evidence suggests that interbreeding was occurring at least occasionally before the recent change in the human population (see Ingolfsson 1970, Jehl MS), there is increasing evidence that human activity is an important factor facilitating breakdown in mechanisms that prevent interbreeding (see Smith 1966 for review of isolating mechanisms). For example, human activity is thought to be primarily responsible for the mass immigration of *argentatus* to Iceland, which resulted in extensive hybridization with *hyperboreus* (Ingolfsson 1970). Similarly, hybridization between *argentatus* and Glaucous-winged Gulls (*L. glaucescens*), another coastal breeder, is most common near human settlements associated with Alaskan fisheries (Williamson and Peyton 1963, Patten 1980). Further study of isolating mechanisms and continued monitoring of phenotype frequencies are needed, however, to identify and assess all factors responsible for interbreeding between these species.

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Histological Evidence for the Systematic Position of *Hesperornis* (Odontornithes: Hesperornithiformes)

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In his original description of *Hesperornis*, O. C. Marsh (1880) noted similarities between this Cretaceous toothed "diver" and modern ratites (Struthioniformes). Subsequently, Heilmann (1927) correctly demonstrated the ecomorphological similarity of *Hesperornis* to loons (Gaviiformes), but, in so doing, he incorrectly renounced the similarities of *Hesperornis* and ratites. Eventually, Gingerich (1973) described *Hesperornis* as possessing a paleognathous palate, but, from Gingerich's own reconstruction, the palate of *Hesperornis* did not satisfy the criteria that collectively diagnose the paleognathous palate as described by Bock (1963) (Brodkorb 1976, McDowell 1978, Cracraft 1980, Balouet 1983). Cracraft's treatment of *Hesperornis* is exemplary of the uncertainty that still exists about its systematic position. Cracraft (1982) concluded that *Hesperornis* was a member of a monophyletic clade that includes the neognathous loons and grebes (Podicipediformes), but, more recently, he (in press) considered it as the sister group of *Ichthyornis* plus Neornithes.

I examined the histological structure of *Hesperornis* bone as part of an effort to determine the correct polarity of histological characters in the bones of paleognathous and neognathous birds, which I treated elsewhere (Houde in press a). I was surprised to find

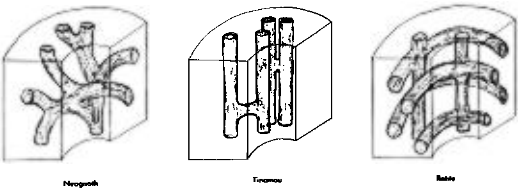

Fig. 1. Schematic representation of the patterns of primary osteons that are characteristically observed in the compacta of the tibiotarsi of neognathous birds, tinamous, and ratite birds, following Amprino and Godina (1944). See text for details.

that the character state of bone histology in *Hesperornis* is clearly like that of neognathous birds and unlike that of paleognathous birds.

The differences in bone histology between paleognathous and neognathous birds were determined by Amprino and Godina (1944, 1947) and Zavattari and Cellini (1956). The work of Amprino and Godina (1947), however, contained editorial errors in its discussion of paleognathous birds. The characters of greatest importance to my study were found in the femur, fibula, and tibiotarsus. In neognathous birds the vascular canals of primary osteons are "reticular" (Enlow and Brown 1956, 1957), generally branching and anastomosing randomly (Figs. 1 and 2). In tinamous, vascular canals are "longitudinal" (Enlow and Brown 1956) and predominantly oriented parallel to the longitudinal axis of the bone (Figs. 1 and 2). In ratites, the majority of vascular canals are "plexiform" or "laminar" (Enlow and Brown 1956), arranged in closely packed concentric circles that course in the transverse plane of the bone (Figs. 1 and 2).

