

## SHORT COMMUNICATIONS

### A NEW PARTIAL MANDIBLE OF *ICHTHYORNIS*

PHILIP D. GINGERICH

Peabody Museum of Natural History  
Yale University  
New Haven, Connecticut 06520

In 1872, O. C. Marsh described a new Cretaceous bird *Ichthyornis dispar* based on a postcranial skeleton (Marsh 1872a). Later in the same year, he described a new reptilian genus *Colonosaurus* for two toothed jaws found associated with the type specimen of *Ichthyornis dispar* (Marsh 1872b). In the following year, Marsh referred the toothed "*Colonosaurus*" jaws to *Ichthyornis dispar* stating that: "On subsequently removing the surrounding shale, the skull and additional portions of both jaws were brought to light, so that there cannot now be a reasonable doubt that all are parts of the same bird" (Marsh 1873). This assignment was accepted until 1952 when J. T. Gregory compared the jaws of *Ichthyornis dispar* to those of mosasaurs. Gregory (1952) concluded that the toothed jaws assigned to *Ichthyornis* by Marsh were actually the jaws of a small mosasaur which had accidentally been deposited together with the skeleton of a bird. The recent classifications of fossil birds by Storer (1960), Romer (1966, 1968), and Brodkorb (1967) all follow Gregory and removed *Ichthyornis* from the toothed birds.

After careful study of the toothed jaws associated with the type specimen of *Ichthyornis dispar* (Yale Peabody Museum [YPM] 1450) M. V. Walker (1967) recently stated his opinion that until further proof is available the toothed jaws should be considered to belong to *Ichthyornis*. Fortunately, Walker has since found a second partial skeleton of *Ichthyornis*, again with associated toothed jaws. The jaws associated with Walker's partial skeleton consist only of portions of the toothed dentaries; the quadrate articulations of both jaws are unfortunately missing (Walker, unpubl.).

I recently discovered an additional mandibular fragment of *Ichthyornis* (*I. cf. dispar*) which was catalogued together with bones of a specimen of the much larger Cretaceous bird *Hesperornis* (YPM 1478) in the Yale Peabody Museum collection. This new mandibular fragment of *Ichthyornis* is the only known specimen revealing the morphology of the quadrate articulation. It presumably was collected together with YPM 1478, which was collected by B. F. Mudge from the Upper Cretaceous Niobrara Chalk, Wallace County, Kansas in 1876. The new mandibular fragment of *Ichthyornis* is now catalogued as YPM 6264.

#### DESCRIPTION OF MANDIBLE

Mandibles of *Ichthyornis* are divided into anterior and posterior segments by an intramandibular articulation, between the splenial and angular bones, permitting limited flexion similar to that in the mandibles of *Hesperornis*, mosasaurs, varanoid lizards, and

snakes. The recently recognized mandibular fragment is an almost complete posterior segment of a left mandible consisting of angular, surangular, articular, and prearticular bones (fig. 1). The intramandibular articular surface of the angular is well preserved. The quadrate articular surface of the articular is also well preserved, although its postero-medial portion, including the posterior articular cotylus, is displaced slightly forward and upward.

Most of the sutures separating individual bones are closed in this posterior mandibular segment, indicating that the jaw belonged to a mature individual. As nearly as can be determined, the individual bones making up the segment are very similar to those of *Hesperornis* in arrangement. The angular forms the ventral margin of the segment. It extends posteriorly from the intramandibular articulation, tapering to a point below the glenoid fossa. This appears to be the condition in *Hesperornis* also (the skull of *Hesperornis* is presently being restudied). The surangular forms the lateral wall of the segment; it is broken anteriorly and dorsally. The articular constitutes most of the posterior portion of the fragment. A small medial process of the articular is present; however, there was no well-developed retroarticular process in *Ichthyornis*. Two distinct oblique articular cotylia are present in the mandibular glenoid fossa for articulation with a double-keeled quadrate. The prearticular is fused posteriorly with the articular, anteriorly it forms the medial surface of the jaw segment. The prearticular is also broken anteriorly and dorsally.

