the second is ovoid (fig. 53A,B). The linear scar is identified as possibly corresponding with a feature in Aves related to the attachment of the lig. transversarium radioulnare (Baumel and Raikow, 1993).

The most conspicuous feature of the proximal radius is the ovoid pit-shaped fossa (fig. 53A) that Marsh (1880) described. It appears topologically equivalent to the radial insertion of the m. biceps brachii in Aves (tuberculum bicipitale radii; Baumel and Witmer, 1993) on a projected "bicipital tubercle" (Howard, 1929). The bicipital scar, however, is a pronounced pit. It is connected to the proximal tip of the radius by a narrow-angling ridge that also appears to be a point of muscle attachment (fig. 53A). The strongly developed tubercle, both on the proximal ulna (see above) and the radius in *Ichthyornis*, may be related to the paired insertions of the m. biceps brachii. These features are also conspicuously developed in other avialans (commented on for the radius only, Clarke and Chiappe, 2001) but not in Aves (appendix 1, character 133). Conspicuously

less demarcated biceps insertions may be synapomorphic of Aves relative to *Ichthyornis* and indicate a shift in some aspect of the function, or functional importance, of the m. biceps brachii.

The proximal end of the radial shaft in *Ichthyornis dispar* (e.g., YPM 1741, YPM 1733, YPM 1773) is not strongly bent or notched (fig. 53A,B) anteroproximally as it is, for example, in *Sterna maxima*. In this character, it resembles the comparatively straight, unnotched radii of more basal avialans (e.g., *Apsaravis ukhaana*, Norell and Clarke, 2001; *Confuciusornis sanctus*, Chiappe et al., 1999) and the condition in other Aves (e.g., *Eudromia elegans* and *Crax pauxi*). In *Ichthyornis* (e.g., YPM 1741), the posterior surface of the shaft has a narrow, flat face and a ventral intermuscular line extending much of its length.

Serenio et al. (2002) commented that a deep groove on the posterior surface of the radius, considered synapomorphic of Enantiornithes (e.g., Chiappe and Calvo, 1994), was developed in *Ichthyornis*. However, no such groove is present; rather, there is a flat scar that is also seen in Aves and elsewhere within Avialae (Norell and Clarke, 2001). Zusi and Bentz (1978) identify the origin of one head of the m. extensor pollicis longus as arising from the proximal and middle part of the posterior radius to insert on the extensor process of metacarpal I in the Labrador duck (*Camptorhynchus labradorius*). Ghetie et al. (1976) appears to refer to the same muscle, figuring the origin of a deep head of the m. extensor metacarpi radialis (i.e., m. extensor carpi radialis; Vanden Berge and Zweers, 1993) from the posterior proximal and middle portion of the radial shaft and inserting with the humeral or superficial head of the m. extensor metacarpi radialis in the galliform *Meleagris gallopavo*. Regardless of the identity of this muscle, a muscular origin and associated scar in Aves appears to correspond with the elongate scar in *Ichthyornis* and with the groove in Enantiornithes (e.g., Chiappe and Calvo, 1994). The identified synapomorphy of Enantiornithes may relate to the different conformation of one of the manus extensors discussed above.

A long, linear scar extending along most of the ventral surface of the radius may cor-

respond to the origin of the m. extensor indicis longus (Zusi and Bentz, 1978). A nutrient foramen considered to correspond to that present in Aves (Gilbert et al., 1981) is visible slightly more than one-third the length of radius from its proximal end (fig. 53A).

The diameter of the radius as measured close to the distal end in the holotype of *Ichthyornis dispar* is 2.1 mm as compared to the same measure of the *Ichthyornis validus* holotype ulna (3.1 mm). The same measures for *Sterna maxima* are 2.5 mm and 4.4 mm, respectively, for a ratio of 0.47. Chiappe (1996) gave this ratio across a sample of avian taxa as 0.49–0.65; however, he gave a ratio of 0.60 for *Ichthyornis victor* referring to the specimen number “YPM 1452”. As mentioned, YPM 1452, the holotype of *Ichthyornis victor*, does not include a radius or ulna. Further, despite Marsh’s (1880) obfuscating statements in the text of *Odontornithes*, the figures in *Odontornithes* (Marsh, 1880) are of elements from different specimens of different sizes. This ratio (Chiappe, 1996) is probably based on the illustrated ulna (YPM 1740) from the subadult individual represented by the holotype specimen of *Ichthyornis validus* and the illustrated radius of YPM 1733. This radius is from a specimen (that would appear to be adult) larger than the holotype of *Ichthyornis dispar* but smaller than the majority of the YPM *Ichthyornis* material.

On the dorsal surface of the radius, at approximately its midpoint, four or five evenly spaced ovoid scars similar to those related to the insertion of the follicular ligaments (papillae remigales; Baumel and Witmer, 1993) are present. It is odd that these should be on the radius; nonetheless, they closely resemble the ulnar scars in spacing and development (fig. 53B).

The illustration of the posteroventral surface of the distal radius of *Ichthyornis* in Marsh (1880: pl. XXX, fig. 10) differs from the holotype of *Ichthyornis dispar* (YPM 1450) and YPM 1758, YPM 1770, YPM 1773, and YPM 1775. An autapomorphy of *Ichthyornis* is not shown. There is a prominent ovoid scar in the center of the posterior surface of the distal radius (in the depressio ligamentosa of Aves; Baumel and Witmer,

1993) seen in YPM 1450, YPM 1758, YPM 1770, YPM 1773, and YPM 1775 (fig. 53C,D). It is not preserved in the one specimen (YPM 1733) that Marsh illustrated (Marsh, 1880: pl. XXX, fig. 10) nor was it illustrated for the holotype of *Ichthyornis dispar* (Marsh, 1880: pl. XXIV, figs. 9, 10) although it is present.

Just ventral to the prominent ovoid scar described above is a second ovoid scar that varies in development from strongly demarcated (e.g., YPM 1741) to less visible (e.g., YPM 1758 and especially YPM 1450). On the posterior surface of the distal radius in *Ichthyornis*, ventral to the articular surface for the radiale, there is a process that appears topologically equivalent to the ligamental process (tuberculum aponeurosis ventralis; Baumel and Witmer, 1993).

One shallow tendinal groove is conspicuous on the anterodorsal surface of the radius, with a second impression on the distal portion of the shaft that may indicate a second narrower impression (e.g., YPM 1741). Tendinal grooves for the extensors of the manus are also shallow, with the impression of a larger groove and a narrower dorsal groove that is poorly delineated in tinamous (e.g., *Nothura darwinii* and *Eudromia elegans*) and *Anhima cornuta*, while in *Anas platyrhynchos* the second ridge is slightly more strongly developed, and in galliforms it often appears that no such groove or one faint dorsal groove is developed. However, in *Sterna maxima*, for example, the two grooves are closer to equal in development and both are conspicuous, separated by a stout ridge.

PROXIMAL CARPALS

No free carpals have previously been described for *Ichthyornis*. Sereno and Rao (1992) commented on the morphology of the radiale and ulnare of *Ichthyornis* citing Marsh (1880); however, they must have been referring to the morphology of the proximal carpals represented in a specimen (YPM 1734) herein designated the holotype of *Iaceornis marshi* and previously referred (Marsh, 1880) to *Apatornis celer*. The proximal carpals of YPM 1734 are the only ones illustrated or discussed in Marsh (1880), and no others are known from the YPM material.

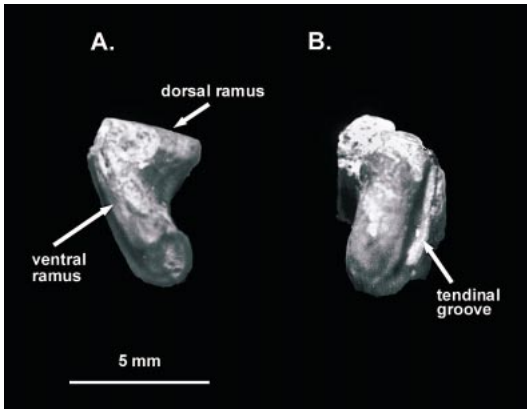


Fig. 54. The right ulnare of *Ichthyornis dispar* (SMM 2503) in (A) anterior and (B) ventral views.

YPM 1734, here named and diagnosed as *Iaceornis marshi*, appears to be more closely related to the crown clade than to *Ichthyornis dispar*. Thus, the carpals of YPM 1734 do not bear on the condition in *Ichthyornis dispar*.

However, a partial skeleton of *Ichthyornis dispar* from the Sternberg Memorial Museum (SMM 2503) includes a right ulnare (fig. 54). A small part of tip of the dorsal ramus, or short arm, is missing. The ventral ramus is a flat, elongate process with a deep tendinal groove that runs the length of its long axis at approximately the midpoint of its ventral surface (fig. 54). Such a groove is variably developed in Aves and present in at least some Enantiornithes (Clarke and Chiappe, 2001). It is also present in *Iaceornis marshi* and *Limenavis patagonica* (Clarke and Chiappe, 2001).

CARPOMETACARPUS

The carpometacarpus is represented in 12 YPM specimens (1208, 1209, 1450, 1724, 1730, 1736, 1751, 1752, 1755, 1769, 1771, 1773, and 1775). The distal left carpometacarpus of the holotype of *Ichthyornis dispar* (YPM 1450) is illustrated in *Odontornithes* (Marsh, 1880: pl. XXIV, figs. 11, 12). That figured as *Ichthyornis victor* (Marsh, 1880: pl. XXXI, figs. 12–15) and included in the *Ichthyornis victor* panel mount was determined to be YPM 1724. Faint numbers indicating “1724” are visible on the carpo-

metacarpus from the mount and an empty block of matrix otherwise comprised YPM 1724 with an element evidently excavated from it. This excavation fits the complete right carpometacarpus removed from the mount. In this case, Gibb’s notes on the contents of the mount are incorrect. They place the word “metacarpal” next the number YPM 1464. However, the word “metacarpal” is included in the list of hind limb elements of the annotated Marsh (1880: fig. 3) figure and YPM 1464 does not include a carpometacarpus. On Gibb’s annotated illustration from Marsh (1880: fig. 3) “1464” is placed on the tarsometatarsus. By contrast, the word “metatarsal” is placed next to the number YPM 1739 in his list of forelimb elements and next to the carpometacarpus of the annotated Marsh (1880) figure. However, these identifications would require YPM 1464 to have had two right tarsometatarsi. Further, it would also leave no specimen among the material to correspond to YPM 1739, the box top of which is labeled “metatarsal” and no other numbered YPM *Ichthyornis* specimen boxes lack a corresponding specimen.

Marsh’s (1880: pl. XXIV, figs. 11, 12; pl. XXXI, figs. 12–15) illustrations and description of the carpometacarpus correspond well to the actual material. However, several of the measurements (e.g., the diameter of the distal end of YPM 1208 and all measures of YPM 1730) given in the text of *Odontornithes* (Marsh, 1880) are useless, as they are of severely crushed or distorted specimens. There seems to be some variation in the length of the carpometacarpus among otherwise similarly sized individuals. Contrast the shorter carpometacarpus of YPM 1755 with the longer but otherwise similarly proportioned one of YPM 1773 (39.4 mm). These two specimens include radii that are approximately the same diameter with their nutrient foramina the same distance from the proximal end. The only specimen with a complete carpometacarpus in which it was possible to measure multiple forelimb elements was YPM 1755. In that specimen, the humerus is approximately 70.6 mm, the carpometacarpus is 36.6 mm, and the first phalanx of the second digit is 21.2 mm.

The isolated carpometacarpi (YPM 1208,

YPM 1209, YPM 1724, YPM 1736, YPM 1751, YPM 1752, YPM 1769, and YPM 1771) are referred to *Ichthyornis* based on overall similarity with the holotype of *Ichthyornis dispar* (YPM 1450), and the other specimens (e.g., YPM 1773, YPM 1775) are referred for that reason, as well as the fact that they include other elements referable to *Ichthyornis*. All of these carpometacarpi are larger than the holotype of *Ichthyornis dispar*.

The proximal and distal carpometacarpus bear many small foramina (e.g., YPM 1450, YPM 1724). As Marsh (1880) noted, the carpal trochlea (trochlea carpalis; Baumel and Witmer, 1993) is flat (fig. 55A,B); no groove is developed. No ulnocarpal articular face is developed, unlike the well-developed projection in tinamous and galliforms or the more weakly developed projection in Anhimidae (Clarke and Chiappe, 2001). A large, proximodistally elongate scar lies in the same position as the intermetacarpal tuberosity, where developed, or a scar for the insertion of m. extensor metacarpi ulnaris (Baumel and Witmer, 1993) in Aves.

Metacarpal I is elongate compared to the condition in Aves, extending to approximately the distal end of the proximal metacarpal symphysis (fig. 55A,B), whereas in the tinamous, galliforms, and anseriforms surveyed as well as in YPM 1734, metacarpal I is much shorter (fig. 55C). The extensor process is also less projected anteriorly than in tinamous, galliforms, anseriforms, and neoavians (e.g., *Sterna maxima*, *Burhinus capensis*) surveyed. The pisiform process is relatively small, connected to metacarpal III by a faint ridge, and directed slightly anteriorly (fig. 55B). This process, often situated at the same level as approximately the midpoint of metacarpal I in Aves (Clarke and Chiappe, 2001), is situated more relatively proximally in *Ichthyornis*. There is a pronounced pitlike scar for muscle insertion on the proximoventral edge of metacarpal III that is also seen, although less well developed, in tinamous and, for example, in *Anhima cornuta*. The anterior (YPM 1724) and posterior (YPM 1775, YPM 1752) carpal fossae are comparatively shallow. The anterior fossa, by contrast, is deep in *Apsaravis ukhaana* (Norell and Clarke, 2001). The in-

fratrochlear fossa (fossa infratrochlearis; Baumel and Witmer, 1993) on the proximoventral surface is moderately deep in *Ichthyornis* (Clarke and Chiappe, 2001), but shallow in *Apsaravis ukhaana* (Norell and Clarke, 2001). On the dorsal surface, the supratrochlear fossa (fossa supratrochlearis; Baumel and Witmer, 1993) and a proximal notch commented on in Clarke and Chiappe (2001) are visible (fig. 45A). The notch is for the lig. radiocarpo-metacarpale in Aves, connecting the radiale to the proximal carpometacarpus (Baumel and Raikow, 1993). Its absence in more basal avialans was noted in Clarke and Chiappe (2001). The supratrochlear fossa in Aves marks the attachment of a ligament connecting the ulnare and proximal carpometacarpus (Baumel and Raikow, 1993).

The diameter of metacarpal III is significantly less than half the diameter of metacarpal II, an apomorphy that arose within Avialae and is ancestral for Aves (Norell and Clarke, 2001). Metacarpal III is subparallel to metacarpal II and the intermetacarpal space is narrow (fig. 55B). While metacarpal III is somewhat more bowed in *Apsaravis ukhaana* (Norell and Clarke, 2001) and tinamous, the intermetacarpal space is comparatively narrow relative to that of Galliformes. Interestingly, Mayr (1999) described an outgroup of Galliformes with a relatively straight metacarpal III and narrow intermetacarpal space.

Metacarpals II and III are approximately equal in distal extent in *Ichthyornis dispar* (e.g., YPM 1450, YPM 1724; appendix 1, character 148). As noted in a comparative context by Clarke and Chiappe (2001), grooves that appear topologically equivalent to those for the m. interosseus dorsalis and that for the m. interosseus ventralis in Aves (Stegmann, 1978) are indicated by short ridges on the dorsal surface of the distal end (e.g., YPM 1450, YPM 1724).

A large dorsal process (Howard, 1929) on the anterodorsal tip of the distal end of the carpometacarpus (fig. 55A) is visible in the holotype of *Ichthyornis dispar* (YPM 1450) and all other referred carpometacarpi where preserved. The development of this process is related to the development of the m. abductor indicus in Aves (Stegmann, 1978; m.

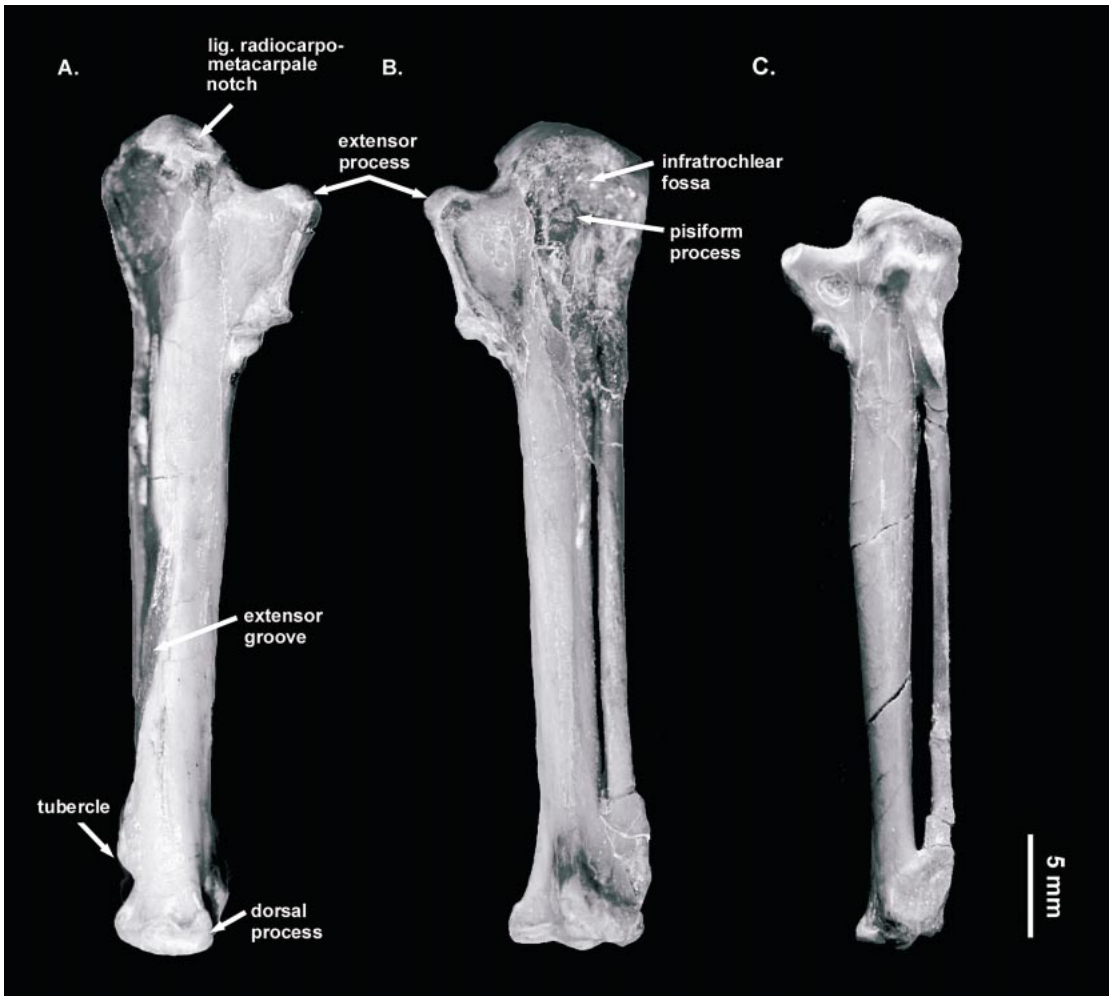


Fig. 55. The right carpometacarpus of (A, B) *Ichthyornis dispar* (YPM 1724) and (C) *Iaceornis marshi* (YPM 1734) in (A) dorsal and (B, C) ventral views.

abductor digiti majoris, Vanden Berge and Zweers, 1993). A process in the same position also appears well developed in basal avialans (e.g., *Confuciusornis sanctus*, JM Ukr-1997/1) and because the dorsal process is positioned on the edge of the articulation of the first phalanx of the second digit, its development in basal avialans may also be related to the presence of more robust ginglymous articulation generally. A dorsal process is well projected, but with a slightly different conformation in tinamous, and it is poorly developed in galliforms and Anhimidae, though it is moderately developed in *Anas platyrhynchos*. In Charadriiformes, such as

Sterna maxima and *Burhinus capensis*, it is well projected. A scar that appears topologically equivalent with the passage of m. abductor indicis in Aves (Stegmann, 1978) is also present in *Ichthyornis* on the anterior edge of the ventral surface (e.g., YPM 1724).

The distal carpometacarpus also displays a feature interpreted as a synapomorphy of *Ichthyornis* (fig. 55A). A large tubercle is developed close to the articular surface for the first phalanx of the second digit (Marsh, 1880), where the tendinal groove ends as the tendon for the m. extensor digitorum communis passes distally to insert on the first phalanx (fig. 55A). The tubercle may be re-

lated to the attachment of the ligament that holds the tendon in place as it shifts direction (Stegmann, 1978). In tinamous, this repositioning ligament is not present, the m. extensor digitorum communis groove is very weakly developed and nearly straight throughout its length, and the tendon of this muscle does not change direction at the distal end of the carpometacarpus to insert on the anteroventral tip of the first phalanx, but rather inserts dorsally (Stegmann, 1978). Thus, the motion that this muscle effects does not include supination of the distal portion of the second digit in Tinamidae, only extension of the manus (Stegmann, 1978). This condition was interpreted as ancestral for Aves by Stegmann (1978), who also noted the dorsal insertion of the extensor in Cuculiformes as testament to the latter group's basal position within Aves. However, the conspicuous, even hypertrophied, tubercle developed in *Ichthyornis*, plus a well-developed extensor groove with distal flexion, unlike the condition in Tinamidae, renders this character equivocal for the base of Aves. The extensor groove in *Apsaravis ukhaana* is not preserved, nor is most of the distal tip of the carpometacarpus exposed.

Either conformation seen in neognaths (including Galliformes) with a distinct distal twist is locally apomorphic of *Ichthyornis*, with the tinamou condition being ancestral to Aves, or the tinamou condition of an untwisted condition is derived. Unfortunately, so far these morphologies for more basal taxa are either not preserved (e.g., *Patagopteryx deferrariisi*, *Hesperornis regalis*, *Baptornis advenus*), not described (e.g., Enantiornithes, *Confuciusornis sanctus*), or the groove itself is apparently not present (e.g., *Archaeopteryx lithographica*, Dromaeosauridae). The hypertrophied tubercle is not seen in tinamous and galliforms (Stegmann, 1978) or anseriforms (e.g., *Anhima cornuta* and *Anas platyrhynchos*). It is not developed in more basal taxa with this portion of metacarpal II preserved (e.g., *Neuquenornis volans* or *Confuciusornis sanctus* or in *Iaceornis marshi* and *Limenavis patagonica*). It is found to be autapomorphic of *Ichthyornis*. Extant charadriiforms have a tubercle in approximately the same position as *Ichthyornis* related to a portion of the lig. digito-metacarpale (Steg-

mann, 1978), part of which constrains the passage of m. extensor digitorum communis (Stegmann, 1978) and part of which passes directly distally to insert on the distal, dorsal tip of phalanx II:1 in Aves.

MANUAL PHALANGES

PHALANX I:1

The element placed as phalanx I:1 in the *Ichthyornis victor* mount appears to be, indeed, manual phalanx I:1. The element is thin and narrow, with an ovoid articular surface (fig. 56E). However, it may be from YPM 1759, which is referred to *Ichthyornis dispar*, or it may be from YPM 1734 (the holotype of *Iaceornis marshi*). Phalanx I:1 is not mentioned or figured in *Odontornithes* (Marsh, 1880) for either *Ichthyornis* or YPM 1734, which Marsh referred to *Apatornis celer*. The element from the mount articulates better with the first metacarpal of *Ichthyornis* (e.g., YPM 1724) than it does with that of YPM 1734. Indeed, it appears too large to be part of YPM 1734.