Transverse lapidary "thin sections" of the diaphysis or distal metaphysis, or both, were made from tibiotarsi of (1) *Lithornis* sp. [National Museum of Natural History (USNM) 290554] (Lithornithidae), (2) *Paracathartes howardae* (USNM 361407) (Lithornithidae), (3) an unidentified moa [Yale Peabody Museum of Natural History (YPM PU) 11905] (Dinornithidae), (4) *Eudromia elegans* (USNM 345016) (Tinamidae), (5) *Rhynchotus rufescens* [Princeton University (PU) 728] (Tinamidae), (6) *Rhea americana* (unnumbered) (Rheidae), (7) *Casuarius casuarius* (USNM 429823) (Casuariidae), (8) *Apteryx australis* (USNM 289727) (Apterygidae), (9) *Hesperornis* sp. (YPM PU 22443) (Hesperornithidae), (10) *Eobucco* sp. (USNM 336571) (Eobucconidae), (11) *Plegadis falcinellus* (unnumbered) (Threskiornithidae), (12) *Crax rubra* (USNM 19918) (Cracidae), (13) *Anas platyrhynchos* [American Museum of Natural History (AMNH) 11133] (Anatidae), (14) *Cygnus olor* (unnumbered) (Anatidae), (15) *Thambetochen* sp. (USNM 386234) (Anatidae), (16) *Gallus gallus* (store-bought) (Phasianidae), and (17) *Bonasa umbellus* (unnumbered) (Phasianidae). Specimens 1–8 are paleognathous birds; 10–17 are neognathous; 1–3, 10, and 15 are fossils of known systematic position to serve as controls for the possible effects of fossilization on bone microstructure; 11, 13, and 16 are juveniles and serve as controls for the possible effects of ontogeny on bone microstructure; and 13–15 serve as controls for the possible effect of overall size between confamilial species and also as controls for the possible effects of flightlessness (15 is flightless) between closely related species.

Lapidary thin sections were made as follows. Free specimens were embedded in Epon epoxy and allowed to cure for several days at room temperature. Specimens were then cut on a diamond lapidary saw. Care was taken to ensure that the plane of the cut was consistently transverse across all of the tibiotarsi.

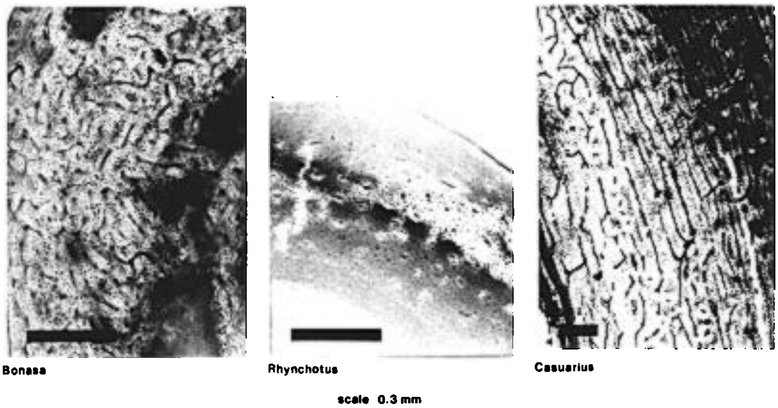

Fig. 2. Bright field photomicrographs of transverse lapidary thin sections through the tibiotarsi of a neognathous bird (*Bonasa*, unnumbered), a tinamou (*Rhynchotus*, PU 728), and a ratite (*Casuarius*, USNM 429823). All sections are through the diaphysis, near the distal metaphysis. Vascular canals appear as thin dark lines or spots. Large dark regions are more opaque regions of bone.

The cut surface was ground with successively finer slurries of aluminum oxide on a lapidary wheel. Adherent abrasive was removed from cavities with an ultrasonic cleaner. Next, the ground surface was polished with a slurry of tin oxide on a cloth-covered lapidary wheel. The polished surface was glued to a glass slide with Epon epoxy and allowed to cure for at least 24 h at room temperature. The process was then repeated on the other side of the specimen. The grinding and polishing processes were monitored periodically and assessed by examination through a light microscope to determine when the specimen was thin enough to transmit light and to resolve structures and to avoid obliterating the specimen by excessive grinding. The thickness of the specimens was not measured. Cover-slips were used and glued to the specimen with Epon epoxy.

Specimens were examined with bright field microscopy. Photographs of thin sections were enlarged by different amounts from the original negative size so that bone microstructures in different photographs appeared to be of comparable size.