The newly discovered jaw segment was compared directly with the jaws associated with the type specimen of *Ichthyornis dispar* (YPM 1450). The left mandible associated with the type specimen consists of a complete dentary-splenial segment, but only the most anterior portion of the posterior mandibular segment. The right mandible of the type specimen, including parts of the posterior segment, is mounted on a plaque for exhibition. The quadrate articular region of this jaw was removed from the plaque and cleaned to allow direct comparison with the new specimen (fig. 2). The two specimens agree closely in morphology although the new specimen is from an individual slightly larger than the type. Unfortunately, the anterior and lateral portion of the articular region of the type specimen is badly distorted. By comparison with the new segment it is clear, however, that the quadrate articular region of the type specimen also had the two oblique articular cotylia characteristic of birds.

#### DISCUSSION

As evidence of affinity with mosasaurs, Gregory (1952) stated that the jaws associated with the type of *I. dispar* have a suture on the upper edge of the surangular for a distinct coronoid bone. I can find no trace of this suture on either the left or the right jaw. The surangular itself is well preserved in both jaws associated with the type specimen. This region of the new mandibular segment is not preserved. The following characters cited by Gregory as evidence of

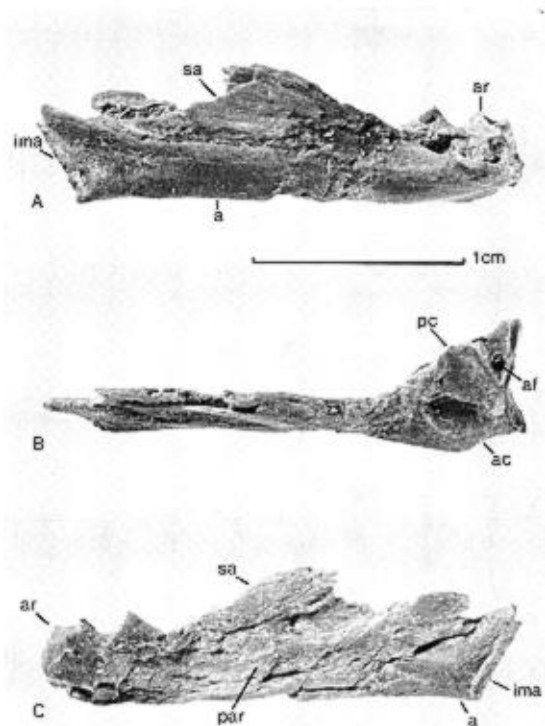


FIGURE 1. Newly discovered posterior segment of a left mandible of *Ichthyornis* (YPM 6264) in lateral (A), dorsal (B), and medial (C) view. (a = angular, af = articular foramen, ar = articular, ima = intra-mandibular articulation, par = prearticular, sa = surangular, ac and pc = anterior cotylus and posterior cotylus for articulation with the quadrate).

affinity with mosasaurs are also present in the bird *Hesperornis*, which Gregory (1951) has shown had in fact converged remarkably in skull morphology with mosasaurs. In both *Ichthyornis* and *Hesperornis* the angular tapers to a point below the articular cotylia. In both, the anterior end of the angular has a facet along its front edge for articulation with the splenial. In both, the splenial is visible posteriorly on the external edge of the jaw where it articulates with the angular. In both, the anterior ends of the dentaries apparently lack any symphysis. The prearticular is similar in both *Ichthyornis* and *Hesperornis*. It extends forward from the articular and is inserted between the splenial and dentary. Thus many of the characters shared by *Ichthyornis* and mosasaurs are also present in *Hesperornis* and are a result of evolutionary convergence. They do not indicate close relationship between *Ichthyornis* and mosasaurs.

The new mandibular segment cannot belong to *Hesperornis* because of the great difference in size (all known posterior mandibular segments of *Hesperornis* are approximately three times the length of this segment). *Ichthyornis* and *Hesperornis* further differ in that there is no retroarticular process and the teeth are set individually in sockets in *Ichthyornis*, whereas in *Hesperornis* there is a large retroarticular process and the teeth are set in grooves. These differences are relatively minor and may be functionally related.