As further discussed below (see Phalanx II:2), Gibb's annotated image of *Ichthyornis victor* from Marsh (1880; fig. 3) placed the number "1759" on Phalanx II:2. But this element from the mount appears to be part of YPM 1734, not YPM 1759 (holotype of *Iaceornis marshi*; previously referred to *Apatornis celer*) that was figured in *Odontornithes* as *Apatornis celer* (Marsh, 1880: pl. XXXI, figs. 9–11). Thus, it is possible that this specimen number (i.e., YPM 1759) corresponds with the similarly shaped phalanx I:1 that had no number applied to it in Gibb's notes (fig. 3).

PHALANX II:1

The first phalanx of digit II (fig. 56A) is represented in five YPM *Ichthyornis dispar* specimens (1463, 1726, 1755, 1759, and 1775). The morphology of these phalanges is consistent insofar as they could be compared. All are from individuals significantly larger than the *Ichthyornis dispar* holotype and approximately the size of the *Ichthyornis victor* holotype. One phalanx identified as *Ichthyornis victor* is figured in *Odontornithes* (Marsh, 1880: pl. XXXI, figs. 16–18). The

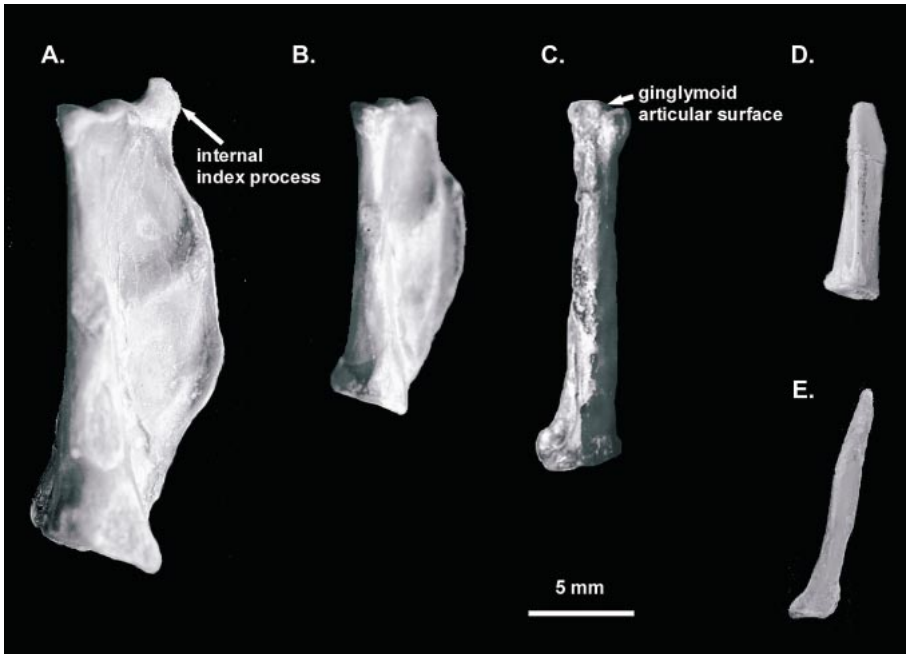


Fig. 56. Manual phalanges of *Ichthyornis dispar* and *Iaceornis marshi*: (A) phalanx II:1 of *Ichthyornis dispar* (YPM 1726) and (B) *Iaceornis marshi* (YPM 1734) in dorsal view; (C) phalanx II:2 of *Ichthyornis dispar* (SMM 2503) and (D) *Iaceornis marshi* (YPM 1734) in dorsal view; (E) phalanx I:1? of *Ichthyornis dispar* (YPM 1759) in dorsal view. The distal ends of all phalanges are pointed toward the top of the page.

phalanx illustrated is probably from YPM 1726, which is the best preserved of the five specimens and the only one that currently matches the pictured element. This specimen was also included in the *Ichthyornis victor* panel mount as indicated by Gibb's notes (fig. 3).

The limited comments on this element in *Odontornithes* (Marsh, 1880) are consistent with the morphology preserved: certain details of the articular surfaces and that the phalanx thins posteriorly. Several morphologies Marsh (1880) did not describe or mentioned only briefly are discussed here.

A subtriangular muscle scar is developed on the proximal edge of the anterodorsal surface, with an oblong scar just distal to it on the same edge (fig. 56A). A third, larger, ovoid scar is well developed on approximately the midpoint of the dorsal surface of the anterodorsal edge of the element (fig. 56A). The scar has a raised distal edge and is moderately deep. A conspicuous scar is developed in the same position on the pha-

lanx of *Iaceornis marshi* (YPM 1734), which, otherwise, little resembles that of *Ichthyornis*. Among the Aves surveyed (i.e., *Crypturellus noctivagus*, *Anhima cornuta*, *Anas platyrhynchos*, *Crax pauxi*, and *Meleagris gallopavo*, *Burhinus capensis*, and *Sterna maxima*), none had a prominent scar in the position observed in *Ichthyornis* and *Iaceornis marshi* (YPM 1734). A weakly developed scar did appear to be present in *Crypturellus noctivagus* and in *Sterna maxima*, for example, but no such scar appears present in *Apsaravis ukhaana* (Norell and Clarke, 2001). The distribution of this scar should be further investigated.

A strong, proximally directed process is developed on the anteroventral corner of the proximal edge of phalanx II:1 (fig. 56A). This process is developed in tinamous and Galliformes. It is not as well developed in Anseriformes. It has not been described for more basal avialans and does not appear present in *Apsaravis ukhaana*. It is possible that this process is synapomorphic of *Ichthyornis*

dispar + Aves, although scrutiny of more basal avialans is necessary to determine if it is synapomorphic at a more or less inclusive level.

Additionally, an internal indicus process (Stegmann, 1978) is present on the posterior edge of the distal end of the phalanx. As discussed in a comparative context by Stegmann (1978) and Clarke and Chiappe (2001), an internal “indicus” process is otherwise only seen in Neoaves. It is not known in *Asaravis ukhaana* (Norell and Clarke, 2001) or for more basal taxa. It is found to be an autapomorphy of *Ichthyornis dispar* (see Taxonomic Revision). An internal indicus process is not present in *Iaceornis marshi* (fig. 56B) or in *Limenavis patagonica* (Clarke and Chiappe, 2001).

PHALANX II:2

Marsh (1880) did not discuss the second phalanx of the second manual digit in *Ichthyornis dispar*, though he did comment on the morphology of this element in YPM 1734 (the holotype of *Iaceornis marshi*), which he referred to *Apatornis celer*. Phalanx II:2 is represented in a partial skeleton discussed above in the context of the furcula (SMM 2503; fig. 56C). This element is significantly more robust and elongate than II:2 in YPM 1734 (named as the holotype of *Iaceornis marshi*; see Taxonomic Revision), for example (compare figs. 56C and D). It bears a relatively well-developed ginglymoid articular surface for the third phalanx (ungual) of this digit (fig. 56C). Its base is excavated by strong depressions for muscular attachment. Thus, it would appear that this digit had a well-developed claw. The length of this phalanx is subequal to that of II:1.

No mention is made in *Odontornithes* (Marsh, 1880) of the manual phalanx II:2 of *Ichthyornis*. It is not represented among the YPM material. However, two manual phalanges besides II:1 were included in the *Ichthyornis victor* panel mount placed in the positions of II:2 as well as I:1.

Gibb’s notes indicate that the element placed in the mount as manual phalanx II:2 belonged to YPM 1759 (fig. 3). However, when this element was removed from the mount, it matched phalanx II:2 as figured for

Iaceornis marshi (YPM 1734) in *Odontornithes* (Marsh, 1880: pl. XXXI, figs. 9–11). YPM 1734 was referred to *Apatornis celer* and is named as the holotype of *Iaceornis marshi*. The illustrated digit of YPM 1734 has a small projection on its proximal end matched by the phalanx placed as II:2 (fig. 56D). It appears that, again, Gibb’s notes are misleading: The phalanx placed as II:2 of *Ichthyornis* and identified by Gibb as belonging to YPM 1759 appears to be II:2 of YPM 1734, which is not closely related to *Ichthyornis dispar* (Part II, Results).

PHALANX III:1

As mentioned by Marsh (1880), phalanx III:1 in *Ichthyornis dispar* is preserved in YPM 1775 (fig. 57D). Both the right and left phalanges are represented. The anatomy of this element does not agree with its representation in the reconstruction of *Ichthyornis victor* in *Odontornithes* (Marsh, 1880: pl. XXXIV). In that figure, it is presented as a simple, narrow element (fig. 57C), as, for example, in *Sterna maxima*. In fact, the phalanx is a flat, robust element with a pronounced, posteriorly directed flexor process (Butendieck and Wissdorf, 1981) and is much closer in structure to the same element in Tinamidae (e.g., *Eudromia elegans* and *Crypturellus undulatus*; fig. 57B), while in *Sterna maxima* (and Charadriiformes generally; Stegmann, 1978) the flexor process is a diminutive (fig. 57A). In *Ichthyornis dispar* and tinamous (and an array of other avian taxa; Stegmann, 1978) it is a broad, flange-like process. This tubercle associated with the m. flexor digiti III insertion in Aves (Chamberlain, 1943; Stegmann, 1978). Phalanx III:1 has an ovoid, slightly concave surface for articulation with metacarpal III (fig. 57D).

PELVIC GIRDLE

Parts of the ilium, ischium, and pubis of *Ichthyornis dispar* are represented by the relatively well-preserved pelvis of YPM 1732 (fig. 42) and possibly in a second specimen (YPM 1733) as a fragment from part of the acetabulum border. One pelvis illustrated in *Odontornithes* (Marsh, 1880: pl. XXXII, figs. 2–3) is from YPM 1732, a specimen

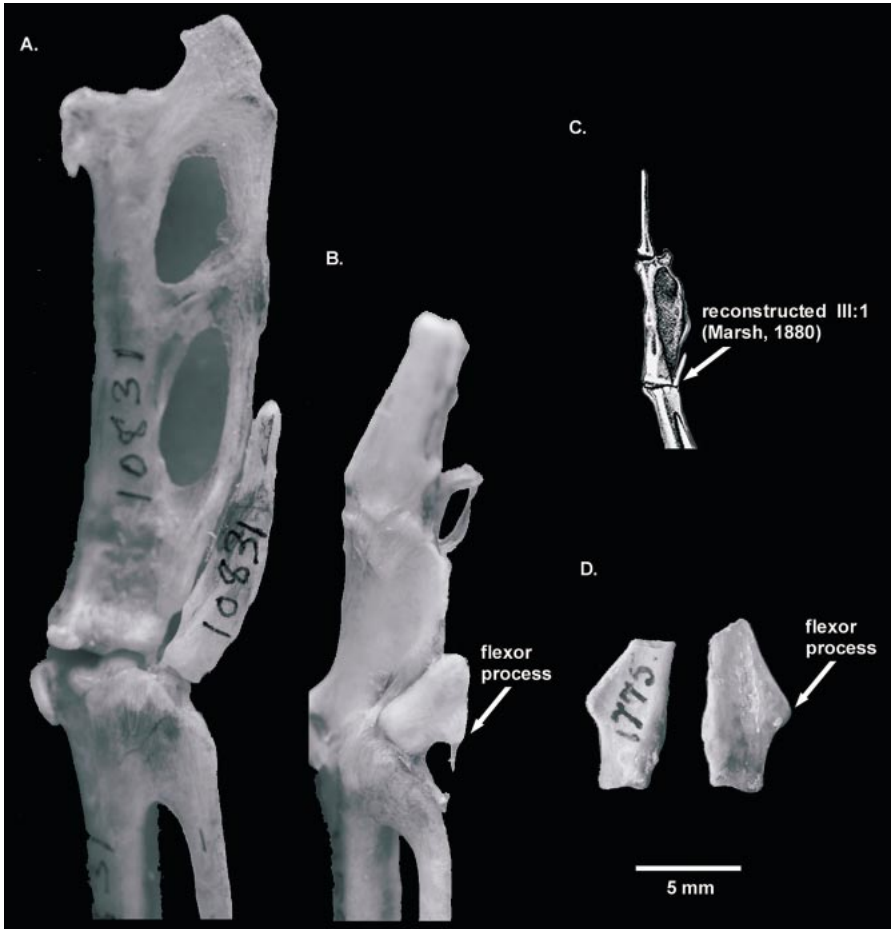


Fig. 57. Manual phalanx III:1 of (A) *Sterna maxima* and (B) *Crypturellus undulatus* compared to that of *Ichthyornis dispar* (C) as reconstructed by Marsh (1880) and (D) as preserved in YPM 1775. The distal ends of the phalanges in D (YPM 1775) are missing. The flexor process of III:1 (B, D) is prominent in *Ichthyornis dispar* (contra Marsh, 1880) and in *Crypturellus undulatus*.

referred to *Ichthyornis dispar*. However, a second pelvis (Marsh, 1880: pl. XXXII, fig. 1) was identified as from a specimen referred to *Apatornis celer*, YPM 1734, here named as the holotype of *Iaceornis marshi*.

The pelvis of YPM 1732 was included in the *Ichthyornis victor* panel mount (fig. 42A). When it was removed from the mount, it was embedded in wax and prepared to expose the ventral surface. The dorsal and lateral surfaces of the pelvic elements were studied from casts and photographs of the *Ichthyornis victor* panel mount (fig. 42A). Only the right pelvic elements are currently

preserved (fig. 42B,D), although Marsh (1880: pl. XXXII, figs. 2–3) illustrated them as preserved for both the right and left sides (fig. 42C).

The anterior portion of the ventral surface of the pelvis in YPM 1732 was not illustrated in *Odontornithes* (Marsh, 1880: pl. XXXII, fig. 3), and the morphology of the pelvis currently differs from its illustration and description in *Odontornithes*. As already noted, 12 sacral vertebrae, not 10 (Marsh, 1880), are present in YPM 1732. The preacetabular ilium is described as being considerably longer than its postacetabular portion, and the

ischium is described as extending farther posteriorly than the ilium (Marsh, 1880: 163). However, no part of the postacetabular ilium is preserved (fig. 42B,D). It is, in fact, illustrated as missing in *Odontornithes* (Marsh, 1880: pl. XXXII).

Several of Marsh's (1880) brief comments on the pelvic elements of YPM 1732 were confirmed on restudy of the material: The ischium is broad "medially" (i.e., it has a conspicuous dorsal process); the ilium and ischium were unfused posteriorly (fig. 42B,D); and the pubis lacks a pectineal process (processus pectinealis; Baumel and Witmer, 1993). As inferred from the orientation of the costal strut in the area of the acetabulum and the preserved sliver of the postacetabular ilium in YPM 1732 (fig. 42B,D), the postacetabular ilia appear to have been directed laterally, as they are illustrated (Marsh, 1880), rather than being oriented dorsoventrally.

The preacetabular ilium is 20 mm in length as reported by Marsh (1880). The preserved portion of the ischium, lacking its distal end, is 19.6 mm, not the 22.5 mm Marsh reported.

The ilium of YPM 1732 has a subtly rounded anterior terminus (fig. 42A,B). The first sacral vertebra (or last thoracic, per Marsh, 1880) lies almost entirely anterior to the ilium, unlike its illustration in *Odontornithes* (Marsh, 1880; fig. 42C). Ossified tendons extend anteriorly from the transverse processes of the left side of this vertebra (fig. 42B). Intertransverse fenestrae (fenestrae intertransversariae; Baumel and Witmer, 1993) are visible between the transverse processes of the first three sacral vertebrae on the left side, and between those of the eighth and ninth on the right. The the paired iliosynsacral sulci appear open (rather than dorsally enclosed to form canals) in YPM 1732 as illustrated by Marsh (1880: pl. XXXII, fig. 2). The proximal end of the femur lies in the right acetabulum and the capital ligament fossa (fovea lig. capitis; Baumel and Witmer, 1993) on the femoral head is visible through the acetabulum. The antitrochanter is well developed and lies posterodorsal to the acetabulum.

The pointed dorsal process of the ischium in YPM 1732 (fig. 42D) approaches the mor-

phology of the element in more basal avialans (e.g., *Confuciusornis sanctus*). A similarly shaped ischium is also seen in *Lithornis plebius* (USNM 336534) but not, apparently, in other *Lithornis* species (Houde, 1988). A diminutive projection of the ischium appears to demarcate the area of the obturator foramen distally; it was not closed posteriorly.

The remains of the pubis are severely crushed; however, it would have been relatively robust (fig. 42D). Its diameter as preserved is 2.4 mm. It does not appear to have closely paralleled the ventral margin of the ischium posteriorly, but rather to have curved ventrally. In *Apsaravis ukhaana*, the pubis and ischium are parallel, even appressed, posteriorly (Norell and Clarke, 2001). The postacetabular extent of the pubis is currently 7.1 mm. Thus, the reported length (26 mm) of this element (Marsh, 1880) could not be confirmed, as most of it is presently missing (fig. 42B,D).

FEMUR

Parts of the femur are represented in three YPM specimens, the *Ichthyornis dispar* holotype (YPM 1450) as well as in YPM 1732 and YPM 1775, which are larger individuals than the majority of the YPM material. The nearly complete, but severely crushed, left femur of the *Ichthyornis dispar* holotype (YPM 1450) was figured in *Odontornithes* (Marsh, 1880: pl. XXV, figs. 1–4). Marsh mentions that the femur of *Ichthyornis victor* is illustrated in plate XXXIII of *Odontornithes* (Marsh, 1880: 171), but it is not included in that or any other plate.

The distal portion of the right femur from the *Ichthyornis dispar* holotype (YPM 1450) was incorrectly mounted as the right distal tibiotarsus in the *Ichthyornis dispar* panel mount. The left femur of YPM 1450 was mounted as the right in the mount, and, when removed, differed from its presentation in *Odontornithes* (Marsh, 1880) as uncrushed. It appears largely to have been reconstructed. Much if not all of the dorsoventral crushing and distortion of the specimen appears to be the original state of preservation of the specimen and not recent damage. The measurements given (Marsh, 1880: 172) differ from

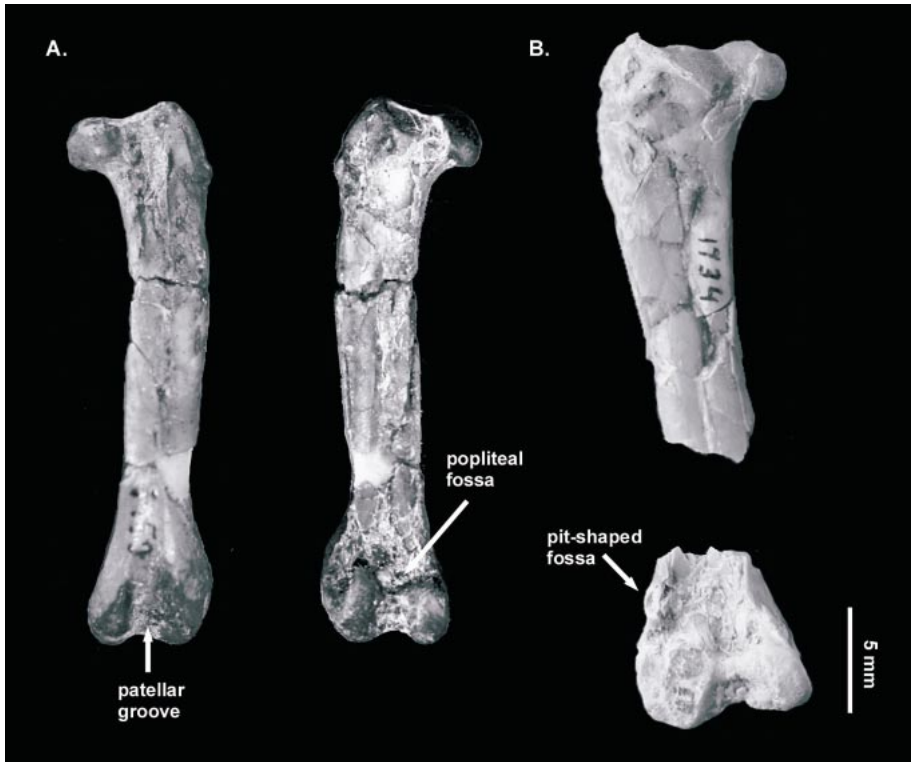


Fig. 58. The left femur of the (A) *Ichthyornis dispar* holotype (YPM 1450; right: anterior view, left: posterior view) and (B) *Iaceornis marshi* (YPM 1734; posterior view).

those of the element as currently preserved. Its total length is 24.7 mm (vs. 30.5 mm, Marsh, 1880: 172) The diameter of the head is 2.6 mm (vs. 2.8 mm, Marsh, 1880: 172).

A well-developed capital ligament fossa (fovea lig. capitis; Baumel and Witmer, 1993) is visible on the head of the femur in YPM 1450 (fig. 58A) and YPM 1732. The development of the trochanteric crest in *Ichthyornis dispar* (YPM 1450, YPM 1732) approximates its representation in *Odontornithes* for the holotype of *Ichthyornis dispar* (Marsh, 1880: pl. XXIV, figs. 1–4). It was not proximally or anterodorsally projected. The lateral surface of the left femur of YPM 1450 is largely destroyed. The features illustrated as present that appear to be muscle impressions (Marsh, 1880: pl. XXV, fig. 4) are not visible in the material and could not be confirmed. Only a small tubercle (Marsh, 1880: pl. XXV, figs. 1, 3) is discernable on the anterior edge of the lateral surface (fig.

58A) of the left femur of YPM 1450. This femur of YPM 1450 is bowed, and, as currently preserved, is approximately half the length of the humerus (contra Marsh, 1880).

The distal end is preserved for the right and left femurs in YPM 1450 (i.e., the holotype of *Ichthyornis dispar*) and in the left femur of YPM 1775. The distal left femur in YPM 1775 is less crushed than either femur of YPM 1450. In both specimens, the fibular trochlea and popliteal fossa are visible (fig. 58A). No scars associated in Aves with the attachment of the ansae m. iliofibularis (impressiones ansae m. iliofibularis; Baumel and Witmer, 1993) or m. gastrocnemius lateralis (tuberculum m. gastrocnemius lateralis; Baumel and Witmer, 1993) are preserved. However, a fossa that is associated with the attachment of the tendon of the m. tibialis cranialis in Aves (fovea tendinis m. tibialis cranialis; Baumel and Witmer, 1993) is visible on the lateral edge of the patellar groove

near the distal end of the femur. It was not figured or mentioned in *Odontornithes* (Marsh, 1880). The intercondylar groove and patellar groove are developed on the distal and anterodistal surfaces, respectively. No potential apomorphies of *Ichthyornis* from the femur were identified.

TIBIOTARSUS

The tibiotarsus is represented in five YPM specimens: the holotype of *Ichthyornis dispar* (YPM 1450), YPM 1723, YPM 1732, YPM 1754, and YPM 1775. YPM 1723 was referred to *Ichthyornis dispar*, while the remaining specimens were referred to *Ichthyornis victor*. These referrals, as previously noted (see Taxonomic Revision), appear arbitrary; YPM 1723 is approximately the same size as the other three referred tibiotarsi and no morphological differences were noted.

Marsh (1880: pl. XXV, figs. 5–8) illustrated a proximal right tibiotarsus that he indicated was from *Ichthyornis dispar* but is not among the YPM material. Only a fragment of a left proximal tibiotarsus from the *Ichthyornis dispar* holotype (YPM 1450) closely matches the approximate length and detail of the illustrated fragment. It is possible that an illustration of this left tibiotarsus from YPM 1450 was inverted to present the right side for consistency, as only a right distal tibiotarsus is preserved. Otherwise, a proximal right tibiotarsus from YPM 1450 has been lost subsequent to the publication of Marsh (1880). Marsh (1880) also illustrated the presence of both a left and a right distal tibiotarsus as preserved in the holotype of *Ichthyornis dispar* (Marsh, 1880: pl. XXVI), but a distal left tibiotarsus is not preserved. It appears that a distal femur was included in the *Ichthyornis dispar* panel mount as a second distal tibiotarsus (see Femur).

