

CRANIAL KINESIS IN THE LATE CRETACEOUS BIRDS *HESPERORNIS* AND *PARAHESPERORNIS*

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ABSTRACT.—A recently discovered skull of the Cretaceous toothed diving bird *Hesperornis* permits evaluation of previous descriptions of the skull, analysis of cranial kinesis in hesperornithid birds, and discussion of the evolution of avian cranial kinesis. We found no evidence in hesperornithids for mesokinesis, a system that in lizards involves relative movement of the frontals and parietals. "Maxillokinesis," the fore-aft movements of the palato-maxillary arcade, was also rejected. Evidence for cranial kinesis in hesperornithid birds involves the presence of a streptostylic quadrate bone of virtually modern morphology, three types of flexion zones at the posterior end of the upper jaw, and a hiatus in the nasal-interorbital septum. Among the forms of kinesis found in modern birds, prokinesis, in which the upper jaw moves as a unit, was the dominant type of cranial kinesis in hesperornithids as indicated by the rigid construction of the upper jaw, the position of the holorrhinal nostril, and the anteriorly truncate mesethmoid bone; rynchokinesis and amphikinesis were not possible. Prokinesis is considered primitive for at least the group including Hesperornithiformes and later birds. Discovery of prokinesis in *Hesperornis* represents the first time all of the morphological correlates of prokinesis have been identified in a bird plesiomorphically lacking pterygoid segmentation. Received 23 April 1987, accepted 5 October 1987.

The skulls of birds have long been recognized as being capable of intracranial mobility (Hérissant 1748). After Nitzsch's (1816–1817) analysis, study of avian cranial kinesis received little attention until the beginning of the 20th century (Versluys 1910, 1912). The general patterns of avian kinesis, prokinesis and rynchokinesis, have been described for modern birds (e.g. Hofer 1949, Bock 1964, Bühler 1981, Zusi 1984). The analyses of the evolution of cranial kinesis in birds, however, have been largely theoretical. In part this is due to lack of sufficient fossil data on the early stages of avian cranial anatomy. A newly discovered fossil bird from the Triassic of Texas was examined by two of us (LDM and LMW) and, although streptostylic, was found to lack the morphological features characteristic of modern avian cranial kinesis. Before the discovery of Triassic birds, the late Jurassic bird *Archaeopteryx* was the oldest and most primitive known member of the Aves. The anatomy of *Archaeopteryx* has been the focus of previous studies involving the evolution of cra-

nial kinesis in birds (Bock 1964, Wellnhofer 1974, Whetstone 1983, Bühler 1985). Unfortunately, only three specimens of *Archaeopteryx* preserve cranial material, and all have important details obscured by crushing. Thus, interpretation of the osteological features associated with kinesis is difficult. One aspect of cranial kinesis in *Archaeopteryx*, namely mesokinesis, can be assessed because of new preparation of the "London" cranium (Whybrow 1982). These findings are discussed below.

Although preservational problems prevent detailed analysis of kinesis in *Archaeopteryx*, one group of Mesozoic birds, the Hesperornithiformes, has sufficiently preserved fossil material. Marsh (1880) described the nominative form *Hesperornis*. Fossils of hesperornithiform birds are currently restricted to Cretaceous strata. These birds had lost the capacity for flight and became such highly specialized foot-propelled divers that they could not bring their legs under their bodies and stand upright (despite Marsh's oft-repeated restoration; Heilmann 1926, Martin 1980). Teeth are associated with all of the cranial specimens, some of which have teeth still implanted in the jaws.

There are four described genera of Hesperornithiformes and others as yet undescribed (Martin MS). Presently, three families are rec-

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ognized: the early Cretaceous Enaliornithidae, including only *Enaliornis* (Seeley 1876); the late Cretaceous Baptonithidae, including only *Baptonis* (Marsh 1880, Martin and Tate 1976); and the late Cretaceous Hesperornithidae, including *Hesperornis* and *Paraesperornis* (Marsh 1880, Martin 1984). Cranial materials of *Baptonis* and *Enaliornis* are fragmentary and are insufficient to address kinesis. Thus, we restrict the following discussion of cranial kinesis to data derived from the hesperornithids *Paraesperornis* and, in particular, *Hesperornis*.