Vascular canals in the tibiotarsi of *Lithornis* and both of the tinamous were oriented primarily in the longitudinal axis of the bone, as previously described for tinamous (Zavattari and Cellini 1956) (Fig. 2). *Paracathartes* and all the ratites showed the pattern described for ratite birds (Amprino and Godina 1944, 1947; Zavattari and Cellini 1956), in which many vascular canals course through the transverse plane of the bone, producing a pattern of concentric circles (Fig. 2). Sections of *Lithornis* and *Paracathartes* bone are illustrated elsewhere (Houde in press b). All the neognathous birds exhibited only the randomly branching pattern of bone vascularization that is generally typical of neognathous birds (Fig. 2). The patterns of bone histology appeared to be correlated only with phylogeny (i.e. tinamou-type, ratite-type, and neognath-type). Fossilization, differences in overall size of the birds, ontogenic stage, and the birds' ability or inability to fly had no noticeable additional effect on patterns of bone vascularization. The pattern exhibited by *Hesperornis* (Fig. 3) is unmistakably like that of the neognathous birds.

Ideally, I would have preferred to use larger samples and to use control groups that varied with respect to only one character each, to ensure independence of characters. Osteological specimens must be sacrificed, however, to make thin sections. It is thus difficult to obtain comparative materials, particularly of rare and valuable fossils. *Ichthyornis* is another toothed fossil bird that ought to be compared with *Hesperornis*, but uncrushed tibiotarsi of *Ichthyornis* were unavailable. Fortunately, the present results were unambiguous.

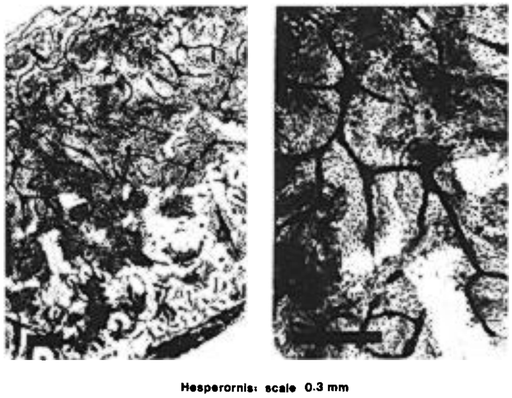

Fig. 3. Bright field photomicrographs of the compacta of the tibiotarsus of *Hesperornis* (YPM PU 22443). Section is transverse through the diaphysis.

A character must be derived and not homoplasious for it to be useful in phylogenetic analysis. The fact that patterns of vascular canals in osteons were not correlated with any of the variables for which I tested suggests that even if the different patterns of vascularization have different adaptive or developmental origins, its character state in birds is phylogenetically consistent. As with any character, caution must nevertheless be exercised in making phylogenetic inferences. The possibility for convergence in patterns of bone histology is underscored by the occurrence of ratite-like vascular patterns in the leg bones of many artiodactyls and therapsids (Enlow and Brown 1958). Moreover, descriptions of vascular patterns are generalities that simplify variation in character states between individuals and between taxa. The distinction between ratitelike and neognathlike vascular patterns is not always clear-cut in all published illustrations.

Theropod dinosaurs are the logical outgroup to examine to determine polarity of these character states. Although the patterns of bone vascularization in theropod dinosaurs apparently have not previously been directly compared with those of birds, Madsen (1976: fig. 24) illustrated transverse sections of the femur and fibula of *Allosaurus* that are suitable for comparison as a primitive outgroup. In the femur of *Allosaurus*, vascular canals lie parallel to the longitudinal axis of the bone. In the fibula, however, the longitudinally parallel canals are arranged in discrete rows that form concentric circles around the long axis of the bone. Plexiform or laminar patterns of circularly oriented vascular canals, like those of ratites but not as closely packed, were found in other dinosaurs by Enlow and Brown (1957), Ricqlés (1981), and Reid (1985). Assuming dinosaurs to be the correct primitive outgroup of birds, the patterns of bone vascularization exhibited by paleognathous birds are thus the primitive character states within Aves, and the condition in *Hesperornis* and neognathous birds is derived.

Crocodiles also might be considered to be a primitive outgroup of birds, but few researchers still seriously accept a sister-group relationship of crocodiles and birds (Walker 1985). Crocodiles possess longitudinally oriented vascular canals in the diaphyses of the leg bones (Amprino and Godina 1947, Enlow and Brown 1957), most like the condition observed in tinamous. But branching vascular canals, more like those of neognathous birds and *Hesperornis*, can be seen in one illustration of a crocodile femur (Peabody 1961). I cannot account for this variation. It might result if the section was made from an unusual level of the shaft, near the epiphysis, or because the specimen was extremely small. It emphasizes the importance of sample size, which is unfortunately minimal in my study.