Marsh (1880: pl. XXXIII, figs. 6, 7) also illustrated a complete left tibiotarsus identified for *Ichthyornis victor*. In *Odontornithes* (Marsh, 1880), only two tibiotarsi were identified as *Ichthyornis victor*: YPM 1775 and YPM 1732. Both specimens include left tibiotarsi, but neither of them is complete. YPM 1775 consists only of one piece of a distal tibiotarsus, the preservation of which

(e.g., pattern of fractures) does not match the illustrated tibia. The other specimen, YPM 1732, includes a proximal right and a large section of a distal left tibiotarsus, as well as several pieces of the shaft that do not articulate. The preservation of the distal piece approaches the illustration in *Odontornithes* in a fracture on the posterior surface of the distal end, as well as in chipped bone midway up the anterior surface of the shaft. However, no aspects of the morphology of the proximal shaft illustrated (Marsh, 1880: pl. XXXIII, figs. 6, 7) can be confirmed. Nor can Marsh's (1880: 173) measurements of the total length of the tibiotarsus be confirmed for YPM 1732 or YPM 1723, which includes four fragments of a left tibiotarsus that do not articulate.

The distal portion of the left tibiotarsus from YPM 1732 was identified by Gibb (fig. 3) as included as the right tibiotarsus in the *Ichthyornis victor* panel mount. The partial right tibiotarsus from YPM 1734 (formerly referred to *Apatornis celer*; here named as the holotype of *Iaceornis marshi*) was included as the left tibiotarsus in the mount (fig. 59D). The four tibiotarsi referred to *Ichthyornis dispar* (i.e., YPM 1723, YPM 1732, YPM 1754, YPM 1775) correspond in all anatomical detail to each other and to the holotype (YPM 1450), insofar as they are preserved.

Several aspects of the morphology illustrated for the proximal tibiotarsus of YPM 1450 are artifacts of crushing, although this was not indicated by Marsh (1880). The apparent lack of a retropatellar fossa and some exaggeration of the blocklike shape of the proximal end result from the cnemial crests being artifactually pressed toward the lateral and medial articular surfaces (fig. 59A). The shape of the distal condyles is also distorted by breakage (fig. 59B). A fracture runs mediolaterally across these condyles, and they have been shifted slightly proximally. The bend in the medial edge of the distal end is due to compression of the shaft, as is seen in breakage in the base of the extensor groove (fig. 59B).

The morphology of the proximal end of the tibiotarsus is preserved in *Ichthyornis dispar* holotype (YPM 1450; fig. 59A), YPM 1723, and YPM 1732. The lateral articular

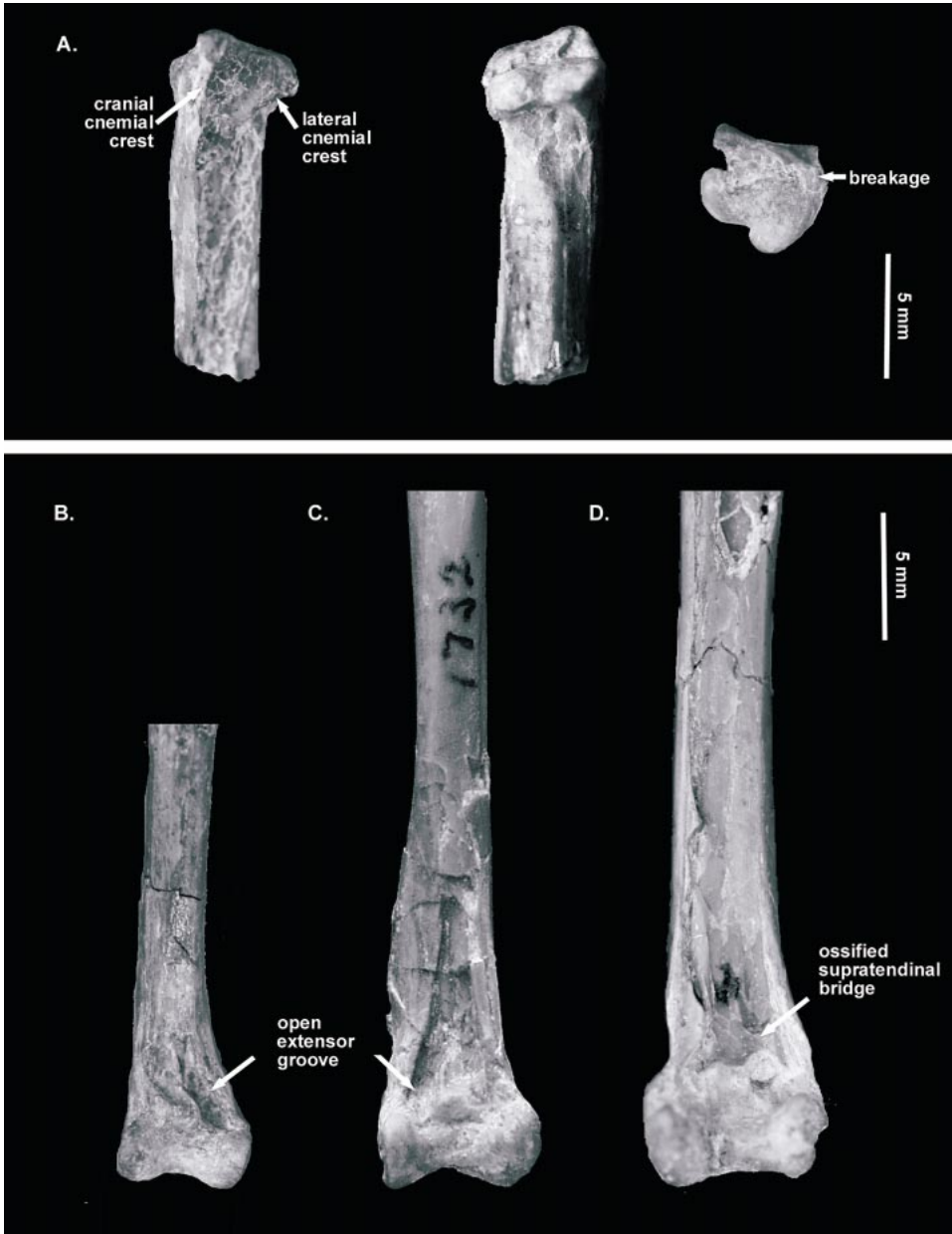


Fig. 59. The tibiotarsus of *Ichthyornis dispar* (YPM 1450, YPM 1732) and *Iaceornis marshi* (YPM 1734): (A) the proximal left tibiotarsus of the *Ichthyornis dispar* holotype (YPM 1450) in anterior, posterior, and proximal views (left to right); (B) the distal right tibiotarsus of the *Ichthyornis dispar* holotype (YPM 1450) in anterior view; (C) the distal left tibiotarsus of a specimen referred to *Ichthyornis dispar* (YPM 1732) in anterior view; (D) the distal right tibiotarsus of the *Iaceornis marshi* holotype specimen (YPM 1734) in anterior view.

surface (facies articularis lateralis; Baumel and Witmer, 1993) is convex and larger than the medial (facies articularis medialis; Baumel and Witmer, 1993), which is flat. There is a relatively short fibular crest (crista fibularis; Baumel and Witmer, 1993) visible in YPM 1450 (Marsh, 1880). The anterior and lateral cnemial crests (crista cnemialis cranialis et lateralis; Baumel and Witmer, 1993) are well developed, although the former does not extend significantly proximal to the level of the articular surfaces (fig. 59A) as observed in YPM 1450, the holotype of *Ichthyornis dispar*. That this morphology (a short anterior cnemial crest) is developed in *Ichthyornis dispar*, tinamous, galliforms (Megapodidae, Cracidae, and some phasianids; Ericson, 1997), and basal anseriforms (Anhimidae) may suggest that this morphology is ancestral for Aves. However, the anterior cnemial crest extends relatively far proximally in *Hesperornithes*, and the proximal tibiotarsus is unknown in *Apsaravis ukhaana* (Norell and Clarke, 2001). The lateral cnemial crest observed in YPM 1450 is not strongly hooked (fig. 59A), and it resembles its representation in *Odontornithes* (Marsh, 1880: pl. XXV, fig. 5).

The distal tibiotarsus is represented in YPM 1450, YPM 1723, YPM 1732, YPM 1754, and YPM 1775. It is distorted in each of these specimens, however. An ossified supratendinal bridge over the tendinal groove (sulcus extensorius; Baumel and Witmer, 1993) for m. extensor digitorum longus is clearly not developed in YPM 1723, YPM 1732, and YPM 1775. In the holotype of *Ichthyornis dispar* (YPM 1450) and YPM 1754, the presence of this ossified bridge cannot be precluded, as the region is poorly preserved (fig. 59B). This is especially true in YPM 1754, where the tendinal groove is almost closed by mediolateral crushing.

The attachments of the extensor retinaculum (retinaculum extensorium tibiotarsi; Baumel and Raikow, 1993) are developed as a narrow ridge along the mediodistal surface proximal to the medial condyle and as a raised lateral scar lying medial to the distal terminus of the fibular groove. These attachments are best seen in YPM 1754 and YPM 1775. The retinaculum in Aves directs the passage of m. tibialis cranialis as well as m.

extensor digitorum longus (Baumel and Raikow, 1993). Both a retinaculum and groove are also developed in *Hesperornis regalis*. Although the retinaculum is developed in *Apsaravis ukhaana*, *Patagopteryx deferrariisi*, *Confuciusornis sanctus*, and other basal avialans (Norell and Clarke, 2001), the extensor groove is absent in these taxa (see appendix 1, character 181). The retinaculum, then, developed phylogenetically before the extensor groove. The m. extensor digitorum longus, thus, may have undergone a shift in function to the avian condition after the m. tibialis cranialis took on the conformation seen in Aves.

The medial and lateral condyles are approximately the same width (fig. 59B) with the lateral very slightly broader than the medial (YPM 1450, YPM 1732, YPM 1754, and especially well preserved in YPM 1775). The distal condyles of YPM 1723 are not preserved. Both condyles are also approximately equal in their other dimensions, in their proximal, as well as anterior, extent. The intercondylar groove is broad, making up approximately a third of the anterodistal tibiotarsus. Slightly medial to the lateral condyle in anterior view, there is a projected edge (fig. 59B,C). This edge borders a raised portion of the anterior surface that ends approximately at the distal terminus of the extensor groove. The lateral corner of this raised portion may correspond to one of the attachments of the extensor retinaculum in Aves, mentioned above. Though a similar edged raised area is developed in *Meleagris gallopavo*, it is not present, for example, in *Anas platyrhynchos*. The distribution of this character across Aves should be further scrutinized. The pronounced “wings” of the osteological correlate of the posterior extension of the cartilaginous pad for articulation with the tarsometatarsus (trochlea cartilaginosa tibialis; Baumel and Witmer, 1993) are well developed in *Ichthyornis*.

TARSOMETATARSUS

The tarsometatarsus is represented in four YPM specimens referred to *Ichthyornis* (i.e., 1456, 1464, 1739, and 1771). All of these elements are isolated. They are here referred to *Ichthyornis* by comparison with the figure

in *Odontornithes* (Marsh, 1880) that is identical to a tarsometatarsus associated with other remains referable to *Ichthyornis* (P. J. Lamb, personal commun.). None of the specimens is complete. The proximal and distal portions of a right tarsometatarsus (YPM 1739) were included in the *Ichthyornis victor* panel mount. However, YPM 1464 was identified as included in the mount by Gibb's annotated illustration of *Ichthyornis victor* from Marsh (1880). In this case, Gibb's notes on the contents of the mount are incorrect. Gibb's notes place the word "metacarpal" next to the number YPM 1464. However, the word "metacarpal" is included in the list of hind limb elements. The word "metatarsal" is placed next to the number YPM 1739 in the list of forelimb elements and next to the carpometacarpus of the annotated Marsh (1880) figure. However, these identifications would require YPM 1464 to have had two right tarsometatarsi and this situation is unknown in YPM *Ichthyornis* material (i.e., obviously two individuals labeled as one). Further, it would also leave no specimen among the material to correspond to YPM 1739, the box top of which is labeled "metatarsal" and no other numbered YPM *Ichthyornis* specimen boxes lack a corresponding specimen, as discussed above with reference to the carpometacarpus.

Marsh (1880: 175) gave measurements of the complete length of the tarsometatarsus of this specimen. It is possible that it was complete at the time and the measure given were accurate, but that cannot be confirmed. All four YPM specimens (i.e., 1456, 1464, 1739, 1771) are from individuals of the same size, larger than the holotype of *Ichthyornis dispar*. They are approximately the size of the holotype of *Ichthyornis victor*. This was ascertained by articulating preserved distal tibiotarsi with elements directly comparable in size to the *Ichthyornis victor* holotype (e.g., YPM 1775) with the well-preserved proximal end of the tarsometatarsus of YPM 1739.

The *Ichthyornis* tarsometatarsus is described from the specimens listed above. The distal tarsals are completely ankylosed to metatarsals II–IV that, in turn, are fused to each other (fig. 60). Metatarsal I is not preserved in any of the YPM specimens, and there is no evidence to indicate metatarsal V

was present. The proximal end of metatarsal III is displaced plantarly relative to II and IV, and a relatively short, rounded intercotylar eminence (eminentia intercotylaris; Baumel and Witmer, 1993) projects proximally (fig. 60A). The medial and lateral cotylae are approximately equal in size, and the anterior edge of the lateral is at approximately the same level as that of the medial as opposed to being slightly more distal to it, as in *Crypturellus noctivagus*, *Anhimidae*, *Anas platyrhynchos*, and *Meleagris gallopavo*. Marsh (1880) described the presence of a single proximal foramen between metatarsals III and IV. A large foramen is visible in this position (fig. 60A,B). It opens on the plantar surface just laterodistal to the hypotarsal prominence (fig. 60B). A series of three tiny foramina are also visible on the anterior surface between metatarsals II and III, not described by Marsh (1880). A single, small foramen is seen on the plantar surface just mediodistal to the hypotarsal prominence directly opposite that on the lateral side (fig. 60B). Norell and Clarke (2001) considered *Ichthyornis dispar*, like *Apsaravis ukhaana* and *Patagopteryx deferrariisi* (Chiappe, 1996), to have the single foramen noted by Marsh (1880). However, after further preparation, it appears *Ichthyornis dispar* should be considered to have a second proximal vascular foramen that, though diminutive, appears to penetrate the tarsometatarsus.

The extensor groove is deep and there are two distinct tubercles (fig. 60A) that are topologically correspondent with the m. tibialis cranialis tubercles in Aves (tuberositas m. tibialis cranialis; Baumel and Witmer, 1993). One of these tubercles lies on the dorsolateral surface of metatarsal II and the other on the dorsal surface of metatarsal III, with that on metatarsal II slightly proximal to that at approximately the midpoint of III (fig. 60A). A scar is visible on the proximal tip of the lateral surface of metatarsal IV in the same position as that for the lig. collateralis lateralis in Aves (impressio lig. collateralis lateralis; Baumel and Witmer, 1993). The groove for the avian m. fibularis longus (sulcus m. fibularis longus; Baumel and Witmer, 1993) is developed on the proximal, medioplantar surface of metatarsal II.

The hypotarsus is projected plantarly in

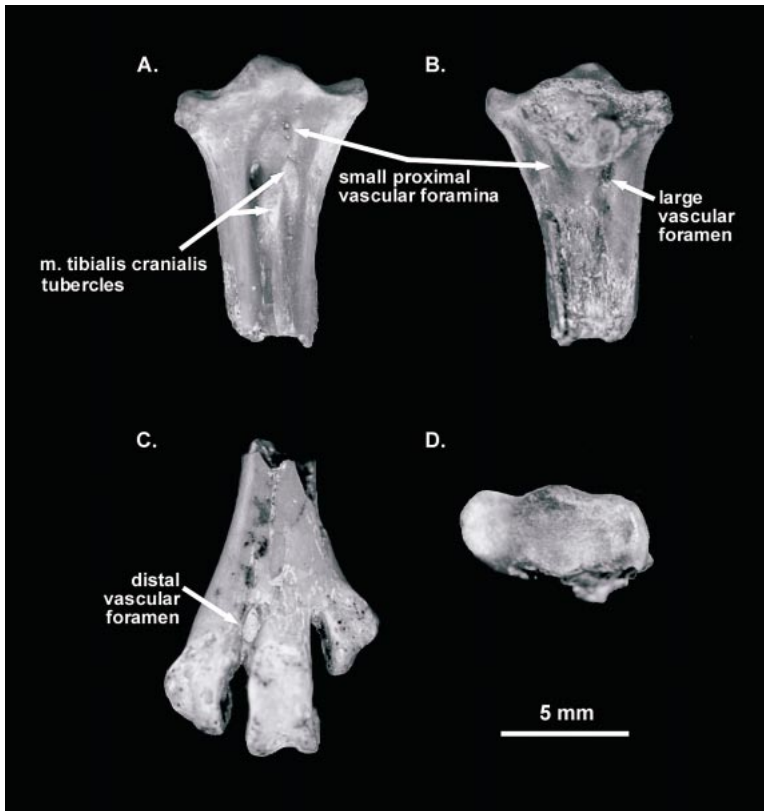


Fig. 60. The tarsometatarsus of *Ichthyornis dispar* (YPM 1739): (A, B, D) proximal and (C) distal ends in (A, C) anterior, (B) plantar, and (D) dorsal views.

Ichthyornis dispar (YPM 1739; fig. 60B). In *Apsaravis ukhaana* (Norell and Clarke, 2001), *Hesperornithes* (Marsh, 1880; Martin and Tate, 1976), and *Patagopteryx deferrariisi* (Chiappe, 1996), in the area of the avian hypotarsus, there is a flat, unprojected, discrete surface. In YPM 1739, a projected lateral portion of the hypotarsus with a flat plantar surface is preserved. Because the medial portion of the hypotarsus is not preserved, it is unclear if there were hypotarsal grooves or ridges (fig. 60B). In both *Crypturellus noctivagus* and *Chauna torquata*, the lateral part of the hypotarsus is essentially flat and little projected, while the medial edge is projected into a hypotarsal ridge. It is possible that either the hypotarsus was completely flat or laterally flat with a medial ridge or groove not preserved.

The distal vascular foramen is enclosed by the fused metatarsals III and IV (fig. 60C). It

has one plantar opening rather than both the distal and plantar openings seen in most Aves. As Marsh (1880) noted, it is a relatively large opening, only partly enclosed distally. In *Ichthyornis*, the plantar opening is directly opposite the dorsal opening. By contrast, in *Apsaravis ukhaana*, the plantar opening is displaced distally relative to the dorsal.

The trochlear surfaces of the distal condyles of metatarsals II–IV are strongly ginglymoid articulations (e.g., YPM 1464). In *Apsaravis ukhaana*, the articular surface of metatarsal II is rounded, as opposed to ginglymoid, as it is in *Crypturellus noctivagus*, *Chauna torquata*, *Alectura lathamii*, and *Meleagris gallopavo*. In *Anas platyrhynchos*, this surface is strongly ginglymoid, whereas in *Ichthyornis dispar*, it is comparatively weakly developed. Norell and Clarke (2001) considered this articulation in *Ichthyornis*

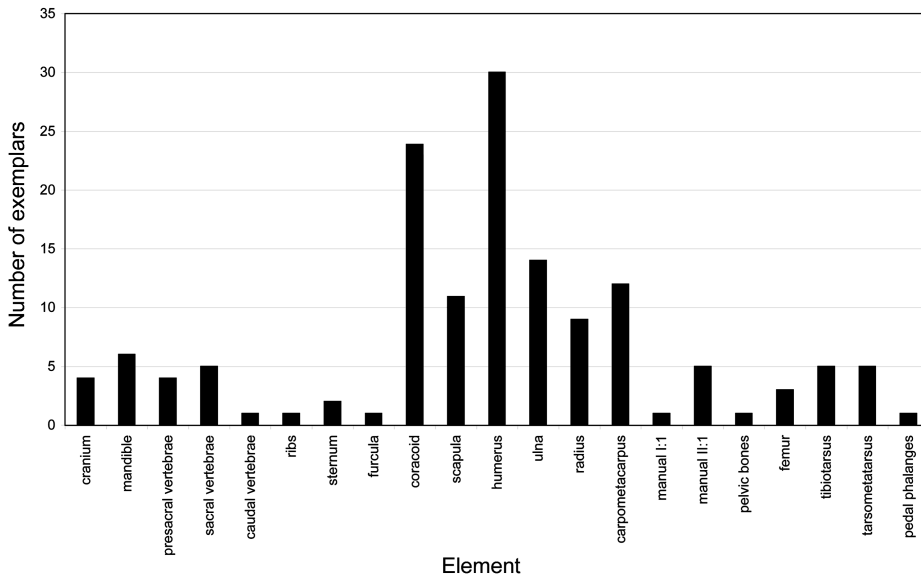


Fig. 61. The number of exemplars of anatomical elements in the YPM *Ichthyornis dispar* material.

dispar to be rounded; however, it is best considered ginglymoid.

Metatarsal III extends farthest distally, with metatarsal II reaching approximately the base of the trochlear surface of metatarsal IV, and deflected slightly more plantarly relative to IV (fig. 60C). Livezey (1997b; character 94) considered metatarsal II as reaching approximately the base of metatarsal IV, as opposed to subequal in distal extent, a derived character of *Anas platyrhynchos* and *Presbyornis pervetus*. He noted that it is also seen in some charadriiforms and in phoenicopteriforms (flamingos). However, the presence of this character in *Ichthyornis dispar*, *Baptornis advenus* (Martin and Tate, 1976), *Hesperornis regalis* (Marsh, 1880), and to a lesser extent in *Apsaravis ukhaana* (Norell and Clarke, 2001) suggests that this condition is basal to Aves. The condition in Tinamidae appears intermediate (Livezey, 1997b). The development of this feature in all of the just named taxa closely approximates that in *Anas platyrhynchos*, with the exception of *Apsaravis ukhaana*, in which metatarsal II extends to about the midpoint of metatarsal IV. As noted in a comparative context by Norell and Clarke (2001), the fossa for “metatarsal I” is developed. It is relatively shallow and lies just proximal to the base of the

trochlea of metatarsal II. One distinct intermuscular line is visible on the distal tarsometatarsus lying parallel to the axis of the shaft just medial to the lateral edge of the plantar surface, and diverging to pass the center of metatarsal IV distally.

PEDAL PHALANGES

One pedal phalanx is known from YPM 1732. It was figured in *Odontornithes* (Marsh, 1880: pl. XXXIII, fig. 8) and is currently slightly less complete than its illustration. It was identified as included in the *Ichthyornis victor* panel mount (fig. 2) in Gibb’s notes (fig. 3). It lacks the right side of the distal articular trochlea. The proximal articular surface of the phalanx is little expanded relative to the width of its shaft, and there are no conspicuous flexor tubercles. These morphologies may suggest that it is not one of the proximal phalanges. Additionally, YPM 1732 is a comparatively large individual of *Ichthyornis* (as represented by the tibiotarsus and sacrum among other elements) and the distal trochlea of the preserved tarsometatarsi are all too large to articulate with the cotyla. The phalanx may be the second phalanx of digit II of Aves, which, in its symmetry, delicate construction, and dimin-

utive distal trochlea, it matches best. Marsh considered this phalanx to be from either the second or third digit. Its proximal articular cotyla is subdivided for a ginglymoid articulation (Marsh, 1880: pl. XXXIII, fig. 8e). The phalanx shaft is almost straight. Distally, the collateral ligament pits are shallow.

PALEOECOLOGY, TAPHONOMY, OR COLLECTING BIAS?

As illustrated in figure 61, the number of forelimb elements represented in the YPM *Ichthyornis dispar* material is much greater than elements from any other part of the skeleton. Most intriguingly, the number of preserved portions of hind limb elements is roughly the same as the number of known cranial elements or presacral vertebrae. For example, the number of specimens including a mandible is the same as those including a tibiotarsus (fig. 61). The robustness of these elements, however, do not compare, the vertebrae and skull being comparatively more fragile than any portion of the hind limb. Also, it is unclear why there would be a collecting bias toward forelimb elements, as, in *Ichthyornis*, the tibiotarsi and tarsometatarsi would seem to be as distinctly recognizable as avialan, as would be the humerus.