Kinematics of the hesperornithid skull were ignored by Marsh (1880). Shufeldt (1915) and Heilmann (1926) did not study the original specimens but restored the palate of *Hesperornis* as being similar to that of a loon. These reconstructions are inaccurate, however, and the hesperornithid palate is unique (Witmer and Martin 1987). Gingerich (1973, 1976) studied the actual fossils described by Marsh (1880), provided a reconstruction (in reality a composite of *Hesperornis* and *Paraesperornis*), and discussed cranial kinesis. Our investigations of hesperornithid birds provide detailed positive evidence for prokinesis in a Mesozoic bird and give insight into the evolution of cranial kinesis in birds.

MATERIALS

Abbreviations: KUVP, Kansas University Vertebrate Paleontology, Lawrence, Kansas; YPM, Yale Peabody Museum, New Haven, Connecticut; USNM, U.S. National Museum, Washington, D.C.

The skulls of the hesperornithids studied were collected from the Upper Cretaceous (Senonian) Smoky Hill Chalk Member of the Niobrara Formation in western Kansas. Four skulls of *Hesperornis regalis* provide data relevant to cranial kinesis; two are virtually complete skulls. The poorest of the four skulls is USNM 4978, which is fragmentary and includes only the premaxilla, left lacrimal, and lower jaws (Lucas 1903).

Marsh (1880) described two of the four skulls of *Hesperornis regalis*. The principal specimen, YPM 1206, was collected by T. H. Russell in 1872 (Marsh 1880). It is a complete skull that was found mostly disarticulated on a slab. Although badly damaged in some areas, the skull provides important data for a study of cranial kinesis. This specimen was employed by Gingerich (1973) in his study of the morphology and kinesis of the skull of *Hesperornis*. The other major specimen is YPM 1207, a well-preserved fragment of the braincase (Marsh 1880) that yields details of quadrate mobility.

Perhaps the best skull of a hesperornithid is KUVP

71012. This specimen is a virtually complete skull of *Hesperornis regalis* found in 1981 in Logan Co., Kansas, by C. R. Bonner and M. C. Bonner. The skull is disarticulated, beautifully preserved, and, except for the partially crushed braincase, undistorted. This was the primary specimen used in our study, although all the specimens were examined.

The other hesperornithid, *Paraesperornis alexi*, is represented by the holotype specimen KUVP 2287, which was collected by H. T. Martin from Graham Co., Kansas, in 1894. KUVP 2287 is mostly complete, partially articulated, but crushed in some areas. Williston (1898) referred the specimen to *Hesperornis gracilis*, but Martin (1984) recognized it as a genus distinct from *Hesperornis*. Lucas (1903) figured the left quadrate and pterygoid (the latter mislabeled as right) of this specimen, and Gingerich (1976) provided photographs of the entire skull and of the left quadrate and pterygoid.

CRANIAL KINESIS

In many groups of birds and lizards the opening of the mouth results not only from depression of the lower jaw but also from elevation of the upper jaw via rotation around intracranial hinges (Nitzsch 1816–1817, 1822). Versluys (1910, 1912, 1936) studied the upper jaw system of extant reptiles and birds and of extinct reptiles such as captorhinomorphs and theropod dinosaurs. Versluys classified the types of intracranial mobility on the position of the hinge. In the metakinetic condition a hinge is developed between the dermal skull roof (dermatocranium) and the endochondral portion of the braincase (the occipital segment). In the mesokinetic condition (*sensu* Versluys), a hinge is situated further anteriorly between dermal bones of the skull roof; the hinge lies above the orbits between the frontal and parietal bones as in some lizards, anterior to the orbits between the frontal and nasal bones as in snakes, or even further anteriorly within the premaxillonasal region as in birds.

The fundamental distinction between the typical mesokinetic condition of lizards (with a hinge within the braincase) and the condition observed in birds and snakes (where the hinge is between the upper jaw and braincase) was noted by Hofer (1949, 1955, 1960). He proposed a modified terminology (Hofer 1949): metakinesis, as defined above; mesokinesis, with the main hinge within the dermal skull roof of the braincase; prokinesis, with a preorbital hinge (or hingelike structure) between the upper jaw

and braincase; and rhynchokinesis, with a hingelike structure further anteriorly within the upper jaw. Simonetta (1960) challenged Hofer, arguing for the use of "mesokinesis" for all birds. Hofer's terminology, however, is reasonable and has been adopted by most workers (Frazzetta 1962, Bock 1964, Bühler 1981, Burton 1985). Meso-, pro-, and rhynchokinesis have been suggested for birds and will be discussed below. Metakinesis will be mentioned only in the discussion of mesokinesis.