If the dichotomy of paleognathous birds and neognathous birds was the earliest divergence among the lineages of modern Aves and if tinamous and gallinaceous birds represent the earliest divergences from their respective superorders (Prager et al. 1976, Prager and Wilson 1980, Sibley and Ahlquist 1981, Stapel et al. 1984), then parsimony suggests that any similarities (e.g. lack of teeth) of tinamous and gallinaceous birds are the result of common ancestry rather than convergence. Because *Hesperornis* possesses teeth, it might be concluded that *Hesperornis* arose before paleognathous and neognathous birds diverged from one another. The combination of paleognathous and neognathous characters of the palate in *Hesperornis* suggests that this could have been so. If so, then its palatal and histological character states could be the primitive conditions for extant birds.

Hesperornis clearly exhibits a pattern of osteons like that of neognathous birds. This pattern seems to be synapomorphous. The patterns of osteons in paleognathous birds resemble those of primitive dinosaurian outgroups. There is no insight gained by asking whether a particular pattern could be hypothetically derived from another. The only objective means of determining this is by examining the distribution of character states in taxa whose phylogeny is assumed to be known. This single character thus suggests that the true affinity of *Hesperornis* lies with neognathous birds or with a predecessor of both neognathous and paleognathous birds. Nevertheless, many other characters do not support a relationship between *Hesperornis* and neognaths or paleognaths (Cracraft in press). Therefore, the condition in paleognaths may also be interpretable as a reversal.

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Ocean Internal Waves as Sources of Small-scale Patchiness in Seabird Distribution on the Blake Plateau

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Seabirds inhabit marine environments that are highly structured by physical processes and features. This physical structure can affect the availability and locations of prey (Haury et al. 1978), in turn ultimately influencing seabird occurrence within marine habitats (Hunt and Schneider 1986). Distributional ecology of seabirds has been interpreted primarily on the basis of large-scale (100-1,000 km) physical variation arising from currents, water masses, and large density fronts (e.g. Brown et al. 1975, Pocklington 1979, Ainley and Jacobs 1981, Gould 1983). Physical structure or patchiness in seabird distribution may occur at much smaller scales, however. Schneider and Duffy (1985) found several seabird species aggregated at spatial scales ranging from 0.3 to 23 km in the Benguela Current region. They did not identify the cause of the aggregations, which could have arisen from species-specific responses to the physical-biological environment (Haney 1986a), variation in flocking or social interactions (Hoffman et al. 1981), or random differences in flock encounters caused by artifacts of sampling during ship-board censusing.

In this paper I describe small-scale (1-10 km) heterogeneity generated by internal waves and its effect on seabird distribution on the Blake Plateau off the coast of the southeastern United States. The Blake Plateau is a topographic anomaly that lies seaward of the continental shelf between Cape Hatteras, North Carolina, and the east coast of Florida. The gently sloping plateau interrupts the continental slope and widens considerably from north to south. As a consequence, waters deeper than 1,000-2,000 m are absent within 150-250 km of the coastline in this region. The Gulf Stream flows over the relatively shallow western third of the plateau, and the current's central axis or region of maximum velocity (6 km/h) occurs approximately 30-40 km east of the continental shelf edge (200-m isobath). The Gulf Stream is altered or deflected where irregular bathymetry on the plateau influences stream flow (Legeckis 1979). Internal waves were observed within the central axis of the stream at two locations with steep bathymetric gradients: the Stetson Mesa (30°20′N, 79°25′W; Fig. 1) and Hoyt Hills (32°00′N, 78°30′W). I censused seabirds at these sites on 1-3 October 1983 and 9-11 May 1984 during investigations of the biological effects of topographic mixing (McGillivary et al. 1986).

Surface turbulence, including that related to internal waves, was conspicuous at both the Hoyt Hills and Stetson Mesa. Internal waves are subsurface waves found between water layers of different density or within water layers with vertical density gradients (LaFond 1959). They can be caused by current flow through straits, around peninsulas, or over irregular bottom (see lower part of Fig. 1), as well as by atmospheric disturbances, tidal forces, and shear flow. Except at wind speeds exceeding 15 knots (Owens 1981), internal waves have visible surface mani-

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