Both Schafer (1972) and Davis and Briggs (1998) documented that one of the early phases of decay of an avian carcass, in a marine environment, is separation of the femur from the pelvis, such that the leg is separated from the rest of the carcass. The remaining portion of the carcass continues to float longer than the hind limb and sternum (Schafer, 1972). One tentative taphonomic explanation of the relative abundances of elements in the Niobrara deposits is that deposited material

was in a relatively advanced state of decay. Thus, it would represent material that had been kept afloat for a considerable length of time.

The Smoky Hill Chalk Member, Niobrara Formation, has been described as representing relatively deep deposits in the epeiric seaway during a period of maximum transgression (Stewart et al., 1990). Feduccia (1996) and others have argued that because *Ichthyornis* is found in such distal, deep marine deposits, they must have had advanced flight capabilities enabling them to head out into the open seas. This capacity, it was argued, might suggest that these animals were metabolically similar to living birds and that this capacity might not be present in other more basal avialans (e.g., Enantiornithes). This proposition was considered further supported by histological evidence (Chinsamy et al., 1998) that *Ichthyornis* is histologically similar to extant birds and unlike more basal taxa such as Enantiornithes or *Patagopteryx deferrariisi*. However, at least one enantiornithine, from the Mooreville Chalk of Alabama, is known from a relatively similar depositional environment (Lamb et al., 1993). Furthermore, Schafer (1972) noted that a drifting avian carcass on the open sea could drift for 27 days without the hind limbs detaching from the rest of the carcass, and that it would commonly take 38 days before the skeleton sank to the sea floor. He also noted that birds that end up on the open sea can be carried out from the near shore by waves and outgoing tides in addition to dying at sea (Schafer, 1972). Thus, the assumption that all or most of the *Ichthyornis* material is from individuals that necessarily flew out to their final resting place seems in error.

PART II: PHYLOGENETIC ANALYSES: THE SYSTEMATIC POSITION OF NIOBRARA AVIALANS

INTRODUCTION

Of the Niobrara avialans that are the focus of this project, *Ichthyornis* has repeatedly been included in phylogenetic analyses of avialan interrelationships (e.g., Cracraft, 1986; Chiappe, 1995a, 1995b, 2001). The re-

lationships of *Apatornis celer* have also been commented upon (e.g., Shufeldt, 1915; Howard, 1955; Olson, 1985; Martin, 1987; Elzanowski, 1995), although this taxon has never been included in a cladistic analysis. By contrast, tellingly, neither Marsh (e.g., 1872b, 1880) nor subsequent workers have hypoth-

esized relationships among the various previously named species of *Ichthyornis* that continued to be recognized.

In the taxonomic revision (Part I), two species were removed from *Ichthyornis* and the rest recognized as junior synonyms of *Ichthyornis dispar*. One of the two species removed from *Ichthyornis* had previously been suggested not to be part of *Ichthyornis* (i.e., *Ichthyornis* [*Austinornis*] *lentus*; Shufeldt, 1915; Martin and Stewart, 1982). The systematic position of the second species removed, *Ichthyornis* (*Guildavis*) *tener*, like the other proposed *Ichthyornis* species (other than *Ichthyornis* [*Austinornis*] *lentus*) has not been commented upon except to continue to list it as part of *Ichthyornis* (e.g., Brodkorb, 1967).

The sole specimen originally referred to *Apatornis celer* was named as part of a new species, *Iaceornis marshi*, in Part I. This specimen is that referenced by nearly all commentary (e.g., Shufeldt, 1915; Howard, 1955; Olson, 1985; Martin, 1987; Elzanowski, 1995) about *Apatornis* and its systematic position.

MATERIALS AND METHODS

A data matrix of 202 morphological characters scored for 24 ingroup terminals and two outgroups (see appendices I and II) was assembled to evaluate the systematic position of *Ichthyornis dispar*, *Apatornis celer*, and the newly identified species (Part I, Taxonomic Revision). Of the 202 characters, approximately 185 were identified as parsimony informative by PAUP*4.0b8 (PPC; Swofford, 2001) depending upon the combination of included taxa (see below). The number of parsimony-informative characters (at least one state shared by two or more but not all terminal taxa) is identified prior to analysis by PAUP*4.0b8 (Swofford, 2001). Three of the included terminals were alternatives for representing the *Ichthyornis dispar* and *Iaceornis marshi* material and were swapped iteratively in separate analyses (see below).

CHARACTERS

Of the 202 characters, 35 are ordered (i.e., 1, 8, 11, 23, 31, 52, 54, 61, 62, 66, 68, 69, 71, 76, 80, 105, 113, 117, 139, 142, 149,

153, 159, 175, 177, 180, 182, 185, 188, 192, 193, 194, 195, 196, 202). These ordered characters are also indicated in appendix 1. Following Slowinski (1993), multistate characters were ordered when there was evidence of a morphocline (sensu Slowinski, 1993; e.g., Metacarpal I, extensor process: [0] absent, no anteroproximally projected muscular process; [1] present, tip of process just surpassed the distal articular facet for phalanx 1 in anterior extent; [2] tip of process conspicuously surpassed the articular facet by approximately half the width of the facet itself, producing a pronounced knob; [3] tip of process conspicuously surpassed the articular facet by approximately the width of the facet itself, producing a pronounced knob).

Of the characters identified as parsimony uninformative, constant characters were included because they have previously been proposed to be synapomorphic of an avialan subclade. After being included and evaluated for the sampled taxa, these characters were either found to be ancestral for at least the included part of Theropoda (i.e., 130, from Chiappe, 1991), or all included taxa are missing data for the character or have the same state (i.e., 45, from Stidham, 1998, and 129, from Chiappe, 1991; the derived state for 129 is only possibly [see Sanz et al., 1995] present in one included taxon, which was scored "0/1").

Of the characters identified by PAUP*4.0b8 (Swofford, 2001) as autapomorphic, some are only known in a single terminal of the ingroup, while others are present only in Dromaeosauridae and have been found in previous analysis to be synapomorphic of *Archaeopteryx lithographica* + the ingroup when the resultant tree is rooted with Dromaeosauridae. In the latter case, these "0"s are assessed as autapomorphies of Dromaeosauridae for the purposes of calculating the number of parsimony-informative characters.

It has been argued that parsimony-uninformative characters (in particular autapomorphies) should be excluded, as they inflate certain tree statistics such as the consistency index (Carpenter, 1988). However, the consistency index has come to be considered more appropriate as a measure of the amount of homoplasy exhibited by included charac-

ters (e.g., Sanderson and Donoghue, 1996) rather than as a metric of support for a particular phylogenetic hypothesis; homoplastic characters can be highly informative of phylogenetic relationship (e.g., Sanderson and Donoghue, 1996; Källersjö et al., 1999). Thus, inflation of the consistency index does not constitute so much an exaggeration of a support measure as an underestimation of the homoplasy exhibited by component characters. Furthermore, characters identified as parsimony uninformative are easily excluded in PAUP*4.0b8 (Swofford, 2001) to recalculate tree statistics. It is also worth noting that in phylogenetic analyses of molecular sequence data, many included characters may be parsimony uninformative, but they are, nonetheless, analyzed.

Including the greatest number of characters possible, on the other hand, brings the most information to bear on the study of morphological change across a clade, summarizes additional characters diagnosing terminal taxa, and provides a more accurate picture of branch lengths. Branch lengths may be of interest as potential indicators of the amount of morphological divergence and the number of missing taxa. Branch lengths would also be important for analyses employing maximum likelihood as an estimator with currently available methodologies (Lewis, 2001). One outcome of excluding autapomorphic characters may be partially responsible for the putative phenomenon of "character exhaustion" (Wagner, 2000) in morphological data sets, by reducing terminal branch lengths in many cases to 0.

Too often, characters proposed by other authors to be informative of avialan interrelationships, once discovered to be constant or autapomorphic for a taxon other than that which was the focus of the analysis have been excluded from analysis and undiscussed. The current analysis is also incomplete, as presumably many more uninformative characters could be included.

TAXON SAMPLING

A species-exemplar approach was taken to represent Aves (sensu Gauthier, 1986; Gauthier and de Queiroz, 2001) in which five species were used. These five include basal

parts of lineages considered to represent its two basal-most divergences: Palaeognathae Pycraft, 1900, and Neognathae Pycraft, 1900, based on previous hypotheses of the relationships within these clades (e.g., Holman, 1964; Cracraft, 1974; Sibley and Ahlquist, 1990; Livezey, 1997a, 1997b). Strong morphological and molecular evidence supports Palaeognathae and Neognathae as the two basal divergences of the crown clade and Galloanserae Sibley et al., 1988 as one of the two basal-most divergences within Neognathae (e.g., Gauthier, 1986; Cracraft, 1988; Sibley and Ahlquist, 1990; Groth and Barrowclough, 1999; van Tuinen et al., 2000; Cracraft and Clarke, 2001). Four exemplars sample basal and derived parts of Galloanserae.

The sister taxon of Galloanserae, Neoaves Sibley et al., 1988, was not sampled; there remains no resolution of the basal relationships within this clade (e.g., Cracraft and Clarke, 2001). Without a hypothesis of in-group relationships, a supraspecific Neoaves terminal representing most of 9000+ species of birds (del Hoyo et al., 1992–1999) would be scored as polymorphic for many, if not most, characters variable for Aves and any exemplars elected would only sample the smallest part of this highly diverse clade. It was decided that whatever exemplars were elected could not with any confidence be deemed to appropriately bracket the ancestral condition. Unfortunately, because of the absence of a Neoavian terminal(s), the states ancestral to Aves may be inaccurately represented in the current analysis for some characters. This issue is further discussed in the Conclusion.

The five species-exemplars for crown clade Aves include *Crypturellus undulatus* (YPM 11564), one of the forest-dwelling tinamous that have been placed as basal within Tinamidae (S. Bertelli, personal commun.), which was used as the exemplar for Palaeognathae Pycraft, 1900. Of Neognathae Pycraft, 1900, *Chauna torquata* (YPM 6046, AMNH-3616) and *Anas platyrhynchos* (YPM 2230, YPM 14369, YPM 14344, AMNH-5847) were used to represent Anseriformes Fürbringer, 1888; *Crax pauxi* (YPM 2104) and *Gallus gallus* (YPM 2106, YPM 6705) were used to represent Galliformes

Garrod, 1873. The included anseriforms and galliforms were chosen to sample both basal divergences (i.e., *Crypturellus*, *Chauna*, and *Crax*) and deeply nested taxa (i.e., *Anas* and *Gallus*) from within these clades based on previous phylogenetic hypotheses (e.g., Holman, 1964; Cracraft, 1974; Sibley and Ahlquist, 1990; Livezey, 1997a, 1997b).

Supraspecific OTUs were used for “*Lithornis*” and the outgroup terminal “Dromaeosauridae”. These two terminals were scored from species considered to comprise them (see Materials and Methods). Both Dromaeosauridae Matthew and Brown, 1922, and *Lithornis* Owen, 1840, have been supported as monophyletic (e.g., Houde, 1988; Gauthier, 1986; although see Norell et al., 2001). In both of these cases, these supraspecific terminals were used to compensate for missing data and because of the availability of multiple specimens. If there was variation among the material studied (see Material and Methods), this was represented as polymorphism (e.g., as “0 and 1”). While not an ideal approach (e.g., Prendini, 2001; Simmons, 2001), the alternative course of evaluating and including as distinct terminals an array of dromaeosaurids and lithornithids was outside the scope of the present analysis. The specimens that formed the basis for the scorings of the two terminals just discussed are indicated below.

The terminal “*Lithornis*” (Owen, 1840) is scored from study of *Lithornis plebius* (USNM-336534, AMNH-21902), *Lithornis promiscuus* (USNM-336535, USNM-424072, AMNH-21903), *Lithornis celetius* (USNM 290601, USNM-290554, USNM 336200, YPM-PU-23485, YPM-PU-23484, YPM-PU-23483, YPM-PU-16961), and supplemented by the description of this material provided by Houde (1988). The paraphyly of the “Lithornithidae” has been proposed (Houde, 1988). However, the “Lithornithidae” included *Paracathartes* and *Pseudocrypturus*, as well as *Lithornis*; the monophyly of *Lithornis* itself has not been disputed. *Paracathartes* and *Pseudocrypturus* material was not scored for the current analysis.

The *Ichthyornis dispar* terminal was scored from all YPM material assessed to be part of that species in the current analysis (see Part I; listed in table 1), as well as from

SMM 2305 and BMNH A905 (see Taxonomic Revision). Two other terminals were employed in a single analysis (see *Ichthyornis dispar* in Results below) to investigate the placement of *Ichthyornis dispar* including and excluding YPM 1732: (1) *Ichthyornis dispar* as known from the holotype and all referred specimens, exclusive of YPM 1732, and (2) *Ichthyornis dispar* as known from YPM 1732 alone. YPM 1732 is considered part of *Ichthyornis dispar* (see Part I) as many morphologies of the femur, tibiotarsus, and sacrum can be compared directly to the *Ichthyornis dispar* holotype. The comparison indicates they are morphologically identical except with regard to the number of sacral vertebrae, which differs. YPM 1732 was used in the scoring of the *Ichthyornis dispar* composite terminal in all but this one analysis.

In addition to the *Ichthyornis dispar* terminal, the other morphologically distinct Late Cretaceous Niobrara Chalk specimens previously considered part of *Ichthyornis* and *Apatornis* (Marsh, 1880) were evaluated: *Ichthyornis (Guildavis) tener* (Marsh, 1880; new clade, Part I) was scored from the holotype, YPM 1760; *Ichthyornis (Austinornis) lentus* Marsh, 1877b (Marsh, 1880; new clade, Part I) was scored from the holotype, YPM 1796; *Apatornis celer* Marsh, 1873a, 1873b, was scored from the holotype, YPM 1451; *Iaceornis marshi* (new clade, new species; Part I) was scored from the holotype specimen, YPM 1734 (which was previously referred to *Apatornis celer*; Marsh, 1880), and from the illustration of the pelvis in *Odontornithes* (Marsh, 1880), as this element is currently missing (Clarke, 2000a; Part I). To explore support for the placement of the *Iaceornis marshii* holotype specimen (YPM 1734) excluding the unverifiable characters scored from the depiction of the missing pelvis in *Odontornithes* (Marsh, 1880), the terminal “*Iaceornis-sacrum*” was swapped in (see Results, below).

Other taxa were included to sample basal Avialae. *Hesperornis regalis* was scored primarily from study of the holotype (YPM 1200) and referred YPM specimens (1206, 1207, 1476), as well as from the description of that taxon in Marsh (1880), Witmer and Martin (1987), Bühler et al. (1988), and Wit-

mer (1990). *Baptornis advenus* was scored primarily from Martin and Tate (1976), although the holotype of that taxon (YPM 1465) was also consulted. *Apsaravis ukhaana* (Norell and Clarke, 2001) was scored from the holotype specimen, IGM 100/1017. *Patagopteryx deferrariisi* was scored from MACN-N-03 (holotype), MACN-N-10, MACN-N-11, and MACN-N-14, as well as from Chiappe (1996). *Vorona berivotrensis* was scored from Forster et al. (1996). *Confuciusornis sanctus* was scored based on the study of numerous IVPP and GMV specimens referenced in Hou (1997) and Chiappe et al. (1999).

Enantiornithes (Walker, 1981; converted clade name, Sereno, 1998) was represented by taxa referred to it by previous authors (e.g., Zhou et al., 1992; Chiappe and Calvo, 1994; Sanz et al., 1995; Chiappe, 1995a, 1996; Norell and Clarke, 2001). The four taxa included as exemplars were chosen because (1) they are known from relatively complete and/or multiple specimens, (2) they sample Early and Late Cretaceous identified parts of the clade, and (3) they are geographically and morphologically diverse.

The four exemplar taxa chosen are the following: *Cathayornis yandica* (Zhou et al., 1992) was scored from the holotype specimen (IVPP V-9769A, B) and two referred specimens (IVPP 10890, IVPP 10916). *Concornis lacustris* (Sanz and Buscalioni, 1992; Sanz et al., 1995) was scored from the holotype specimen, LH 2814, and from Sanz et al. (1995). *Neuquenornis volans* was scored from Chiappe and Calvo (1994). *Gobipteryx minuta* was scored from Elzanowski (1974, 1977, 1995), Chiappe et al. (2001), and from the description of the holotype of "*Nanantius valifanovi*" (Kurochkin, 1996), considered to be a junior synonym of *Gobipteryx minuta* (Chiappe et al., 2001). Unfortunately, because relationships among Enantiornithes remain largely unresolved (e.g., Padian and Chiappe, 1998; Chiappe, 2001, 2002), sampling taxa closest to the base of the clade, as recommended in exemplar choice (e.g., Pren dini, 2001 and references therein) was problematic.

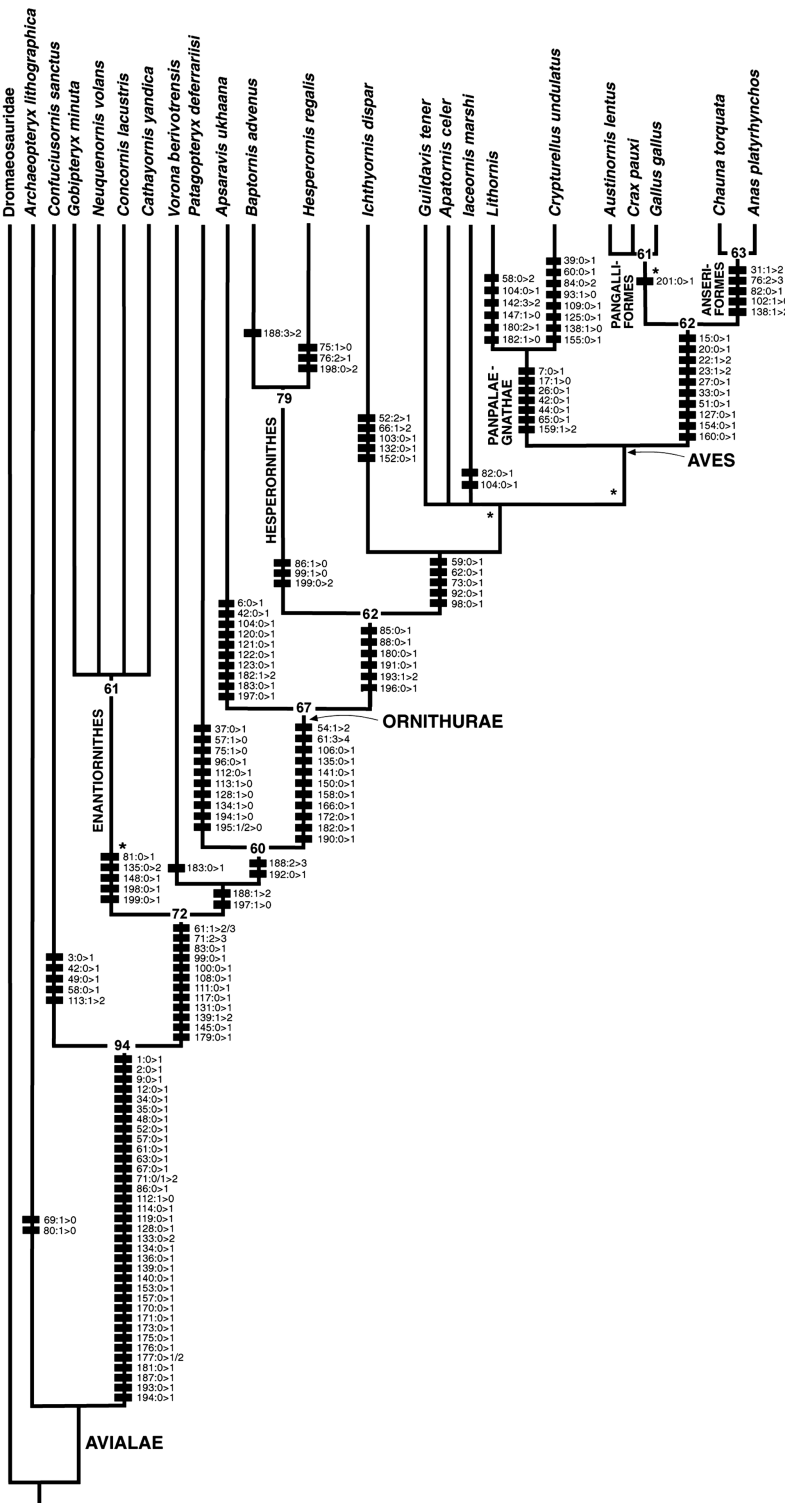
Outgroup terminal *Archaeopteryx lithographica* (Meyer, 1861) was scored based on study of the London and Berlin specimens

and from descriptions provided in Wellnhofer (1974, 1993), Ostrom (1976), Witmer (1990), and Elzanowski and Wellnhofer (1996). Dromaeosauridae (Matthew and Brown, 1922; sensu Gauthier, 1986) was represented primarily by studied specimens of *Deinonychus antirrhopus*, *Dromaeosaurus albertensis*, and *Velociraptor mongoliensis* cited in Ostrom (1969), Norell et al. (1992), Colbert and Russell (1969), Currie (1995), and Norell and Makovicky (1997, 1999), as well as from descriptions provided in those publications.

The data set was analyzed in PAUP*4.0b8 (PPC; Swofford, 2001). All searches were branch and bound. Several settings were altered from the PAUP defaults in all searches: "amb-" in the "Parsimony Settings" menu was selected so that internal branches with a minimum length of 0 were collapsed to form a soft polytomy; by contrast, the PAUP* default is to collapse only internal branches with a maximum length of 0. Additionally, when interpreting entries with more than one state, ambiguity (e.g., "state 1 or 2") was distinguished from polymorphism (e.g., "states 1 and 2"). Bootstrap support values from 1000 replicates (10 random sequence additions per replicate) were computed with all the same settings as in the other branch and bound searches (see above). The bootstrap scores greater than 50% for the all analyses are reported at the internodes in figures 62–63.

RESULTS

Analysis of the 23 primary terminal taxa (i.e., excluding the alternate scoring of *Ichthyornis dispar* and *Iaceornis marshi*) produced two MPTs 396 steps in length including uninformative characters, and the tree statistics for these MPTs were CI: 0.67, RI: 0.81, and RC: 0.55 (fig. 62). Excluding uninformative characters, tree length was 383 steps, and the tree statistics were CI: 0.66, RI: 0.81, and RC: 0.54. The two trees differ only in enantiornithine interrelationships. The other polytomies are present in both of the shortest trees and are present because internal nodes with a minimum branch length of 0 were collapsed (see Analyses referenced above). If these 0-length internal branches



were allowed, more MPTs would have resulted.

Austinornis lentus is placed within Aves in a trichotomy with the included galliforms. *Ichthyornis dispar* is placed as more closely related to Aves than is *Hesperornithes* (fig. 62). *Iaceornis marshi*, *Apatornis celer*, and *Guildavis tener* are placed in a polytomy as more closely related to Aves than *Ichthyornis dispar*. These three taxa share no parts and/or scored characters in common; thus, no more can be said about their relative phylogenetic positions. *Iaceornis marshi* does not include a sacrum, and no single character could be scored in both of the partial sacrum holotypes of *Apatornis celer* and *Guildavis tener*. Comments on the support for the relationships of these taxa in the current analysis and on the previously proposed hypotheses of their relationships are given below.

ICHTHYORNIS DISPAR MARSH, 1872b

Marsh (1873b, 1880) considered *Ichthyornis* to be most closely related to *Hesperornithes*, forming part of his lineage of “toothed birds”, the “Odontornithes”. Subsequently, most authors placed *Ichthyornis* as more closely related to Aves than to *Hesperornithes* (e.g., Martin, 1983; Cracraft, 1986, 1988; Chiappe, 1995a, 2001). Others, however, have suggested that *Hesperornis* is more closely related to Aves than *Ichthyornis* (e.g., Elzanowski, 1995) or have followed Marsh (1873b, 1880) in considering *Hesperornithes* + *Ichthyornis* to be a clade (e.g., Elzanowski et al., 2000).