The paired, oblique articular cotylia for articulation

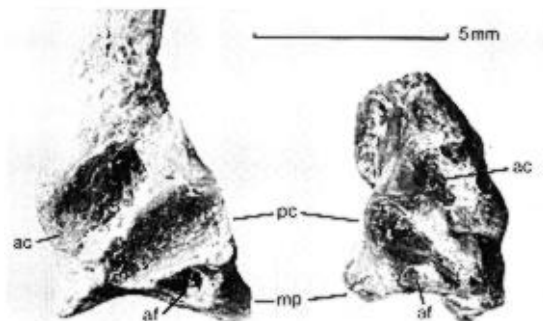


FIGURE 2. Comparison of the new left mandibular segment (left, YPM 6264) with the right mandibular segment associated with the type specimen of *Ichthyornis dispar* (right, YPM 1450). The anterior and lateral margins of the type specimen (right) are broken and highly distorted. (mp = medial process of the articular, other abbreviations as in fig. 1).

with the quadrate in the mandible of *Ichthyornis* (and in *Hesperornis* and most living birds) differ from the transverse articular cotylus of mosasaurs and other reptiles. The morphology of the quadrate articulation of the new specimen described above and of the right mandible associated with *Ichthyornis* by Marsh is the best anatomical evidence that these jaws belonged to a bird. The discoveries by Marsh and Walker of toothed jaws associated with *Ichthyornis* skeletons further confirm that *Ichthyornis* was a toothed bird.

Bock (1969) has recently questioned whether the teeth associated with *Hesperornis* actually belong to that bird, stating that no teeth have been found in place in the jaws. The left mandible of the most complete *Hesperornis* skull (YPM 1206) does in fact have three teeth in place in the dental groove as Marsh (1880) illustrated them in his original reconstruction of this skull. Both *Ichthyornis* and *Hesperornis* were toothed birds. They are the latest surviving birds known to have had true teeth.

I thank John Ostrom for his assistance in reviewing the manuscript, Craig Black for the loan of the skull of *Hesperornis* from University of Kansas, and C. E. Ray for the loan of the skull of *Hesperornis* from the U.S. National Museum. Myrl V. Walker kindly sent me a copy of his preliminary description of the newly discovered *Ichthyornis* skeleton.

#### ADDENDUM

Dr. Hildegard Howard has recently called my attention to an additional left posterior mandibular segment of *Ichthyornis* (YPM 1761) among specimens presently on loan to Dr. Pierce Brodkorb. Dr. Brodkorb has kindly made this specimen available to me. The quadrate articular region of YPM 1761 is crushed dorsoventrally and the specimen is slightly larger than YPM 6264; it is otherwise morphologically identical to YPM 6264 described here.

#### LITERATURE CITED

- BOCK, W. J. 1969. The origin and radiation of birds. *Ann. New York Acad. Sci.* 167:147-155.  
 BRODKORB, P. 1967. Catalogue of fossil birds: Part

- 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). Bull. Florida State Mus. 11:99-220.
- GREGORY, J. T. 1951. Convergent evolution: the jaws of *Hesperornis* and the mosasaurs. Evolution 5:345-354.
- GREGORY, J. T. 1952. The jaws of the Cretaceous toothed birds, *Ichthyornis* and *Hesperornis*. Condor 54:73-88.
- MARSH, O. C. 1872a. Notice of a new and remarkable fossil bird. Amer. J. Sci., 3rd ser. 4:344.
- MARSH, O. C. 1872b. Notice of a new reptile from the Cretaceous. Amer. J. Sci., 3rd ser. 4:406.
- MARSH, O. C. 1873. On a new sub-class of fossil birds (Odontornithes). Amer. J. Sci., 3rd ser. 5: 161-162.
- MARSH, O. C. 1880. Odontornithes: a monograph

- on the extinct toothed birds of North America. Yale Univ. Peabody Mus. Mem. 1:1-201.
- ROMER, A. S. 1966. Vertebrate paleontology. Third ed. Univ. Chicago Press, Chicago.
- ROMER, A. S. 1968. Notes and comments on vertebrate Paleontology. Univ. Chicago Press, Chicago.
- STOREY, R. W. 1960. The classification of birds, p. 57-93. In A. J. Marshall (ed.) Biology and comparative physiology of birds. Vol. 1. Academic Press, New York.
- WALKER, M. V. 1967. Revival of interest in the toothed birds of Kansas. Trans. Kansas Acad. Sci. 70:60-66.

Accepted for publication 8 October 1971.