Five unambiguous synapomorphies (59, 62, 73, 92, 98) place *Ichthyornis dispar*, from the Late Cretaceous Niobrara Chalk of Kansas (Marsh, 1872b, 1880), as more closely related to Aves than *Hesperornithes* (fig. 62). These five synapomorphies supporting *Ichthyornis dispar* + Aves relative to *Hesperornithes* include: (59:1) thoracic vertebrae with

ossified connective tissue bridging between transverse processes, (62:1) midseries sacral vertebrae with dorsally projected transverse processes that give the appearance of being absent, (73:1) a pneumatic foramen on midline on dorsal surface of the sternum, (92:1) the presence of a lateral process of the coracoid (discussed in Martin, 1987), and (98:1) lack of a depression at the medial opening of n. supracoracoideus foramen (evaluated to have a different distribution by previous authors; e.g., Chiappe and Calvo, 1994). Of these five synapomorphies, three (i.e., 59, 62, 73) are newly brought to bear on basal avialan relationships.

Five unambiguous autapomorphies of *Ichthyornis dispar* are identified in the phylogenetic analysis (i.e., 52, 66, 103, 132, 152; each is discussed in the Taxonomic Revision of Part I): (52:0) amphicoelous cervical vertebrae, (66:1) proximal free caudal vertebrae with well-developed prezygapophyses clasping the dorsal surface of preceding vertebra, (103:1) unprojected acromion on scapula, (132:1) subequal posterior and distal dimensions of the distal articular surface of ulna, and (152:1) internal index process present. Of these characters, two (i.e., 66, 152) are also seen in Charadriiformes and some other neoavians but not in the included Aves. This distribution, and the absence of these morphologies in other basal avialans, is consistent with the hypothesis (e.g., Marsh, 1880) that several derived aspects of the anatomy of *Ichthyornis dispar* may be convergent on charadriiform morphologies. It does not, however, support these structures, or “shorebird” morphologies generally, as ancestral to Aves, as has often been argued (Feduccia, 1995, 1999).

As noted in Part I, YPM 1732 is morphologically consistent with the holotype and all other referred specimens of *Ichthyornis dispar* except with regard to the number of an-

←

Fig. 62. The strict consensus cladogram of two MPTs from analysis of the core taxa (L: 396; CI: 0.67; RI: 0.81; RC: 0.55). Excluding uninformative characters, tree length was 383 steps and the tree statistics were CI: 0.66, RI: 0.81, and RC: 0.54. * indicates optimization of unambiguous support for clade effected by presence of a soft polytomy; listed characters (those unambiguously optimized in both most parsimonious topologies) represent minimum support for the node. See figures 63–65 for unambiguous synapomorphies of Aves relative to nearest outgroups.

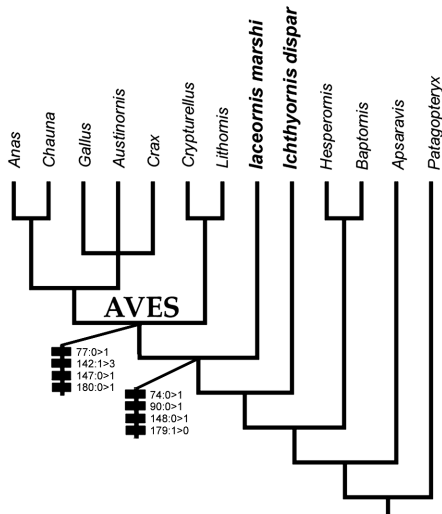


Fig. 63. The relationships of new taxon *Iaceornis marshi* and character support in the primary analysis (fig. 62).

kylosed sacral vertebrae. YPM 1732 is considered on this basis to be a part of *Ichthyornis dispar*, as discussed in Part I. Based on this referral, the *Ichthyornis dispar* terminal is scored as polymorphic for total sacral number. Although total sacral number is often considered intraspecifically conservative, such variation has been described. For example, similar to the case of YPM 1732, a large individual of *Velociraptor mongoliensis* has been described (Norell and Makovicky, 1999) with an additional partially “sacralized” caudal. Additionally, intraspecific variation in sacral number was also early noted in breeds of the domestic pigeon, *Columba livia* (Darwin, 1859).

To investigate the effect of considering YPM 1732 (comprised of thoracic and caudal vertebrae, sacrum, and partial hind limb) not *Ichthyornis dispar*, the “*Ichthyornis dispar*” terminal was removed and replaced with two terminals. One of the swapped-in terminals represented *Ichthyornis dispar* as scored from holotype and referred material with the exception of YPM 1732; the second swapped-in terminal was scored only from YPM 1732.

Analysis resulted in 2MPTs (L: 395; CI: 0.67; RI: 0.81; RC 0.55) with the “*Ichthyornis*-YPM 1732” terminal placed in the

same position as the *Ichthyornis dispar* terminal in the primary analysis. YPM 1732 was placed closer to Aves than to *Ichthyornis dispar* but outside of the polytomy including *Iaceornis marshi*, *Apatornis celer* and *Guildavis tener*. The strict consensus of these two trees, which differ only in enantiornithine interrelationships, is shown in figure 63. The rest of the resultant topology is the same as in the primary analysis.

YPM 1732 is placed closer to Aves than the rest of the YPM material by a derived character state for character 61 (number of ankylosed sacral vertebrae). It is not surprising that it is not supported as most closely related to the other *Ichthyornis dispar* material because, as discussed in Part I, eight of nine identified autapomorphies of *Ichthyornis dispar* are not preserved in YPM 1732 and one character optimized as an autapomorphy of *Ichthyornis dispar* is only preserved in YPM 1732. This character (66:1; proximal free caudal vertebrae with well-developed prezygapophyses clasping the dorsal surface of preceding vertebra) cannot be scored for any *Ichthyornis dispar* specimens other than YPM 1732. Thus, when YPM 1732 is included as a separate terminal, it is optimized as an autapomorphy of YPM 1732.

The unambiguous synapomorphies uniting “*Ichthyornis*-YPM 1732” + Aves are the same as those for the “*Ichthyornis dispar*” terminal (which includes YPM 1732) + Aves, with one exception; character 59:1 (thoracic vertebrae with ossified connective tissue bridging between transverse processes) is ambiguously optimized. Character 59 is not preserved in the holotype or any referred specimens of *Ichthyornis dispar* besides YPM 1732. And it was this material that was scored for the “*Ichthyornis dispar*-YPM 1732” terminal.

AUSTINORNIS MARSH, 1877b AND PANGALLIFORMES (NEW PROVISIONAL CLADE NAME)

Austinornis lentus (*Ichthyornis lentus* of Marsh, 1877b) is a distal tarsometatarsus from the Late Cretaceous (?) of Texas (Marsh, 1877b, 1880). Marsh (1880) considered *Ichthyornis* (*Austinornis*) *lentus* to be part of *Ichthyornis*, a hypothesis that is not supported by the present analysis. Martin and

Stewart (1982) suggested that *Ichthyornis* (*Austinornis*) *lentus* was not part of *Ichthyornis* but offered no hypothesis of its phylogenetic position. Shufeldt (1915) commented that *Ichthyornis* (*Austinornis*) *lentus* had galliform affinities.

Because no stratigraphic and little locality information for the *Austinornis lentus* holotype is available, its putative Cretaceous age should be further investigated (see Part I). The present analysis is the first phylogenetic analysis to include this taxon.

Austinornis lentus is placed in a trichotomy with the included galliforms (fig. 62). It is supported as part of at least the galliform stem clade by one unambiguous synapomorphy, (201:1) asymmetrical development of the edges of the trochlea of metatarsal III (Mayr, 2000). The phylogenetic position of *Austinornis lentus* is, otherwise, supported by the presence of a hierarchical set of unambiguous synapomorphies as part of *Vorona berivotrensis* + Aves, *Patagopteryx deferrariisi* + Aves, Ornithurae, *Hesperornis regalis* + Aves. It is missing data, however, for unambiguous synapomorphies of Aves itself and for Neognathae. Thus, its placement as part of the avian crown clade (indeed, as a neognath and a galliform; fig. 62) is supported by a single character.

The galliform stem clade, that *Austinornis* is supported as a part of, is named in Part I. If new data on the distribution of Cretaceous outcrops in Collin County, Texas and archival data support the provenance of *Austinornis lentus* from these outcrops, then there is evidence of the Pangalliformes in the Cretaceous, but not necessarily for the presence of any part of the crown, Galliformes.

IACEORNIS MARSHI, NEW CLADE, NEW SPECIES

The holotype specimen of *Iaceornis marshi*, a partial postcranial skeleton (YPM 1734) from the Late Cretaceous Niobrara Chalk of Kansas, was previously referred to *Apatornis celer* (Marsh, 1880; see Part I). The previous proposed relationships of YPM 1734, as discussed as *Apatornis celer*, are discussed under the “*Apatornis celer*” heading below. It is also possible that YPM 1734 elements have been mistakenly scored as *Ichthyornis* in other analyses; there is evi-

dence of parts of YPM 1734 figured in *Odontornithes* (Marsh, 1880) being mistaken for parts of *Ichthyornis* (e.g., Sereno and Rao, 1992; see Part I).

Iaceornis marshi is placed outside of Aves (fig. 62) by four unambiguous synapomorphies (fig. 63): (74:1) pneumatic foramina between sternal rib articulations on sternum; (90:1) pneumatization of the coracoid (lost in *Anas platyrhynchos*); (148:1) metacarpal III surpasses II in distal extent (intermediate in *Lithornis*); (179:1) distal condyles of the tibiotarsus equal in anterior extent (optimized as ancestral to Avialae, but as lost in basal avialae). It is possible that increased pneumatization of the skeleton is a single character (as discussed in Gauthier, 1986) and that characters 74 and 90 are linked. However, each of several other characters concerning pneumatization has distinct distributions. For example, the presence of pneumatic foramen on the dorsal midline of the sternum is a synapomorphy of *Ichthyornis* + Aves; additionally, the kinds of postcranial and cranial pneumatization vary significantly across Avialae (Witmer, 1990; Britt et al., 1998). Because distinct air sacs pneumatize the skeleton, different pneumatic features may be expected to have different points of origin related to the evolution of these distinct air sacs (Britt et al., 1998).

Iaceornis marshi shared four derived characters with Aves relative to *Ichthyornis dispar* (fig. 63). These characters are the following: (77:1) paired intermuscular ridges on sternum, (142:2/3) anterior extent of extensor process surpasses articulation of phalanx I:1 by more than half the width of this articulation, (147:1) intermetacarpal space terminates distal to the end of metacarpal I, (180:2) ossified supratendinal bridge on tibiotarsus. An ossified supratendinal bridge has traditionally been considered to diagnose Aves relative to its nearest fossil outgroup (e.g., historically *Ichthyornis*; Cracraft, 1986). Its presence in *Iaceornis marshi* indicates that it is synapomorphic of a more inclusive clade that must include outgroups of Aves. Thus, its presence in other fragmentary tibiotarsi from the Cretaceous should no longer be the basis for necessarily referring these elements to Aves. The absence of a supratendinal bridge in *Lithornis* (placed within Panpa-

laeognathae: Aves) is unambiguously optimized as a derived loss of this feature, which could be discovered to unite this taxon with ratites within which this feature is also lost (e.g., Cracraft, 1979).

Iaceornis marshi is diagnosed by two local autapomorphies: (82:1) a strongly tapering, or pointed, omal tip of the furcula, and (104:1) a hooked scapular acromion process. Character 82 is also seen within Aves (e.g., in Anseriformes) and character 104 is also seen in more basal taxa such as *Apsaravis ukhaana* (Norell and Clarke, 2001) and in *Lithornis* (in which the acromium is otherwise markedly different from that of *Iaceornis marshi* and *Apsaravis ukhaana*).

The characters optimized as autapomorphies of *Iaceornis marshi* and supporting its placement as the sister taxon of Aves, are the same whether or not the illustration of the sacrum in *Odontornithes* (Marsh, 1880) is included as part of the *Iaceornis marshi* holotype.

GUILDAVIS TENER (NEW CLADE NAME; CONVERTED SPECIES NAME [MARSH, 1880])

Ichthyornis (*Guildavis*) *tener* (Marsh, 1880) is an extremely fragmentary sacral series from the Late Cretaceous Niobrara Chalk Formation of Kansas. *Guildavis tener* was placed in an unresolved polytomy with *Apatornis celer* and *Iaceornis marshi* as the sister taxon of Aves. Marsh (1880) considered *Ichthyornis* (*Guildavis*) *tener* more closely related to *Ichthyornis dispar* than to Aves. However, it is here placed as more closely related to Aves than to *Ichthyornis dispar* (figs. 62, 64). This position is supported by one character: (161:1) the ilium overlaps at least one set of ribs, as indicated by a parapophyses visible on the first sacral. It is placed outside Aves by one character. A flat, round anterior articular surface of the centrum of the first sacral indicates that the thoracic series was not entirely heterocoelous (55:0) in *Guildavis tener*. Thus, a completely heterocoelous thoracic series (55:1) is a synapomorphy of Aves relative to *Guildavis tener*.

APATORNIS CELER MARSH, 1873b

The holotype and only known specimen of *Apatornis celer* (Marsh, 1873b, 1880; see

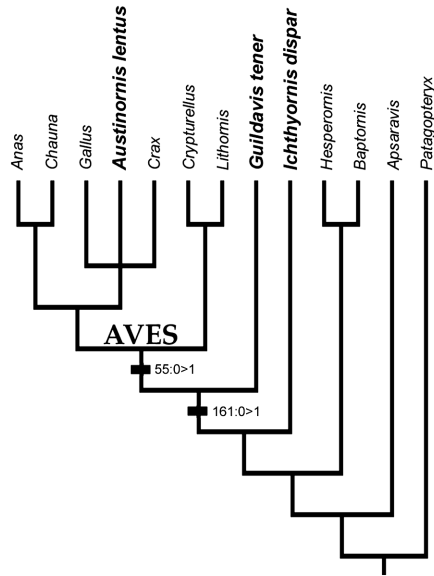


Fig. 64. The relationships of *Austinornis lentus* and *Guildavis tener* and the character support in the primary analysis (fig. 62).

Part I: Taxonomic Revision) consists of an incomplete sacrum (lacking pelvic bones) from the Late Cretaceous Niobrara Chalk Formation of Kansas. *Apatornis celer* has no scored characters in common with *Iaceornis marshi* (pelvic elements but not the sacral series) or *Guildavis tener*. Although *Guildavis tener* and *Apatornis celer* are known exclusively from fragmentary sacra, they cannot be evaluated for any of the same included characters and effectively share no “parts” in common. (As discussed in Part I, new specimens are needed to determine whether one or more of these names may refer to the same taxon).

Apatornis celer was considered by Marsh (1873b, 1880) to be most closely related to *Ichthyornis dispar* as part of his “Ichthyornithes”, and by Brodkorb (1967) as part of his “Ichthyornithiformes”. Howard (1955) suggested that *Apatornis celer* was most closely related to a fossil taxon that was considered to have anseriform “affinities” and that is now placed as part of Aves (*Presbyornithidae*; e.g., Livezey, 1997b). This conclusion was based in large part, if not entirely, on study of the single referred specimen, here designated the holotype of *Iaceornis*.

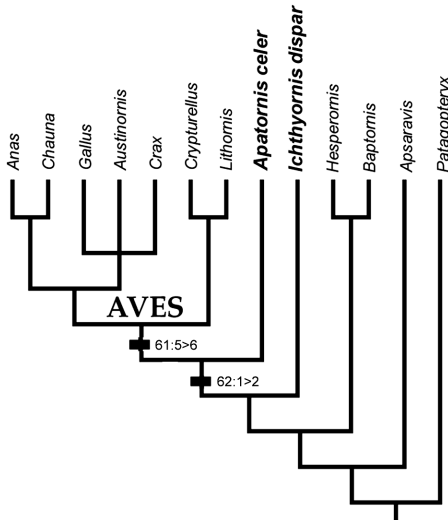


Fig. 65. The relationships of *Apatornis celer* and its character support in the primary analysis (fig. 62).

nis marshi (YPM 1734). Similarly, when Martin (1987) remarked that the elongate acromion seen in “*Apatornis celer*” and *Ambiortus dementjevi* suggested that they may be closely related, he must have been referring to YPM 1734 (holotype of *Iaceornis marshi*) as the *Apatornis celer* holotype does not include a scapula.

The systematic position of *Apatornis celer*, as more closely related to Aves than to *Ichthyornis dispar* (fig. 65) is supported by one character (62:2) the presence of four or more midseries sacral vertebrae with diminutive and dorsally projected transverse processes. *Ichthyornis dispar* has but three such vertebrae. Its placement outside of Aves is also supported by one character, a synapomorphy of Aves relative to *Apatornis celer* (fig. 65). This synapomorphy of Aves absent in *Apatornis celer* is the presence of 15 or more fused sacral vertebrae (61:3). The morphology of the incomplete anterior sacral vertebrae of *Apatornis celer* evidences the presence of only from 11 to possibly 13 fused sacral vertebrae (see Part I).

DISCUSSION

Of the specimens previously referred to *Ichthyornis* (Marsh, 1880), *Ichthyornis* (*Austinornis*) *lentus* is placed in Pangalliformes

as part of Aves; *Ichthyornis* (*Guildavis*) *tener* is placed as more closely related to Aves than to *Ichthyornis dispar*; and YPM 1732, while supported as part of *Ichthyornis dispar*, has one character that would place it closer to the crown than to *Ichthyornis dispar*. YPM 1732, however, is referred to *Ichthyornis dispar* (see Part I), making that species polymorphic for number of sacral vertebrae.

While most of the material Marsh (1880) referred to *Ichthyornis* is determined to be part of that taxon (see Part I), the placement of *Ichthyornis* (*Austinornis*) *lentus* and *Ichthyornis* (*Guildavis*) *tener* suggests that, indeed, “*Ichthyornis*” (sensu Marsh, 1880) was a chimera formed of distinct taxa more closely related to the avian crown clade than to *Ichthyornis dispar*, as suggested by Elzarnowski (1995) and Clarke (2000a). Furthermore, *Apatornis celer* and the single specimen previously referred to that taxon and named as the holotype of *Iaceornis marshi* (Part I) both have synapomorphies of the crown clade relative to *Ichthyornis dispar*. Thus, rather than “*Apatornis celer*” sensu Marsh (1880) being more closely related to *Ichthyornis dispar* (Marsh, 1873a, 1880), both the holotype and the sole previously referred specimen are more closely related to Aves. The specimen named as the holotype of *Iaceornis marshi* shares no overlapping elements with that of *Apatornis celer* and is the sister taxon of Aves. *Apatornis celer*, scored from the holotype (and only known) specimen, is more closely related to Aves than to *Ichthyornis dispar* (contra Marsh, 1873a, 1873b). Thus, Marsh’s groups “*Ichthyornithes*” (Marsh, 1873b) and “*Odontotormae*” (Marsh, 1876) are both polyphyletic.

Austinornis lentus is placed as part of the avian crown clade (contra Marsh, 1880; pro Shufeldt, 1915). *Guildavis tener*, *Apatornis celer*, and *Iaceornis marshi*, while all parts of *Ichthyornis dispar* + Aves, are currently unambiguously placed outside of the crown clade. Of these taxa, the holotype of *Iaceornis marshi* (YPM 1734) was thought to have affinities with *Presbyornis* (e.g., Howard, 1955), which has been placed as part of the crown clade lineage, Anseriformes (Ericson, 1997; Livezey, 1997b).

Guildavis tener, and *Apatornis celer* are placed outside of Aves. However, they ex-

hibit morphologies seen within Neoaves but not among the included avian exemplars. It may be that inclusion of neoavian taxa would change the currently unambiguous placement of these taxa. For example, many Neoaves have less than 15 though more than 11 sacral vertebrae (Verheyen, 1960), as is the case in *Apatornis celer* and one specimen referred to *Ichthyornis dispar* (YPM 1732; Part I). Likewise, an apneumatic humerus is present in Neoaves, as well as in *Ichthyornis* and all more basal avialans.

Most of the above characters are present in Charadriiformes among neoavian lineages, and it is no coincidence that this neoavian lineage is one of the two most often considered present in the Cretaceous (e.g., Olson, 1985; Olson and Parris, 1987; Feduccia, 1995, 1999). Unlike the characters and conclusions just remarked, *Ichthyornis dispar* has characters also seen in Charadriiformes and other Neoaves that are not present in any other avialans (e.g., an internal indicus process and well-developed reverse articulations of the anterior caudal vertebrae). In this case, *Ichthyornis dispar* was often assumed convergent on Charadriiformes (e.g., Martin, 1983; Olson, 1985) in these features, rather than as part of that lineage (although see, e.g., Brodkorb, 1967). One observation hazarded here is that only extremely fragmentary taxa placed within Aves have remained identified as such. Essentially all better preserved Mesozoic avialans, even if they were originally placed within the crown clade, were shortly thereafter removed (see further discussion and comparisons with the Mesozoic record of crown clade placentals or marsupials, e.g., from Novacek et al., 1998, in Clarke and Chiappe, 2001, and the conclusion to this document).

The expectation that apomorphies at each of the levels of interest (e.g., of Aves and its subclades and not of Archosauria) should be evenly distributed to every part of the skeleton such that sufficient and congruent signal will be preserved in small samples of characters from distinct parts of the skeleton appears to conflict with one of the most frequent observations of the pattern of morphological evolution. The broadly noted phenomenon of "mosaic evolution" (de Beer, 1954), or heterogeneity across the skeleton in degree and kind of morphological change, would appear to predict that with some frequency small samples of characters will not preserve characters at the hierarchical level of interest. For example, *Austinornis lentus* with 99% missing data (see appendix 2) could be placed, as its character distributions are congruent and one character is currently optimized, as an apomorphy of an avian subclade.

That single elements and their inherent small samples of characters pose several analytical issues is apparent from the analyses here and from previous work (Clarke, 2000b; Clarke and Chiappe, 2001). First, in phylogenetic analyses of multiple fragmentary specimens, taxa cannot be placed if they have no scored characters in common. There is, for example, no algorithm that can resolve the relationship of an isolated sternum to an isolated femur, if characters in both cases place them in the same least inclusive clade. Strong support for a part of Aves in the Mesozoic requires: (1) locality, horizon, and collection data sufficient to establish the Mesozoic age of the fossil and (2) hierarchical signal-supporting placement within a series of internested clades (e.g., Ornithurae, Aves, Neognathae, Pangalliformes).

COMMENTS AND CONCLUSIONS

The present study of *Ichthyornis dispar* brought to light elements and structures not previously described that allow a new view (fig. 66) of this historically important taxon. The results of the anatomical reevaluation undertaken here are consistent with *Ichthyornis dispar* being a small bird with powerful wings, an elongate rostrum, and small legs and feet as previously described (Marsh, 1880: 120–121; fig. 66). Whether *Ichthyornis dispar* had aquatic habits similar to that of a tern (e.g., *Sterna maxima*, Marsh, 1880: 120–121) will never be known with certainty, although several with morphological characters also seen in Charadriiformes are optimized as apomorphies of *Ichthyornis dispar* (Parts I and II).

Restudy revealed issues of misidentification and misrepresentation of elements in the landmark description of *Ichthyornis* in *Odonornithes* (Marsh, 1880) as well as its significant contributions. The original referral of specimens to the distinct species of *Ichthyornis* in Marsh (1880) appears to have been arbitrary in many cases. However, most of the material used in the original description of *Ichthyornis* (Marsh, 1880) is assessed to represent individuals more closely related to the holotype of *Ichthyornis dispar* (YPM 1450) than to Aves. Many exceedingly fragmentary specimens do not preserve one or more of the four apomorphies used in the definition of the apomorphy-based (de Queiroz and Gauthier, 1992) clade name “*Ichthyornis*”. Thus, these are established as part of *Ichthyornis* as a result of their referral to the species *Ichthyornis dispar*. Referral to *Ichthyornis dispar* was based on both apomorphy and morphological correspondence. Decisions concerning the number of taxa represented by the *Ichthyornis* material is contingent upon the assumptions made about its physiology and growth, amount of anagenetic change across approximately 15 million years, and upon interpretations of the taxonomic significance of morphological differences.

Material incorporated in the YPM “*Ichthyornis victor*” panel mount formed a chimera of at least 14 specimens including parts of the *Iaceornis marshi* holotype and parts of

a specimen that, although referred to *Ichthyornis dispar* (Part I), is morphologically distinct from the holotype of that taxon (YPM 1450; Clarke, 1999, 2000a). Furthermore, the named species previously considered part of *Ichthyornis* by Marsh (1880) do not form a clade. Two of these species, *Guildavis tener* and *Austinornis lentus*, are placed as more closely related to Aves than to *Ichthyornis dispar*, and the latter as part of Aves. Additionally, “*Ichthyornithes*” (sensu Marsh, 1873b) is polyphyletic: *Apatornis celer*, which was placed with *Ichthyornis* in this taxon (Marsh, 1873b), is discovered more closely related to Aves than to *Ichthyornis dispar*. The results of these analyses have implications for inferences concerning the timing and pattern of avian diversification in addition to allowing revised diagnoses of these taxa.

The timing and pattern of the earliest divergences of the avian crown clade are currently much debated (Chiappe, 1995a; Feduccia, 1995; Hedges et al., 1996; Cooper and Penny, 1997; Bleiweiss, 1998; Dingus and Rowe, 1998; Stidham, 1998; Dyke and Mayr, 1999; Marshall, 1999). The structure of the debate is paralleled in arguments over the origin of crown placentals and marsupials (Novacek et al., 1998; Foote et al., 1999; Rich et al., 1999). In both cases, arguments from molecular data invoking a clocklike model of sequence evolution have placed most if not all of the divergences between extant lineages in the early Cretaceous (≈ 120 mya; Hedges et al., 1996; Cooper and Penny, 1997; Rambaut and Bromham, 1998; Mindell et al., 1999; Waddell et al., 1999; although see Groth and Barrowclough, 1999).

Estimates dating avian divergences using cladogram topology and fossil data (even with gap analyses to extend “error bars” on these estimates to account for potential preservational biases) place them in the early Tertiary, with the possibility of several basal divergences occurring in the latest Cretaceous (Bleiweiss, 1998; Novacek et al., 1998; Marshall, 1999).

Because of the substantial difference between these two estimates (≈ 60 million years) in the case of both mammals and birds, explanations with increased generality

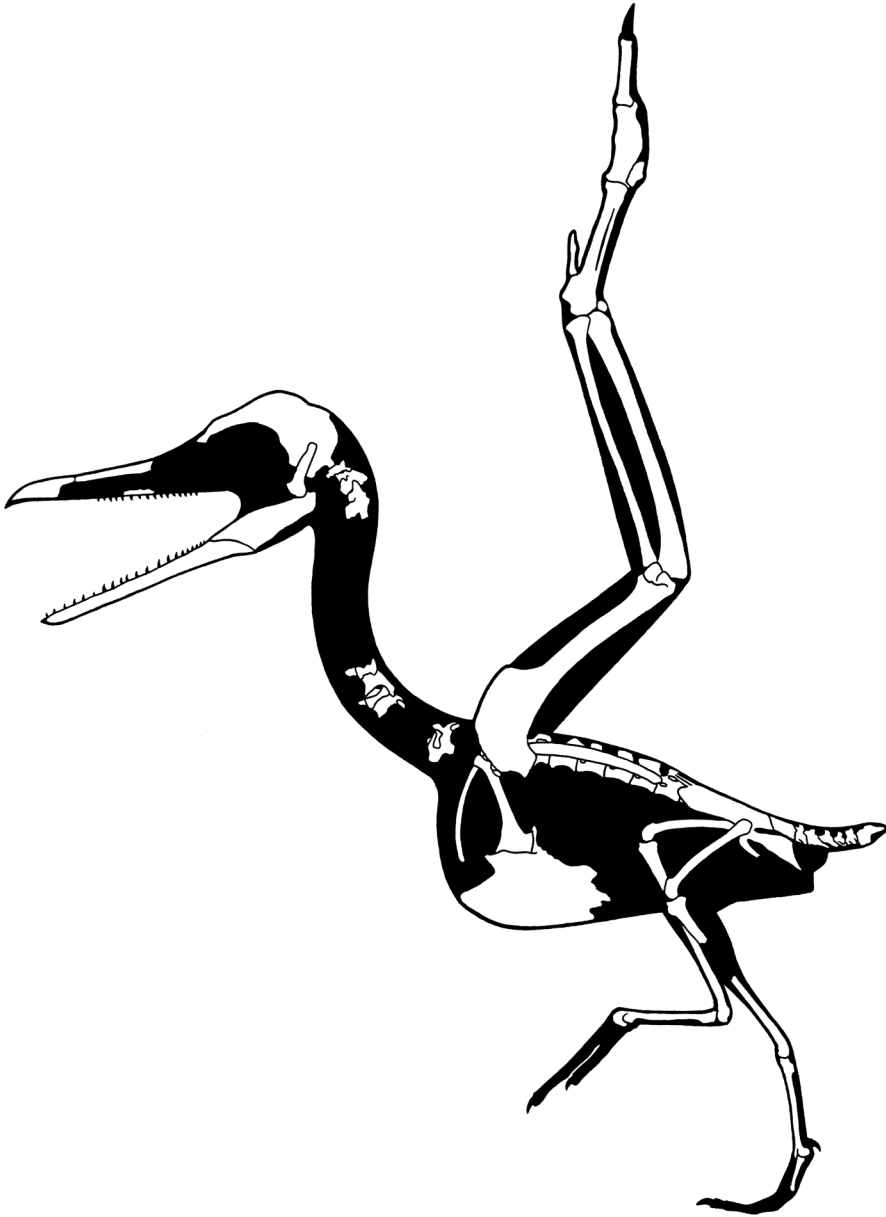


Fig. 66. Two silhouette reconstructions of *Ichthyornis dispar* by Gregory Paul showing the relative proportions of the elements discussed in the anatomical description. Elements known from *Ichthyornis* and discussed in the present monograph are in white.

have been sought. Increasingly, the debate has become one with implications for whether sequence data, morphological data, and fossils are treated as equal forms of evidence (e.g., whether fossil data is “strong” enough to challenge the molecular results and, in-

deed, the molecular clock). On the other hand, the significant difference in estimates has also been considered an issue not simply of methodology but of biology. For example, it has been used as evidence for the disassociation between sequence divergence and

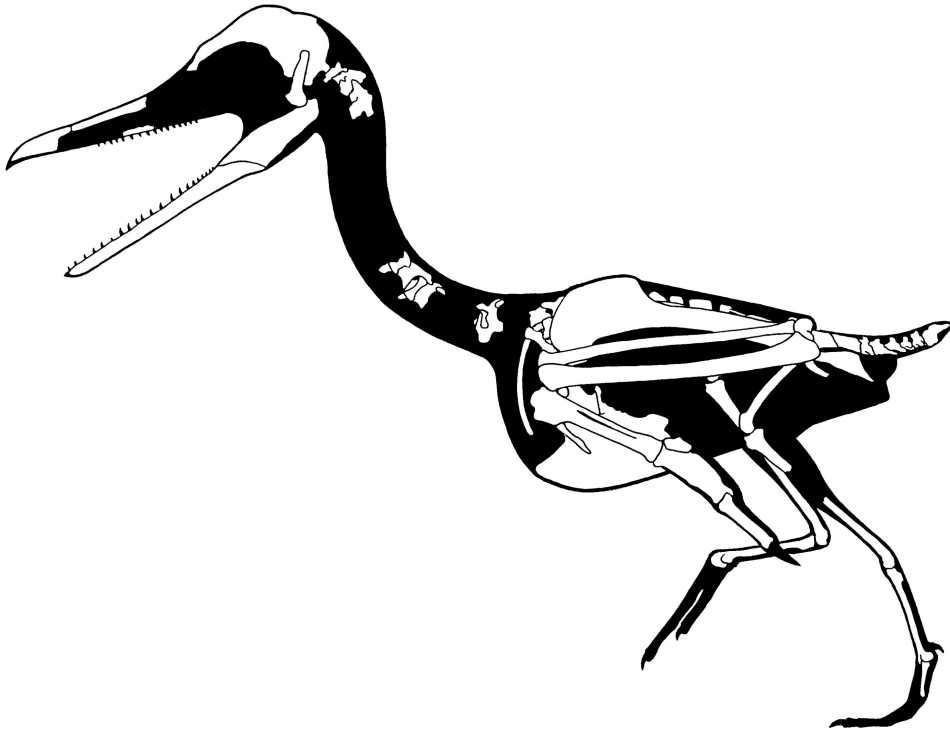


Fig. 66. Continued.

morphological evolution (Cooper and Fortey, 1998).

At issue is the relationship between environmental change, “mass extinction”, and the origin of major clades. It has been suggested that these differences in estimates may be indicative of a larger macroevolutionary phenomenon (e.g., “cryptodiversification”; Cooper and Fortey, 1998). This proposed phenomenon of diversifying lineages early in their phylogenetic history, or during their “fuse” period prior to explosive diversification, involves numerous cladogenic events (with molecular sequence divergence) but with morphological stasis as a result of ecological constraints (Cooper and Fortey, 1998).

Others have suggested a taphonomic explanation for the discrepancy (e.g., van Tuinen et al., 2000), postulating that crown clade birds are diversifying on land and thus go unsampled in the marine environments from which most Cretaceous ornithurines are known (e.g., van Tuinen et al., 2000). Similarly, this concept involves a biological ex-

planation for the data from the fossil record; parts of the crown clade are ecologically restricted, not to the shorelines, in this case, but to the continental interiors.

Biogeographical restriction has also been proposed (e.g., Cracraft, 2001). Crown clade lineages are supposed to be Gondwanan in origin and diversifying in the undersampled Southern hemisphere. Those places that have actually been sampled are proposed to be, by chance, havens of primitive lineages. This hypothesis invokes the historical contingency of the location of the origin of the first crown clade avians as an explanation for their having eluded discovery. Still other hypotheses suggest that the lack or scarcity of identifiable parts of crown clade lineages in the Cretaceous is consistent with the notion of low standing diversity in these lineages (Marshall, 1999), but do not necessarily require that these lineages be ecologically or morphologically constrained.

Whether considered an epistemological or biological issue, the outcome of this debate affects not only our view of the origin of

Aves, but hypotheses that sketch commonalities between the timing of the origins of Aves and Mammalia and take these proposed patterns as the basis for statements of further scope (e.g., macroevolutionary in nature).

As a result of phylogenetic analyses, there is new evidence to bring to bear on the origin of Aves and on previous interpretations of the Mesozoic ornithurine fossil record. The placement of *Iaceornis marshi* and *Apatornis celer* and of *Guildavis tener* as the sister taxon of Aves, its age (late Santonian or early Campanian) and projection of ghost lineages (Norell, 1992) require that the avian stem lineage must also be present in the Late Cretaceous. This inference, however, does not bear on the presence of the avian crown clade in the Cretaceous (Dingus and Rowe, 1998).

Austinornis lentus is the first Mesozoic taxon to be placed as part of Aves in a cladistic analysis. If the Mesozoic age and phylogenetic placement of *Austinornis lentus* are reliable then there is evidence (through inference from cladogram topology) of the three basal-most divergences of the crown clade in the Late Cretaceous. This result is consistent with those tentatively offered by Groth and Barrowclough (1999), who estimated one palaeognath and two neognath lineages to be present in the Late Cretaceous. At the same time, the best hypothesis of *Austinornis lentus*' phylogenetic position is as, minimally, part of Pangalliformes. This placement does not require that extant lineages of Galliformes were present in the Cretaceous, only that the galliform stem lineage was present. However, again, given that *Austinornis lentus* is a fragment of a tarsometatarsus supported by one character as part of Pangalliformes and has none of the unambiguously optimized autapomorphies of Aves or Neognathae, it is not a solid foundation for proposing generalities about the timing and pattern of the origin of Aves. It would be ill advised to use a specimen with little or no available locality or collection data and one synapomorphy of Aves to "set the clock" for analyses of crown clade divergences.

By contrast, the placement as part of Palaeognathae of *Lithornis*, a taxon known from abundant specimens from the late Pa-

leocene and Eocene (Houde, 1988), is strong support for the presence of at least the palaeognath stem lineage in the early Tertiary. The presence of a part of Palaeognathae (sensu Gauthier and de Queiroz, 2001) at this time has already been suggested based on a late Paleocene/early Eocene? rheiform (Alvarenga, 1983). More recently, earlier evidence of *Lithornis*, in the latest Cretaceous or earliest Paleocene, has been described (Parris, 2000).

The results of the current analyses do not support proposed morphological and ecological constraints on the avian stem lineage or a biogeographical explanation for the lack or paucity of crown clade avians in the Cretaceous. If there was a restriction of ornithurines to a shorebird habitus (Cooper and Foret, 1998; Feduccia, 1995, 1996; van Tuinen et al., 2000), an "ecological bottleneck" (Feduccia, 1995), "shorebird" morphologies and ecologies should be able to be bracketed phylogenetically as basal to the crown clade, as well as seen in its nearest outgroups (Clarke and Norell, 2001). However, molecular and morphological evidence places "land birds" at the base of Aves (e.g., tinamous, ratites, galliforms, anseriforms; Sibley and Ahlquist, 1990; Groth and Barrowclough, 1999; van Tuinen et al., 2000; Cracraft and Clarke, 2001). Charadriiformes, the extant lineage referred to as "shorebirds", are placed as derived within Aves as neoavian neognaths (Cracraft, 1986; Sibley and Ahlquist, 1990; Livezey, 1997b; Groth and Barrowclough, 1999; van Tuinen et al., 2000; Cracraft and Clarke, 2001). Thus, bracketing the ecologies and morphologies basal to the crown clade and incorporating possible evidence of the ecologies of the nearest avian outgroups, there is no support for an ecological bottleneck (Clarke and Norell, 2001).

Convergence of Charadriiformes on morphologies seen in *Ichthyornis dispar* and other Mesozoic ornithurines does not make these "shorebird" morphologies indicative of the ecologies outside of Aves any more than flightless ratites share the ecology of "flightless" nonavian theropod dinosaurs. Rather, the results of this analysis suggest that inferences from isolated elements used to place Charadriiformes in the Cretaceous should be restudied, as their morphologies

(but not necessarily their ecology) may be primitive for a part of Avialae such as Ornithurae or *Ichthyornis* + Aves. Indeed, of the two “graculavids”, parts of a “form family” (Olson and Parris, 1987) supposed to be primitive “shorebird-like” ancestors of extant birds (Feduccia, 1996), the one that had a resolved placement fell outside of the crown clade (Clarke, 2002).

Only further taxon sampling outside of Aves, better material, and further resolution of crown clade relationships will enable a more robust assessment of the timing and pattern of early avian diversification. The immediate fossil outgroups of Aves must play an important role in estimating these relationships using morphological data. Unfortunately, all Mesozoic ornithurines described from more than a single bone were included in the phylogenetic analyses, and the total count for such specimens is 13. This is an unlucky number for attempting to ask broad-scale evolutionary questions. It is hoped, then, that the study of the morphology and systematic position of *Ichthyornis dispar*, as well as of the relationships of other basal ornithurines, may be useful in our continued attempts to unravel what is one of the least understood parts of the history of Dinosauria: the origin of Aves.

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APPENDIX 1

The following is a list of the 202 morphological characters used in the phylogenetic analyses (from Clarke, 2002). All characters are unordered except the following 36: 1, 8, 11, 23, 31, 52, 54, 61, 62, 66, 68, 69, 71, 76, 80, 105, 113, 117, 139, 142, 149, 153, 159, 175, 177, 180, 182, 185, 188, 192, 193, 194, 195, 196, and 202. “P.V.” before characters 89 and 97 indicates these are the “previous versions” of characters 88 and 98, respectively, which were excluded from the primary analysis (see text).

1. Premaxillae: (0) unfused in adults; (1) fused anteriorly in adults, posterior nasal [frontal] processes not fused to each other; (2) frontal processes completely fused as well as anterior premaxillae (Ordered).
2. Premaxillary teeth: (0) present, (1) absent.
3. Maxillary teeth: (0) present, (1) absent.
4. Dentary teeth: (0) present, (1) absent.
5. Tooth crown serration: (0) present, (1) vestigial or absent.
6. Dentaries: (0) joined proximally by ligaments, (1) joined by bone.
7. Mandibular symphysis, two strong grooves forming an anteriorly opening “v” in ventral view: (0) absent, (1) present.
8. Facial margin: (0) primarily formed by the maxilla, with the maxillary process of the premaxilla restricted to the anterior tip; (1) maxillary process of the premaxilla extending half of facial margin; (2) maxillary process of the premaxilla extending more than half of facial margin (Ordered).
9. Nasal [frontal] process of premaxilla: (0) short, (1) long, closely approaching frontal.
10. Nasal process of maxilla, dorsal ramus: (0) prominent, exposed medially and laterally; (1) absent or reduced to slight medial and no lateral exposure.
11. Nasal process of maxilla, participation of ventral ramus in anterior margin of antorbital fenestra in lateral view: (0) present, extensive; (1) small dorsal projection of the maxilla participates in the anterior margin of the antorbital fenestra, descending process of the nasals contacts premaxilla to exclude maxilla from nasal margin; (2) no dorsal projection of maxilla participates in anterior margin of the antorbital fenestra. (Ordered).
12. Osseous external naris: (0) considerably smaller than the antorbital fenestra, (1) larger.
13. Ectopterygoid: (0) present, (1) absent.
14. Articulation between vomer and pterygoid: (0) present, well-developed; (1) reduced, narrow process of pterygoid passes dorsally over palatine to contact vomer; (2) absent, pterygoid and vomer do not contact.
15. Palatine and pterygoid: (0) long, antero-posteriorly overlapping, contact, (1) short, primarily dorsoventral, contact.
16. Palatine contacts: (0) maxilla only, (1) premaxilla and maxillae.
17. Vomer contact with premaxilla: (0) present, (1) absent.
18. Coronoid ossification: (0) present, (1) absent.
19. Projecting basisphenoid articulation with pterygoid: (0) present, (1) absent.
20. Basispterygoid processes: (0) long, (1) short (articulation with pterygoid subequal to or longer than amount projected from the basisphenoid rostrum).
21. Basisphenoid–pterygoid articulations: (0) located basal on basisphenoid, (1) located markedly anterior on basisphenoid (parasphenoid rostrum) such that the articulations are subadjacent on the narrow rostrum (the “rostrompterygoid articulation” of Weber, 1993).
22. Basisphenoid/pterygoid articulation, orientation of contact: (0) anteroventral, (1) mediolateral, (2) entirely dorsoventral.
23. Pterygoid, articular surface for basisphenoid: (0) concave “socket”, or short groove enclosed by dorsal and ventral flanges; (1) flat to convex; (2) flat to convex facet, stalked, variably projected. (Ordered).
24. Pterygoid, kinked: (0) present, surface for basisphenoid articulation at high angle to axis of palatal process of pterygoid; (1)

- absent, articulation in line with axis of pterygoid.
25. Osseous interorbital septum (mesethmoid): (0) absent, (1) present.
 26. Osseous interorbital septum (mesethmoid): (0) restricted to posterior or another just surpassing premaxillae/frontal contact in rostral extent does not surpass posterior edge of external nares in rostral extent; (1) extending rostral to posterior extent of frontal processes of premaxillae and rostral to posterior edge of external nares.
 27. Eustachian tubes: (0) paired and lateral; (1) paired, close to cranial midline; (2) paired and adjacent on midline or single anterior opening.
 28. Eustachian tubes ossified: (0) absent, (1) present.
 29. Squamosal, ventral or "zygomatic" process: (0) variably elongate, dorsally enclosing otic process of the quadrate and extending anteroventrally along shaft of this bone, dorsal head of quadrate not visible in lateral view; (1) short, head of quadrate exposed in lateral view.
 30. Orbital process of quadrate, pterygoid articulation: (0) pterygoid broadly overlapping medial surface of orbital process (i.e., "pterygoid ramus"); (1) restricted to anteromedial edge of process.
 31. Quadrate, orbital process: (0) pterygoid articulates with anteriormost tip; (1) pterygoid articulation does not reach tip; (2) pterygoid articulation with no extent up orbital process, restricted to quadrate corpus. (Ordered).
 32. Quadrate/pterygoid contact: (0) as a facet, variably with slight anteromedial projection cradling base; (1) condylar, with a well-projected tubercle on the quadrate.
 33. Quadrate, well-developed tubercle on anterior surface of dorsal process: (0) absent, (1) present.
 34. Quadrate, quadratojugal articulation: (0) overlapping, (1) peg and socket articulation.
 35. Quadrate, dorsal process, articulation: (0) with squamosal only, (1) with squamosal and prootic.
 36. Quadrate, dorsal process, development of intercotylar incisure between prootic and squamosal cotylae: (0) absent, articular surfaces not differentiated; (1) two distinct articular facets, incisure not developed; (2) incisure present, "double headed".
 37. Quadrate, mandibular articulation: (0) bi-
 - condylar articulation with mandible; (1) tricondylar articulation, additional posterior condyle or broad surface.
 38. Quadrate, pneumaticity: (0) absent, (1) present.
 39. Quadrate, cluster of pneumatic foramina on posterior surface of the tip of dorsal process: (0) absent, (1) present.
 40. Quadrate, pneumatization, large, single pneumatic foramen: (0) absent, (1) posteromedial surface of corpus.
 41. Articular pneumaticity: (0) absent, (1) present.
 42. Dentary strongly forked posteriorly: (0) unforked or with a weakly developed dorsal ramus; (1) strongly forked with the dorsal and ventral rami approximately equal in posterior extent.
 43. Splenial, anterior extent: (0) splenial terminates well posterior to mandibular symphysis; (1) extending to mandibular symphysis, though noncontacting; (2) extending to proximal tip of mandible, contacting on midline.
 44. Mandibular symphysis, anteroposteriorly extensive, flat to convex, dorsal-facing surface developed: (0) absent, concave, (1) flat surface developed.
 45. Mandibular symphysis, symphyseal foramina: (0) absent, (1) present.
 46. Mandibular symphysis, symphyseal foramen/foramina: (0) single, (1) paired.
 47. Mandibular symphysis, symphyseal foramen/foramina: (0) opening on posterior edge of symphysis, (1) opening on dorsal surface of symphysis.
 48. Meckel's groove: (0) not completely covered by splenial, deep and conspicuous medially; (1) covered by splenial, not exposed medially.
 49. Anterior external mandibular fenestra: (0) absent, (1) present.
 50. Jugal/postorbital contact: (0) present, (1) absent.
 51. Frontal/parietal suture in adult: (0) open, (1) fused.
 52. Cervical vertebrae: (0) variably dorsoventrally compressed, amphicoelous ("biconcave": flat to concave articular surfaces); (1) heterocoelous anterior (i.e., mediolaterally concave, dorsoventrally convex) and posterior (i.e., mediolaterally convex, dorsoventrally concave) surfaces.
 53. Thoracic vertebrae (with ribs articulating with the sternum), one or more with prominent hypapophyses: (0) absent, (1) present. (This character does not address the presence of hypapophyses on transi-

- tional vertebrae, or “cervicothoracics”, that do not have associated ribs that articulate with the sternum, e.g., Gauthier, 1986; Chiappe, 1996. By contrast, in Aves, well-developed hypapophyses are developed well into the thoracic series, on vertebrae with ribs articulating with the sternum.)
54. Thoracic vertebrae, count: (0) 12 or more, (1) 11, (2) 10 or fewer. (Ordered).
 55. Thoracic vertebrae: (0) at least part of series with subround, central articular surfaces (e.g., amphicoelous/opisthocoelous) that lack the dorsoventral compression seen in heterocoelous vertebrae; (1) series completely heterocoelous.
 56. Thoracic vertebrae, parapophyses: (0) rostral to transverse processes, (1) directly ventral to transverse processes (close to midpoint of vertebrae).
 57. Thoracic vertebrae, centra, length, and midpoint width: (0) approximately equal in length and midpoint width, (1) length markedly greater than midpoint width.
 58. Thoracic vertebrae, lateral surfaces of centra: (0) flat to slightly depressed; (1) deep, emarginate fossae; (2) central ovoid foramina.
 59. Thoracic vertebrae with ossified connective tissue bridging transverse processes: (0) absent, (1) present.
 60. Notarium: (0) absent, (1) present.
 61. Sacral vertebrae, number ankylosed: (0) less than 7, (1) 7, (2) 8, (3) 9, (4) 10, (5) 11 to 14, (6) 15 or more. (Ordered).
 62. Sacral vertebrae, series of short vertebrae, with dorsally directed transverse processes just anterior to the acetabulum: (0) absent; (1) present, three such vertebrae; (2) present, four such vertebrae. (Ordered).
 63. Free caudal vertebrae, number: (0) more than 8, (1) 8 or less.
 64. Caudal vertebrae, chevrons, fusion on at least one anterior caudal: (0) present, (1) absent.
 65. Free caudals; length of transverse processes: (0) subequal to width of centrum or slightly longer, (1) significantly shorter than centrum width.
 66. Anterior free caudal vertebrae: (0) elongate pre/postzygapophyses; (1) pre- and postzygapophyses short and variably non-contacting; (2) prezygapophyses clasping the posterior surface of neural arch of preceding vertebra, postzygapophyses negligible. (Ordered).
 67. Distal caudals: (0) unfused, (1) fused.
 68. Fused distal caudals, morphology: (0) long, more than length of four free caudal vertebrae; (1) medium, equal to or less than the length of four free caudal vertebrae; (2) short, less than two caudal vertebrae in length. (Ordered).
 69. Ossified uncinat processes: (0) absent, (1) present and unfused to ribs, (2) fused to ribs. (Ordered).
 70. Gastralia: (0) present, (1) absent.
 71. Ossified sternal plates: (0) unfused; (1) fused, flat; (2) fused, with slightly raised midline ridge; (3) fused with projected keel. (Ordered).
 72. Sternum, keel or midline ridge: (0) restricted to posterior half of sternum, (1) approaches anterior limit of sternum.
 73. Sternum, dorsal surface, pneumatic foramen (or foramina): (0) absent, (1) present.
 74. Sternum, pneumatic foramina in the depressions (loculi costalis; Baumel and Witmer, 1993) between rib articulations (processi articularis sternocostalis; Baumel and Witmer, 1993): (0) absent, (1) present.
 75. Sternum, coracoidal sulci spacing on anterior edge: (0) widely separated medio-laterally, (1) adjacent, (2) crossed on midline.
 76. Sternum, number of processes for articulation with the sternal ribs: (0) three, (1) four, (2) five, (3) six, (4) seven or more. (Ordered).
 77. Sternum: raised, paired intermuscular ridges (linea intermuscularis; Baumel and Witmer, 1993) parallel to sternal midline: (0) absent, (1) present.
 78. Clavicles: (0) fused, (1) unfused.
 79. Interclavicular angle (clavicles elongate): (0) equal to or greater than 90 degrees, (1) less than 90 degrees.
 80. Furcula, hypocleideum: (0) absent, (1) a tubercle, (2) an elongate process. (Ordered).
 81. Furcula, lateral excavation: (0) absent, (1) present.
 82. Furcula, dorsal (omal) tip: (0) flat or blunt tip, (1) with a pronounced posteriorly pointed tip.
 83. Scapula and coracoid: (0) fused, (1) unfused.
 84. Scapula and coracoid articulation: (0) pit-shaped scapular cotyla developed on the coracoid, and coracoidal tubercle developed on the scapula (“ball and socket” articulation); (1) scapular articular surface of coracoid convex; (2) flat.
 85. Coracoid, procoracoid process: (0) absent, (1) present.