## TERRITORY SIZE, CLUTCH SIZE, AND FOOD IN POPULATIONS OF WRENS

MARTIN L. CODY

Department of Zoology  
University of California  
Los Angeles, California 90024

AND

CHRISTOPHER B. J. CODY

Hope Hall,  
Bramham, Boston Spa  
Yorkshire, England

Island populations of nonmarine birds at high latitudes characteristically show a reduced clutch size over their mainland counterparts (Cody, Ecological Aspects of Reproduction, p. 461. In Farner and King [eds.] Avian Biology. Vol. 1. Academic Press, New York, 1971). The Wren (*Troglodytes troglodytes*)<sup>1</sup> is one species which well illustrates this, as it has reached just about every North Atlantic island. Information on clutch size is reasonably complete and quite intriguing (fig. 1). The usual correlation with latitude exists; further, clutch size decreases with population isolation and the inverse of population size (as measured by distance from the mainland and island size, respectively). In order to evaluate the hypothesis that changes in clutch size are due to geographic differences in food supply, we examined various populations of Wrens during the 1970 breeding season: (a) *T. t. troglodytes*, Hope Hall, Yorkshire, England, early June and late July; (b) *T. t. troglodytes*, Dunvegan, Isle of Skye, Scotland, early July; (c) *T. t. hebridensis*, Isle of Lewis, Outer Hebrides, late June; (d) *T. t. zetlandicus*, Mainland and Mousa, Shetland Islands, mid-July; (e) *T. t. islandicus*, Vaglaskógur, Akureyri, Iceland, early August. We wished to discover if changes in food supply which correspond to changes in habitat and numbers of competitors were compensated by changes in territory size. We also hoped to shed light on an often cited and equally often denied inverse relation between territory size and food density. The data are presented and discussed below.

### METHODS

In each locale, we selected, where possible, areas of uniform habitat in which Wrens held contiguous territories. The Wrens of Lewis and Shetland Islands

were very patchy in their local distribution, and of these we included some Wrens whose territories were not or were only partly contiguous with those of neighbors. In this case, we used the foraging area as a territory size. All Wrens were in vigorous song and defended their territories against interlopers; most were feeding young in the nest or juveniles within the territory, while one or two may have been unmated. Territories were plotted by accumulating activity records on a map, and no area was included which was rarely or never used by foraging Wrens.

The density of all other passerine species in territories of Wrens was noted, and the feeding heights and behaviors of each of these potential competitors were measured as described by Cody (Amer. Nat. 102:107, 1968). This information was used to calculate competition coefficients  $a_i$  between each Wren and the other species with which it shared its territory. The product of four overlap factors—horizontal overlap  $a_H$ , vertical overlap  $a_V$ , bill measurement overlap  $a_B$ , and feeding behavior overlap  $a_F$ —gives an estimated competition coefficient  $a$ . The factors by which densities of Wrens might be increased if each competitor were removed can then be calculated. The carrying capacity of Wrens in the absence of  $(n - 1)$  competitors is given by the vector product  $[1 \ a_2 \ a_3 \ \dots \ a_n]$   $\{N_1 \ N_2 \ N_3 \ \dots \ N_n\}$  where  $N_1$  is the observed density of Wrens and  $N_2-N_n$  the densities of its competitors. Wrens had between zero (in the walls and ruins of Mousa) and 13 (in Yorkshire woods) competitors, 23 different species in all, whose effect was thus evaluated.

To measure food, we set out in territories of Wrens sets of grease-covered plaques, 10 cm  $\times$  10 cm, at various heights which spanned feeding activity of Wrens. Between 42 and 308 plaque-days were recorded at each location. The insects caught on the plaques were removed every 24 hr and classified according to length. A unit of food was taken to be an insect of  $\frac{1}{4}$  inch body length (=  $\frac{1}{8}$  of a  $\frac{1}{2}$  inch insect,  $\frac{1}{27}$  of a  $\frac{3}{4}$  inch insect), and density of food has the units "number of  $\frac{1}{4}$  inch insects/plaque/day." Each feeding site of Wrens, from cracks in banks and walls to tree trunks and foliage, was sampled. A final figure of food density was determined by weighting the insect catch at different heights according to the proportion of its time the Wren fed there.

There are potential sources of error in this estimate of food abundance of Wrens: immobile food items are not sampled; some of the food items caught will be perhaps unusable or unavailable to Wrens; the plaques may be differentially effective in different habitats.

<sup>1</sup> = Winter Wren of N.A.