86. Coracoid: (0) height approximately equal mediolateral dimension; (1) height more than twice width, coracoid "strutlike".
87. Coracoid, lateral margin: (0) straight to slightly concave, (1) convex.
88. Coracoid, dorsal surface (= posterior surface of basal maniraptoran theropods): (0) strongly concave, (1) flat to convex.
89. P. V. Coracoid, dorsal surface, deep fossa: (0) absent, (1) present.
90. Coracoid, pneumatized: (0) absent, (1) present.
91. Coracoid, pneumatic foramen: (0) proximal, (1) distal.
92. Coracoid, lateral process: (0) absent, (1) present.
93. Coracoid, ventral surface, lateral intermuscular line or ridge: (0) absent, (1) present.
94. Coracoid, glenoid facet: (0) dorsal to acrocoracoid process/ "biceps tubercle", (1) ventral to acrocoracoid process.
95. Coracoid, acrocoracoid process: (0) straight, (1) hooked medially.
96. Coracoid, n. supracoracoideus passes through coracoid: (0) present, (1) absent.
97. P. V. Coracoid, passage of foramen n. supracoracoideus opening into a medial groove: (0) absent, (1) present.
98. Coracoid, medial surface, area of the foramen n. supracoracoideus (when developed): (0) strongly depressed, (1) flat to convex.
99. Angle between coracoid and scapula at glenoid: (0) more than 90 degrees, (1) 90 degrees or less.
100. Scapula: (0) posterior tip wider than proximal dorsoventral shaft width, (1) tapering distally.
101. Scapula: (0) straight, (1) dorsoventrally curved.
102. Scapula, length: (0) shorter than humerus, (1) as long as or longer than the humerus.
103. Scapula, acromion process: (0) projected farther anteriorly than the articular surface for coracoid (facies articularis coracoidea; Baumel and Witmer, 1993), (1) projected less anteriorly than the articular surface for coracoid.
104. Scapula, acromion process: (0) straight, (1) laterally hooked tip.
105. Humerus and ulna, length: (0) humerus longer than ulna, (1) ulna and humerus approximately the same length, (2) ulna significantly longer than humerus. (Ordered).
106. Humerus, proximal end, head in anterior or posterior view: (0) straplike, articular surface flat, no proximal midline convexity; (1) head domed proximally.
107. Humerus, proximal end, proximal projection: (0) dorsal edge projected farthest, (1) midline projected farthest.
108. Humerus, ventral tubercle and capital incisure: (0) absent, (1) present.
109. Humerus, capital incisure: (0) an open groove, (1) closed by tubercle associated with a muscle insertion just distal to humeral head.
110. Humerus, anterior surface, well-developed fossa on midline making proximal articular surface appear "V"-shaped in proximal view: (0) absent, (1) present.
111. Humerus, "transverse groove": (0) absent, (1) present, developed as a discrete, depressed scar on the proximal surface of the bicipital crest or as a slight transverse groove.
112. Humerus, deltopectoral crest: (0) projected dorsally (in line with the long axis of humeral head), (1) projected anteriorly.
113. Humerus, deltopectoral crest: (0) less than shaft width, (1) same width, (2) dorsoventral width greater than shaft width. (Ordered).
114. Humerus, deltopectoral crest, proximo-posterior surface: (0) flat to convex, (1) concave.
115. Humerus, bicipital crest, pit-shaped scar/fossa for muscular attachment on anterodistal, distal or posterodistal surface of crest: (0) absent, (1) present.
116. Humerus, bicipital crest, pit-shaped fossa for muscular attachment: (0) anterodistal on bicipital crest, (1) directly ventrodistal at tip of bicipital crest, (2) posterodistal, variably developed as a fossa.
117. Humerus, bicipital crest: (0) little or no anterior projection, (1) developed as an anterior projection relative to shaft surface in ventral view, (2) hypertrophied, rounded tumescence. (Ordered).
118. Humerus, proximal end, one or more pneumatic foramina: (0) absent, (1) present.
119. Humerus, distal condyles: (0) developed distally, (1) developed on anterior surface of humerus.
120. Humerus, long axis of dorsal condyle: (0) at low angle to humeral axis, proximodistally oriented, (1) at high angle to humeral axis, almost transversely oriented.
121. Humerus, distal condyles: (0) subround, bulbous; (1) weakly defined, "straplike".
122. Humerus, distal margin: (0) approximately perpendicular to long axis of humeral

- shaft, (1) ventrodistal margin projected significantly distal to dorsodistal margin, distal margin angling strongly ventrally (sometimes described as a well-projected flexor process).
123. Humerus, distal end, compressed antero-posteriorly and flared dorsoventrally: (0) absent, (1) present.
 124. Humerus, brachial fossa: (0) absent, (1) present, developed as a flat scar or as a scar-impressed fossa.
 125. Humerus, ventral condyle: (0) length of long axis of condyle less than the same measure of the dorsal condyle, (1) same or greater.
 126. Humerus, demarcation of muscle origins (e.g., m. extensor metacarpi radialis in Aves) on the dorsal edge of the distal humerus: (0) no indication of origin as a scar, a pit, or a tubercle, (1) indication as a pit-shaped scar or as a variably projected scar-bearing tubercle or facet.
 127. Humerus, distal end, posterior surface, groove for passage of m. scapulotriceps: (0) absent, (1) present.
 128. Humerus, m. humerotricipitalis groove: (0) absent, (1) present as a well-developed ventral depression contiguous with the olecranon fossa.
 129. Ulna, cotylae: (0) dorsoventrally adjacent, (1) widely separated by a deep groove.
 130. Ulna, dorsal cotyla convex: (0) absent, (1) present.
 131. Ulna, distal end, dorsal condyle, dorsal trochlear surface developed as a semilunate ridge: (0) absent, (1) present.
 132. Ulna, distal end, dorsal condyle, dorsal trochlear surface, extent along posterior margin: (0) less than transverse measure of dorsal trochlear surface, (1) approximately equal in extent.
 133. Ulna, bicipital scar: (0) absent, (1) developed as a slightly raised scar, (2) developed as a conspicuous tubercle.
 134. Ulna, brachial scar: (0) absent, (1) present.
 135. Radius, ventroposterior surface: (0) smooth, (1) with muscle impression along most of surface, (2) deep longitudinal groove.
 136. Ulnare: (0) absent, (1) present.
 137. Ulnare: (0) "heart-shaped", little differentiation into short dorsal and ventral rami, (1) "V"-shaped, well-developed dorsal and ventral rami.
 138. Ulnare, ventral ramus (crus longus, Baumel and Witmer, 1993): (0) shorter than dorsal ramus (crus brevis), (1) same length as dorsal ramus, (2) longer than dorsal ramus.
 139. Semilunate carpal and metacarpals: (0) no fusion, (1) incomplete proximal fusion, (2) complete proximal fusion, (3) complete proximal and distal fusion. (Ordered).
 140. Semilunate carpal, position relative to metacarpal I: (0) over entire proximal surface, (1) over less than half proximal surface.
 141. Metacarpal III, anteroposterior diameter as a percent of same dimension of metacarpal II: (0) approximately equal to or greater than 50%, (1) less than 50%.
 142. Metacarpal I, extensor process: (0) absent, no anteroproximally projected muscular process; (1) present, tip of extensor process just surpassed the distal articular facet for phalanx 1 in anterior extent; (2) tip of extensor process conspicuously surpasses articular facet by approximately half the width of facet, producing a pronounced knob; (3) tip of extensor process conspicuously surpasses articular facet by approximately the width of facet, producing a pronounced knob. (Ordered).
 143. Metacarpal I, anterior surface: (0) roughly hourglass-shaped proximally, at least moderately expanded anteroposteriorly, and constricted just before flare of articulation for phalanx 1, (1) anterior surface broadly convex.
 144. Metacarpal I, distal articulation with phalanx I: (0) ginglymoid, (1) shelf.
 145. Pisiform process: (0) absent, (1) present.
 146. Carpometacarpus, ventral surface, supratrochlear fossa deeply excavating proximal surface of pisiform process: (0) absent, (1) present.
 147. Intermetacarpal space (between metacarpals II and III), (0) reaches proximally as far as the distal end of metacarpal I, (1) terminates distal to end of metacarpal I.
 148. Carpometacarpus, distal end, metacarpals II and III, articular surfaces for digits: (0) metacarpal II subequal or surpasses metacarpal III in distal extent; (1) metacarpal III extends farther.
 149. Intermetacarpal process or tubercle: (0) absent, (1) present as scar, (2) present as tubercle or flange. (Ordered).
 150. Manual digit II, phalanx 1: (0) subcylindrical to subtriangular; (1) strongly dorsoventrally compressed, flat caudal surface.
 151. Manual digit II, phalanges: (0) length of phalanx II:1 less than or equal to that of II:2, (1) longer.

152. Manual digit II, phalanx 2, "internal index process" (Stegmann, 1978) on posterodistal edge: (0) absent, (1) present.
153. Ilium, ischium, pubis, proximal contact in adult: (0) unfused, (1) partial fusion (pubis not ankylosed), (2) completely fused. (Ordered).
154. Ilium/ischium, distal coossification to completely enclose the ilioischadic fenestra: (0) absent, (1) present.
155. Ischium: (0) forked (dorsal process present); (1) straight, no dorsal process.
156. Ischium, dorsal process: (0) does not contact ilium, (1) contacts ilium.
157. Ischium and pubis: (0) not subparallel, pubis directed nearly directly ventrally; (1) subparallel, pubis posteriorly directed.
158. Laterally projected process on ischiadic peduncle (antitrochanter): (0) directly posterior to acetabulum, (1) posterodorsal to acetabulum.
159. Preacetabular pectineal process (Baumel and Witmer, 1993): (0) absent, (1) present as a small flange, (2) present as a well-projected flange. (Ordered).
160. Preacetabular ilium: (0) approach on anterodorsal midline, open, or cartilaginous connection, (1) coossified, dorsal closure to form "iliosynsacral canals".
161. Preacetabular ilium extends anterior to first sacral vertebrae: (0) no free ribs overlapped, (1) one or more ribs overlapped.
162. Postacetabular ilium: (0) dorsoventrally oriented, (1) mediolaterally oriented.
163. Postacetabular ilium, ventral surface, renal fossa developed: (0) absent, (1) present.
164. Ilium, m. cuppedicus fossa as broad, mediolaterally oriented surface directly anteroventral to acetabulum: (0) present; (1) surface absent, insertion variably marked by a small entirely lateral fossa anterior to acetabulum.
165. Ischium, posterior demarcation of the obturator foramen: (0) absent; (1) present, developed as a small flange or raised scar contacting/fused with pubis and demarcating the obturator foramen distally.
166. Pubis: (0) suboval in cross section, (1) compressed mediolaterally.
167. Pubes, distal contact: (0) contacting, variably coossified into symphysis, (1) non-contacting.
168. Distal end of pubis: (0) expanded, flared; (1) straight, subequal, in proportion with rest of pubis.
169. Femur, fossa for insertion of lig. capitis femoris: (0) absent, (1) present.
170. Femur, posterior trochanter: (0) present, developed as a slightly projected tubercle or flange; (1) hypertrophied, "shelflike" conformation (in combination with development of the trochanteric shelf; see Hutchinson, 2001); (2) absent. (Ordered).
171. Femur, lesser and greater trochanters: (0) separated by a notch, (1) developed as a single trochanteric crest.
172. Femur, patellar groove: (0) absent, (1) present.
173. Femur: (0) ectocondylar tubercle and lateral condyle separated by deep notch, (1) ectocondylar tubercle and lateral condyle form single trochlear surface.
174. Femur, posterior projection of the lateral border of the distal end, continuous with lateral condyle: (0) absent, (1) present.
175. Laterally projected fibular trochlea: (0) absent; (1) present, developed as small notch; (2) a shelflike projection. (Ordered).
176. Femur, popliteal fossa: (0) a groove open distally and bounded medially and laterally by narrow condyles, (1) closed distally by expansion of both condyles (primarily the medial).
177. Calcaneum and astragalus: (0) unfused to each other or tibia in adult, (1) fused to each other, unfused to tibia, (2) completely fused to each other and tibia. (Ordered).
178. Tibia, cnemial crest(s): (0) lateral crest only, (1) lateral and anterior crests developed.
179. Tibia/tarsal formed condyles: (0) medial condyle projecting farther anteriorly than lateral, (1) equal in anterior projection.
180. Tibia/tarsal formed condyles, extensor canal: (0) absent, (1) an emarginate groove, (2) groove bridged by an ossified supratendinal bridge. (Ordered).
181. Tibia/tarsal formed condyles, tuberositas retinaculi extensoris (Baumel and Witmer, 1993) indicated by short medial ridge or tubercle proximal to the condyles close to the midline and a more proximal second ridge on the medial edge: (0) absent, (1) present.
182. Tibia/tarsal formed condyles, mediolateral widths: (0) medial condyle wider, (1) approximately equal, (2) lateral condyle wider. (Ordered).
183. Tibia/tarsal formed condyles: (0) gradual sloping medial constriction of condyles, (1) no medial tapering of either condyle.
184. Tibia/tarsal formed condyles, intercondylar groove: (0) mediolaterally broad, ap-

- proximately one-third width of anterior surface, (1) less than one-third width of total anterior surface.
185. Tibia, extension of articular surface for distal tarsals/tarsometatarsus: (0) no posterior extension of trochlear surface, or restricted to distal-most edge of posterior surface; (1) well-developed posterior extension, sulcus cartilaginis tibialis of Aves (Baumel and Witmer, 1993), distinct surface extending up the posterior surface of the tibiotarsus; (2) with well-developed, posteriorly projecting, medial and lateral crests. (Ordered).
 186. Tibia, distalmost mediolateral width: (0) wider than midpoint of shaft, giving distal profile a weakly developed triangular form, (1) approximately equal to shaft width, no distal expansion of whole shaft, although condyles may be variably splayed mediolaterally.
 187. Fibula: (0) reaches tarsal joint articulating into distinct socket formed between proximal tarsal and tibia, (1) reduced in length, does not reach tarsal joint.
 188. Distal tarsals and metatarsals, fusion: (0) distal tarsals fuse to metatarsals, (1) distal tarsals fuse to metatarsals and proximal metatarsals coossify, (2) distal tarsals fuse to metatarsals, and metatarsals fuse to each other proximally and distally, (3) extreme distal fusion, distal vascular foramen closed (Martin, 1983; Cracraft, 1986). (Ordered)
 189. Metatarsal V: (0) present, (1) absent.
 190. Metatarsal III: (0) proximally in plane with II and IV, (1) proximally displaced plantarly, relative to metatarsals II and IV.
 191. Tarsometatarsus, intercotyler eminence: (0) absent; (1) well developed, globose.
 192. Tarsometatarsus, projected surface on proximoposterior surface with/without grooves (associated with the passage of tendons of the pes flexors in Aves; hypotarsus): (0) absent, (1) developed as posterior projection with flat posterior surface, (2) projection, with distinct crests and/or grooves, (3) projection, at least one groove enclosed by bone. (Ordered).
 193. Tarsometatarsus, proximal vascular foramen(foramina): (0) absent, (1) one, between metatarsals III and IV, (2) two. (Ordered).
 194. Metatarsal I: (0) straight; (1) curved or distally deflected but not twisted, ventral surface convex; (2) deflected and twisted such that the ventromedial surface is concave proximal to trochlear surface for phalanx I. (Ordered).
 195. Metatarsal II tubercle (associated with the insertion of the tendon of the m. tibialis cranialis in Aves): (0) absent; (1) present, on approximately the center of the proximodorsal surface of metatarsal II; (2) present, developed on lateral surface of metatarsal II, at contact with metatarsal III or on lateral edge of metatarsal III. (Ordered).
 196. Metatarsal II, distal plantar surface, fossa for metatarsal I (fossa metatarsi I; Baumel and Witmer, 1993): (0) absent, (1) shallow notch, (2) conspicuous ovoid fossa. (Ordered).
 197. Metatarsal II, articular surface for first phalanx: (0) ginglymoid, (1) rounded.
 198. Metatarsals, relative mediolateral width: (0) metatarsal IV approximately the same width as metatarsals II and III, (1) metatarsal IV narrower than MII and MIII, (2) metatarsal IV greater in width than either metatarsal II or III.
 199. Metatarsals, comparative trochlear width: (0) II approximately the same size as III and/or IV, (1) II wider than III and/or IV, (2) II narrower than III and/or IV.
 200. Distal vascular foramen: (0) simple, with one exit, (1) forked, two exits (plantar and distal) between metatarsals III and IV.
 201. Metatarsal III, trochlea in plantar view, proximal extent of lateral and medial edges of trochlea: (0) absent, trochlear edges approximately equal in proximal extent; (1) present, lateral edge extends farther.
 202. Metatarsal II, distal extent of metatarsal II relative to metatarsal IV: (0) approximately equal in distal extent; (1) metatarsal II shorter than metatarsal IV, but reaching distally farther than base of metatarsal IV trochlea; (2) metatarsal II shorter than metatarsal IV, reaching distally only as far as base of metatarsal IV trochlea. (Ordered).

APPENDIX 2
DATA MATRIX: MODIFIED FROM CLARKE (2002)^a

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Anas platyrhynchos</i>	2	1	1	1	?	1	0	2	1	1	2	1	1	1	1	1	1
<i>Chauna torquata</i>	1	1	1	1	?	1	0	2	1	1	2	1	1	1/2	1	1	1
<i>Gallus gallus</i>	1	1	1	1	?	1	0	2	1	1	2	1	1	2	1	1	1
<i>Crax pauxi</i>	2	1	1	1	?	1	0	2	1	1	2	1	1	2	1	1	1
<i>Crypturellus undulatus</i>	2	1	1	1	?	1	1	2	1	1	2	1	1	0/1	0	1	0
<i>Lithornis</i>	2	1	1	1	?	1	1	2	1	1	2	1	1	0	0	?	0
<i>Iaceornis marshi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Iaceornis minus sacrum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	1/2	1	0	0	1	0	?	1	1	?	?	?	?	?	?	?	?
<i>Ichthyornis minus YPM 1732</i>	1/2	1	0	0	1	0	?	1	1	?	?	?	?	?	?	?	?
<i>YPM 1732</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	1	0	0	1	0	?	1	1	1	1	1	1	2	0	0	1
<i>Baptornis advenus</i>	1/2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Patagopteryx deferrariisi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Cathayornis yandica</i>	0/1	0	0	0	1	0	?	0	1	?	?	1	?	?	?	?	?
<i>Concornis lacustris</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Neuquenornis volans</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gobipteryx minuta</i>	1	1	1	1	?	1	0	0	1	0	0	0	0	?	0	0	1
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	?	?	?	1	?	1	0	?	?	?	?	?	?	?	?	?	?
<i>Confuciusornis sanctus</i>	1	1	1	1	?	0&1	0	0	1	0	0	1	0	?	?	?	?
<i>Archaeopteryx lithographica</i>	0	0	0	0	1	0	?	0	0	0	0	0	0	0	0	0	?
<i>Dromaeosauridae</i>	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
<i>Anas platyrhynchos</i>	1	0	1	1	2	2	1	1	0	2	1	1	1	2	1	1	1
<i>Chauna torquata</i>	1	0	1	0	2	2	1	1	0	1	1	1	1	2	1	1	1
<i>Gallus gallus</i>	1	0	1	1	2	2	1	1	0	1	1	1	1	1	1	1	1
<i>Crax pauxi</i>	1	0	1	1	2	2	1	1	0	1	1	1	1	1	1	1	1
<i>Crypturellus undulatus</i>	1	0	0	0	1	1	1	1	1	0	1	0	1	1	0	0	1
<i>Lithornis</i>	1	0	0	0	1	1	1	1	1	0	1	0	1	1	0	?	1
<i>Iaceornis marshi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Iaceornis minus sacrum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	0	?	?	?	?	?	?	1	0	0/1	1	?	1	1	1	0	1
<i>Ichthyornis minus YPM 1732</i>	0	?	?	?	?	?	?	1	0	0/1	1	?	1	1	1	0	1
<i>YPM 1732</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	?	1	?	0	?	1	0	1	0	?	?	1	1	1	0	0	1
<i>Baptornis advenus</i>	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	1
<i>Patagopteryx deferrariisi</i>	?	0	?	0	?	1	?	?	?	?	?	?	0	0	?	?	1
<i>Cathayornis yandica</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Concornis lacustris</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Neuquenornis volans</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gobipteryx minuta</i>	?	1	?	0	?	1	0	?	?	?	?	?	0	0	?	?	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
<i>Confuciusornis sanctus</i>	?	?	?	?	?	?	?	1	0	?	?	0	0	?	?	0	1
<i>Archaeopteryx lithographica</i>	?	0	0	0	1	1	0	?	?	0	0	?	0	?	?	0	0
<i>Dromaeosauridae</i>	0	0	0	0	0	0	0	0	?	0	0	0	0	0	?	0	0

APPENDIX 2
Continued

	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
<i>Anas platyrhynchos</i>	1	1	1	1	0	1	1	0	0	0	1	1	1	1	0	1	1
<i>Chauna torquata</i>	1	1	1	1	0	1	1	0	0	0	1	1	1	1	0	1	1
<i>Gallus gallus</i>	1	1	1	1	0	1	1	0	0	0	1	1	0	1	0	1	1
<i>Crax pauxi</i>	1	1	1	1	0	1	1	0	0	0	1	1	0	1	0	1	1
<i>Crypturellus undulatus</i>	1	0	1	1	1	1	1	1	1	1	1	0	0	1	0	1	0
<i>Lithornis</i>	1	0/1	1	1	0	1	?	1	1	1	1	?	0	1	?	1	0
<i>Iaceornis marshi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Iaceornis minus sacrum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	1	1	0	1	0	0	1	0	2	0	?	?	?	?	1	0	1
<i>Ichthyornis minus</i> YPM 1732	1	1	0	1	0	0	1	0	2	0	?	?	?	?	1	0	1
YPM 1732	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	1	0	0	?	?	0	0	?	0	?	?	?	1	0	1	0
<i>Baptornis advenus</i>	?	?	0	0	?	?	1	?	?	?	?	?	?	?	?	?	?
<i>Patagopteryx deferrariisi</i>	1	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?
<i>Cathayornis yandica</i>	?	?	?	?	?	?	?	0	?	?	?	?	?	?	0	?	?
<i>Concornis lacustris</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Neuquenornis volans</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Gobipteryx minuta</i>	?	?	0	?	?	?	0	?	?	0	?	?	?	?	1	?	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	1	0/1	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?
<i>Confuciusornis sanctus</i>	1	2	0	0	?	?	0	1	1/2	0	1	1	1	1	1	0	0
<i>Archaeopteryx lithographica</i>	0	?	0	0	?	?	?	0	0	0	?	?	?	0	0	?	0
Dromaeosauridae	0	?	0	0	?	?	0	0	0	0	?	?	?	0	0	0	0

	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
<i>Anas platyrhynchos</i>	2	1	2	1	0	1	0	1	0	6	2	1	1	0	1	1	1
<i>Chauna torquata</i>	2	1	2	1	0	1	2	1	0	6	2	1	1	0	1	1	1
<i>Gallus gallus</i>	2	1	2	1	0	1	0	1	1	6	2	1	0	0	1	1	1
<i>Crax pauxi</i>	2	1	2	1	0	1	0	1	1	6	2	1	1	0	1	1	1
<i>Crypturellus undulatus</i>	2	1	2	1	0	1	0	1	1	6	2	1	0	1	1	1	2
<i>Lithornis</i>	2	1	2	1	0	1	2	?	0	5&6	1	1	?	1	?	1	1/2
<i>Iaceornis marshi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Iaceornis minus sacrum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	5	2	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	0/1	1	2	0	0	1	1	1	?	4&5	1	1	0	0	2	1	1/2
<i>Ichthyornis minus</i> YPM 1732	0/1	1	2	0	0	1	1	?	?	4	1	?	?	?	?	?	?
YPM 1732	?	?	?	0	0	1	1	1	?	5	1	1	0	0	2	1	1/2
<i>Hesperornis regalis</i>	2	1	2	1	0	1	1	0	0	5	0	1	0	0	1	1	2
<i>Baptornis advenus</i>	2	1	2	1	0	1	1	0	0	4	0	1	0	0	1	1	2
<i>Patagopteryx deferrariisi</i>	2	0	1	0	0	0	0	0	0	3	0	?	?	?	?	?	?
<i>Cathayornis yandica</i>	?	?	?	0	1	1	1	?	?	2	0	1	?	0	?	1	0
<i>Concornis lacustris</i>	?	?	?	0	1	1	1	?	?	?	?	?	?	?	?	1	0
<i>Neuquenornis volans</i>	?	?	?	0	1	1	0	?	?	?	?	?	?	?	?	?	?
<i>Gobipteryx minuta</i>	?	?	?	?	?	?	?	?	?	3/4	?	?	?	?	?	1	0
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	2	?	2	0	0	1	0	?	0/1	4	0	1	0	0	1	1	?
<i>Confuciusornis sanctus</i>	1	0	0	0	0	1	1	0	?	0	1	0	1	0	0	1	0
<i>Archaeopteryx lithographica</i>	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	?
Dromaeosauridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?

APPENDIX 2
Continued

	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
<i>Anas platyrhynchos</i>	2	1	3	1	1	1	1	3	1	0	1	1	0	1	1	0	1
<i>Chauna torquata</i>	1	1	3	1	1	1	1	4	0	0	1	0/1	0	1	1	0	1
<i>Gallus gallus</i>	1/2	1	3	1	1	1	1	2	1	0	1	2	0	0	1	2	1
<i>Crax pauxi</i>	2	1	3	1	1	1	1	2	1	0	1	2	0	0	1	2	1
<i>Crypturellus undulatus</i>	2	1	3	1	1	1	1	2	?	0	1	0	0	0	1	2	1
<i>Lithornis</i>	1/2	1	3	1	1	1	2	2	1	0	1	0	0	?	1	0	1
<i>Iaceornis marshi</i>	?	?	3	1	?	0	2	2/3	1	?	?	?	?	?	1	1	0
<i>Iaceornis minus sacrum</i>	?	?	3	1	?	0	2	2/3	1	?	?	?	?	?	1	1	0
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	?	?	3	1	1	0	2	2	0	0	?	0	0	?	1	0	1
<i>Ichthyornis minus YPM 1732</i>	?	?	3	1	1	0	2	2	0	0	?	0	0	?	1	0	1
YPM 1732	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	1	?	1	?	0	0	0	1	0	1	0	?	0	0	1	?	?
<i>Baptornis advenus</i>	1	?	1/2/3	?	?	0	1	2	?	?	?	?	?	?	?	1	0
<i>Patagopteryx deferrariisi</i>	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	1	0
<i>Cathayornis yandica</i>	?	?	3	0	?	?	1/2	?	?	0	1	2	1	?	1	1	0
<i>Concornis lacustris</i>	?	?	3	0	?	?	1	?	0	0	1	2	1	0	1	1	0
<i>Neuquenornis volans</i>	?	?	3	1	?	?	?	?	?	0	1	1	1	?	1	?	0
<i>Gobipteryx minuta</i>	?	?	?	?	?	?	?	?	?	?	1	2	1	?	1	1	0
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	?	?	3	1	?	?	1	?	?	?	?	?	?	?	?	1	0
<i>Confuciusornis sanctus</i>	0&1	0	2	0	0	0	1	2	0	0	0	1	?	0	0	?	0
<i>Archaeopteryx lithographica</i>	0	0	0/1	?	?	?	?	?	?	0	0	0	0	0	0	?	0
Dromaeosauridae	1	0	0	?	0	0	0	0	0	0	0	1	0	0	0	?	0

	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102
<i>Anas platyrhynchos</i>	1	0	1	0	0	?	1	0/1	1	1	1	0	1	1	1	1	0
<i>Chauna torquata</i>	1	0	1	0	1	1	1	1	1	0	1	0	1	1	1	1	0
<i>Gallus gallus</i>	1	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1
<i>Crax pauxi</i>	1	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1	1
<i>Crypturellus undulatus</i>	1	0	1	0	1	0	1	0	1	1	1	0	1	1	1	1	1
<i>Lithornis</i>	1	0	1	0	1	0	1	1	1	1	0	0	1	1	1	1	?
<i>Iaceornis marshi</i>	1	0	1	0	0	?	1	1	1	1	0	0	1	1	1	1	?
<i>Iaceornis minus sacrum</i>	1	0	1	0	0	?	1	1	1	1	0	0	1	1	1	1	?
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	1	0	1	0	0	?	1	1	1	1	0	0	1	1	1	1	1
<i>Ichthyornis minus YPM 1732</i>	1	0	1	0	0	?	1	1	1	1	0	0	1	1	1	1	1
YPM 1732	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	0	?	1	0	0	?	0	?	?	?	0	0	0	0	0	1	0
<i>Baptornis advenus</i>	0	?	1	0	0	?	0	?	?	?	0	0	0	0	?	?	?
<i>Patagopteryx deferrariisi</i>	1	0	?	?	?	?	?	0	1	0	1	?	?	1	1	1	1
<i>Cathayornis yandica</i>	1	1	?	?	?	?	?	0	1	0	?	1	0	1	1	0	0
<i>Concornis lacustris</i>	1	1	?	?	0	?	0	0	1	0	0	1	0	1	?	0	?
<i>Neuquenornis volans</i>	1	1	0	1	0	?	0	0	1	?	0	1	0	1	?	0	?
<i>Gobipteryx minuta</i>	1	0	0	1	0	?	0	?	1	0	0	1	0	1	1	0	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	1	0	0	1	0	?	0	?	1	0	0	1	0	1	1	1	1
<i>Confuciusornis sanctus</i>	1	0	0	1	0	?	0	?	?	0	?	?	?	0	0	0	0
<i>Archaeopteryx lithographica</i>	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0
Dromaeosauridae	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2
Continued

	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119
<i>Anas platyrhynchos</i>	0	0	0	1	1	1	0	0	1	1	0	0	1	2	0	1	1
<i>Chauna torquata</i>	1	0	2	1	1	1	0	0	1	1	0	0	1	2	0	1	1
<i>Gallus gallus</i>	0	0	1	1	1	1	1	0	1	1	0	0	1	2	0	1	1
<i>Crax pauxi</i>	0	0	1	1	1	1	1	0	1	1	0	0	1	2	0	1	1
<i>Crypturellus undulatus</i>	0	0	1	1	1	1	1	0	1	1	0	0	1	2	0	1	1
<i>Lithornis</i>	0	1	1	1	1	1	0	0	1	1	0	0	1	1/2	1	1	1
<i>laceornis marshi</i>	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>laceornis minus sacrum</i>	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	1	0	1	1	1	1	0	0	1	0	1	1	1	1	1	0	1
<i>Ichthyornis minus YPM 1732</i>	1	0	1	1	1	1	0	0	1	0	1	1	1	1	1	0	1
YPM 1732	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?
<i>Baptornis advenus</i>	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?
<i>Patagopteryx deferrariisi</i>	0	0/1	0	0	?	?	?	0/1	?	1	0	?	?	?	?	0	1
<i>Cathayornis yandica</i>	0	0	1	0	0	1	0	1	1	0	0/1	?	1	0	2	0	1
<i>Concornis lacustris</i>	?	?	0/1	0	0	1	?	1	1	0	?	?	1	0	2	?	1
<i>Neuquenornis volans</i>	?	?	1/2	?	?	1	?	?	?	0	1	?	?	?	?	0	?
<i>Gobipteryx minuta</i>	0	0	1/2	0	0	1	?	1	?	0	1	1	?	?	?	0	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	0	1	1	1	1	1	?	0	1	0	1	1	1	0	1/2	0	1
<i>Confuciusornis sanctus</i>	?	0	0	0	0	0	?	0	0	0	2	1	?	?	0	0	1
<i>Archaeopteryx lithographica</i>	?	0	0	0	0	0	?	0	0	1	1	0	0	?	0	0	0
Dromaeosauridae	?	0	0	0	0	0	?	0	0	1	0	0	0	?	0	0	0
	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136
<i>Anas platyrhynchos</i>	0	0	0	0	1	0	1	1	1	0	1	1	1	1	1	1	1
<i>Chauna torquata</i>	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	1	1
<i>Gallus gallus</i>	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	1	1
<i>Crax pauxi</i>	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	1	1
<i>Crypturellus undulatus</i>	0	0	0	0	1	1	1	0	1	0	1	1	0	1	1	1	1
<i>Lithornis</i>	0	0	0	0	1	0	1	0	1	0	1	1	0	1	1	1	1
<i>laceornis marshi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>laceornis minus sacrum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	0	0	0	0	1	0	1	0&1	1	0	1	1	1	2	1	1	1
<i>Ichthyornis minus YPM 1732</i>	0	0	0	0	1	0	1	0&1	1	0	1	1	1	2	1	1	1
YPM 1732	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hesperornis regalis</i>	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Baptornis advenus</i>	?	?	?	?	?	?	?	?	?	0	1	?	?	0/1	1	0/1	?
<i>Patagopteryx deferrariisi</i>	0	0	0	0	0	?	0/1	0	0	0	1	?	?	1/2	0	0	?
<i>Cathayornis yandica</i>	1	1	1	1	0	?	0/1	?	1	?	?	1	?	?	?	2	1
<i>Concornis lacustris</i>	?	?	?	1	0	?	?	?	1	0/1	1	?	?	1/2	?	?	?
<i>Neuquenornis volans</i>	?	?	?	?	0/1	?	?	?	1	?	1	1	?	?	?	2	?
<i>Gobipteryx minuta</i>	?	?	?	?	?	?	?	?	?	?	?	1	1	?	1	2	1
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	1	1	1	1	0	0	0	0	1	0	1	1	0	2	1	1	1
<i>Confuciusornis sanctus</i>	0	0	0	0	0	0	0	0	1	0	1	0	0	2	1	0	1
<i>Archaeopteryx lithographica</i>	?	?	0	0	0	?	0	0	0	0	1	0	0	0	0	0	0
Dromaeosauridae	?	?	0	0	0	?	0	0	0	0	1	0	0	0	0	0	0

APPENDIX 2

Continued

	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153
<i>Anas platyrhynchos</i>	1	2	3	1	1	3	0	1	1	0	1	0	1	1	1	0	2
<i>Chauna torquata</i>	1	2	3	1	1	3	0	1	1	0	1	1	1	1	1	0	2
<i>Gallus gallus</i>	1	1	3	1	1	3	0	1	1	0	0	1	2	1	1	0	2
<i>Crax pauxi</i>	1	1	3	1	1	3	0	1	1	0	1	1	2	1	1	0	2
<i>Crypturellus undulatus</i>	1	0	3	1	1	3	0	1	1	0	1	1	1	1	1	0	2
<i>Lithornis</i>	1	1	3	1	1	2	0	1	1	1	0	0/1	1	1	1	0	2
<i>Iaceornis marshi</i>	1	1	3	1	1	3	0	1	1	1	1	0	1	1	1	0	2
<i>Iaceornis minus sacrum</i>	1	1	3	1	1	3	0	1	1	1	1	0	1	1	1	0	?
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	1	?	3	1	1	1	0	1	1	1	0	0	1	1	?	1	2
<i>Ichthyornis minus YPM 1732</i>	1	?	3	1	1	1	0	1	1	1	0	0	1	1	?	1	?
<i>YPM 1732</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
<i>Hesperornis regalis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
<i>Baptornis advenus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
<i>Patagopteryx deferrariisi</i>	?	?	3	?	0	?	?	?	?	?	?	?	?	0	0	?	2
<i>Cathayornis yandica</i>	0	1	2	1	0	0	1	?	1	?	0	1	?	0	1	0	1
<i>Concornis lacustris</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?
<i>Neuquenornis volans</i>	?	?	2	1	0	0	1	?	?	?	0	1	?	?	?	?	?
<i>Gobipteryx minuta</i>	?	?	0/1/2	?	0	?	?	?	?	?	?	1	?	0	?	?	1
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Apsaravis ukhaana</i>	0	?	2/3	1	1	1	0	1	1	0	0	?	1	1	?	?	2
<i>Confuciusornis sanctus</i>	0	1	1	1	0/1	0	1	0	0	?	0	0	0	0	0	0	1
<i>Archaeopteryx lithographica</i>	?	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0
<i>Dromaeosauridae</i>	?	?	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0

	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170
<i>Anas platyrhynchos</i>	1	?	?	1	1	1	1	1	1	0	1	1	1	1	1	1	?
<i>Chauna torquata</i>	1	?	?	1	1	1	1	1	1	1	1	1	1	1	1	1	2
<i>Gallus gallus</i>	1	?	?	1	1	2	1	1	1	1	1	1	1	1	1	1	2
<i>Crax pauxi</i>	1	?	?	1	1	1	1	1	1	1	1	1	1	1	1	1	2
<i>Crypturellus undulatus</i>	0	1	?	1	1	2	0	1	1	0	1	1	1	1	1	1	2
<i>Lithornis</i>	0&1	0	0	1	1	2	0	1	1	0	1	1	1	1	1	1	2
<i>Iaceornis marshi</i>	0	0	0	1	1	0	?	?	1	?	1	1	?	1	1	1	2
<i>Iaceornis minus sacrum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	2
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	0	0	0	1	1	0/1	0	0	1	0	1	?	1	1	?	1	2
<i>Ichthyornis minus YPM 1732</i>	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	1	2
<i>YPM 1732</i>	0	0	0	1	1	0/1	0	0	1	0	1	?	1	1	?	1	2
<i>Hesperornis regalis</i>	0	1	?	1	1	1	0	0	0	0	1	1	1	1	1	1	2
<i>Baptornis advenus</i>	0	1	?	1	1	1	0	0	0	0	1	1	1	1	1	1	2
<i>Patagopteryx deferrariisi</i>	0	0	0	1	0	0	0	?	0	1	1	0	1	1	?	?	2
<i>Cathayornis yandica</i>	0	0	1	1	?	?	0	?	0	0	0	?	0	0	0	?	1
<i>Concornis lacustris</i>	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?
<i>Neuquenornis volans</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
<i>Gobipteryx minuta</i>	?	?	?	?	?	?	?	?	?	?	0	?	0	0	1	?	?
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?
<i>Apsaravis ukhaana</i>	0	1	?	1	1	0/1	0	0	1	0	1	1	1	1	1	1	?
<i>Confuciusornis sanctus</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Archaeopteryx lithographica</i>	0	0	0	0	0	0	0	?	0	?	0	0	0	0	0	?	0
<i>Dromaeosauridae</i>	0	0	0	0	0	0&1	0	0	0	0	0	0&1	0	0	0	0&1	0

APPENDIX 2
Continued

	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187
<i>Anas platyrhynchos</i>	1	1	1	0	1	1	2	1	0	2	1	1	0	0	2	1	1
<i>Chauna torquata</i>	1	1	1	0	2	1	2	1	0	2	1	2	0	0	2	1	1
<i>Gallus gallus</i>	1	1	1	0	2	1	2	1	0	2	1	1	0	0	2	1	1
<i>Crax pauxi</i>	1	1	1	0	2	1	2	1	0	2	1	1	0	0	2	1	1
<i>Crypturellus undulatus</i>	1	1	1	0	2	1	2	1	0	2	1	1	0	0	2	1	1
<i>Lithornis</i>	1	1	1	0	2	1	2	1	0	1	1	0	0	0	2	1	1
<i>laceornis marshi</i>	1	1	1	0	2	1	2	?	1	2	1	1	0	0	2	1	1
<i>laceornis minus sacrum</i>	1	1	1	0	2	1	2	?	1	2	1	1	0	0	2	1	1
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Austinornis lentus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ichthyornis dispar</i>	1	1	1	0	2	1	2	1	1	1	1	1	0	0	2	1	1
<i>Ichthyornis minus YPM 1732</i>	1	1	1	0	2	1	2	1	1	1	1	1	0	0	2	1	1
YPM 1732	1	1	1	0	2	1	2	?	1	1	1	1	0	0	2	1	1
<i>Hesperornis regalis</i>	1	1	1	0	2	1	2	1	1	1	1	1	0	0	2	1	1
<i>Baptornis advenus</i>	1	1	1	0	2	1	2	1	1	1	1	1	0	0	2	1	1
<i>Patagopteryx deferrariisi</i>	?	0	?	?	?	?	2	0	?	0	?	0	0	0	1/2	1	1
<i>Cathayornis yandica</i>	1	?	?	?	1	1	1/2	0	?	0	?	0	?	1	0/1	1	?
<i>Concornis lacustris</i>	?	?	?	?	?	?	2	0	?	0	?	0	0	?	?	1	1
<i>Neuquenornis volans</i>	1	0	?	1	?	1	?	0	?	?	?	?	?	?	?	1	?
<i>Gobipteryx minuta</i>	?	0	?	?	?	?	1	?	1	0	?	0	0	1	1	1	1
<i>Vorona berivotrensis</i>	?	?	?	?	?	?	1	0	1	0	1	0	1	1	1	1	1
<i>Apsaravis ukhaana</i>	1	1	1	0	?	?	2	?	1	0	1	2	1	1	2	1	1
<i>Confuciusornis sanctus</i>	1	0	1	0	1	1	2	0	0	0	1	0	0	0	1	1	1
<i>Archaeopteryx lithographica</i>	0	0	0	0	0	0	0	0	?	0	0	?	0	?	0/1	1	0
Dromaeosauridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	188	189	190	191	192	193	194	195	196	197	198	199	200	201	202	% missing data	
<i>Anas platyrhynchos</i>	3	1	1	1	2/3	2	2	2	1	0	0	0	1	0	2	2.5	
<i>Chauna torquata</i>	3	1	1	1	2	2	2	2	2	1	0	0	1	0	0	1.5	
<i>Gallus gallus</i>	3	1	1	1	3	2	2	2	2	1	0	0	1	1	1	1.5	
<i>Crax pauxi</i>	3	1	1	1	3	2	2	2	2	1	0	0	1	1	0	1.5	
<i>Crypturellus undulatus</i>	3	1	1	1	2	2	2	2	1	0/1	0	0	1	0	1	1.5	
<i>Lithornis</i>	3	1	1	1	2	2	2	2	1	1	0	0	1	0	0&1	5.4	
<i>laceornis marshi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	63.4	
<i>laceornis minus sacrum</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	69.4	
<i>Apatornis celer</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	99.0	
<i>Guildavis tener</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	99.0	
<i>Austinornis lentus</i>	3	?	1	?	?	?	?	?	2	1	0	0	1	1	1	95.5	
<i>Ichthyornis dispar</i>	3	1	1	1	1/2	2	?	2	1	0	0	0	0	0	2	15.3	
<i>Ichthyornis minus YPM 1732</i>	3	1	1	1	1/2	2	?	2	1	0	0	0	0	0	2	24.8	
YPM 1732	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	77.7	
<i>Hesperornis regalis</i>	3	1	1	1	1	2	2	2	1	0	2	2	0	0	2	34.7	
<i>Baptornis advenus</i>	2	1	1	1	1	?	2	2	1	?	0	2	0	?	2	51.9	
<i>Patagopteryx deferrariisi</i>	3	1	0	0	1	1	0	0	0	0	0	0	0	?	0/1	48.5	
<i>Cathayornis yandica</i>	0/1	?	0	?	?	?	?	?	?	0	?	?	?	?	?	47.0	
<i>Concornis lacustris</i>	1	?	0	0	?	?	1	?	?	?	0/1	1	?	?	?	67.3	
<i>Neuquenornis volans</i>	0/1	?	0	?	?	?	1	?	0	1	1	1	?	?	?	72.3	
<i>Gobipteryx minuta</i>	1	1	0	0	0	?	1	1	?	1	1	1	?	0	?	53.5	
<i>Vorona berivotrensis</i>	2	0	0	0	0	1	?	2	0	0	0	0	0	0	0	87.1	
<i>Apsaravis ukhaana</i>	3	1	1	0	1	1	?	2	0	1	0	0	0	?	1	35.1	
<i>Confuciusornis sanctus</i>	1	0	0	0	0	1	1	1	0	1	0	0	?	0	0	15.8	
<i>Archaeopteryx lithographica</i>	1	0	0	0	0	0	0	0	?	1	0	0	?	?	?	21.8	
Dromaeosauridae	0	0	0	0	0	0	0	0/1	0	0	0	0	?	0	0	11.4	

*Slash (/) indicates ambiguous character states; ampersand (&) indicates polymorphism.