MESOKINESIS

The presence of a frontoparietal joint (mesokinesis) has been best described in lizards (Versluys 1912; Frazzetta 1962; Russell 1964; Rieppel 1978, 1979). Hofer (1960) and Frazzetta (1962, 1986) noted that most lizards are amphikinetic (possess two joints) in that both metakinetic and mesokinetic joints are developed. Upon protraction of the palate the upper jaw (including the frontal) rotates dorsally about the mesokinetic joint, while the parietal segment is depressed and rotates ventrally about the metakinetic joint (Fig. 1a). Although this basic pattern is widespread in lizards, some forms fuse the metakinetic joint and are only mesokinetic (Hofer 1960, Frazzetta 1962, Rieppel 1978).

This last form of kinesis, mesokinesis without metakinesis, has been suggested for birds. Bock (1964) acknowledged the poor preservation of the existing specimens of *Archaeopteryx* but postulated the existence of a mesokinetic hinge, primarily on theoretical grounds. Discovery of the Eichstatt specimen of *Archaeopteryx*, with its unfused frontals and parietals, led some workers to believe that *Archaeopteryx* was indeed mesokinetic (Ostrom 1976). Verification of mesokinesis in *Archaeopteryx* was not possible until Whybrow (1982) undertook new preparation of the British Museum (Natural History) specimen of *Archaeopteryx*. Whetstone (1983) studied this braincase and, finding the tight suturing of the frontal to the parietal, rejected mesokinesis for *Archaeopteryx*. Martin (1983) and Bühler (1985) confirmed these findings.

Whetstone discovered the presence of jointlike structures (Fig. 2d) between the frontals and parietals in *Parahesperornis* and *Enaliornis* (Martin 1983). Martin (1984) also suggested mesokinesis for *Parahesperornis*. In KUV 71012 the ventrolateral surface of the frontal (Fig. 3b: fac po pr) is excavated into a troughlike struc-

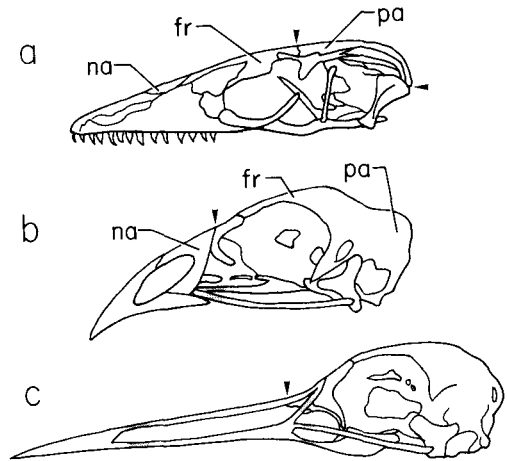


Fig. 1. Kinematic interpretation of mesokinesis, prokinesis, and rhynchokinesis indicating flexion zones (stippling) and hinges between functional units (arrows). (a) Mesokinesis in the skull of the lizard *Varanus*; the anterior arrow indicates the mesokinetic hinge and the posterior arrow the metakinetic hinge. (Redrawn from Rieppel 1978.) (b) Prokinesis in the skull of *Gallus*; the arrow shows the position of the craniofacial hinge dorsal to the mesethmoid, and the stippling shows the palatal and jugal bar bending zones. (c) Rhynchokinesis in the skull of *Grus*; the arrow represents the medial portion of the craniofacial hinge dorsal to the anteriorly protruding mesethmoid, and the stippling indicates the same palatal and jugal bar bending zones as in the prokinetic bird and additional bending zones in the nasal, dorsal, and ventral bars. Abbreviations: fr = frontal bone; na = nasal bone; pa = parietal bone.

ture to receive the cylindrical, polished postorbital process of the parietal (Fig. 3a: po pr). The corresponding surfaces do not match precisely, perhaps indicating persistent cartilage at their juncture.

The frontoparietal contact is quite complex in hesperornithid birds. It may not be simply a case of a plesiomorphically open suture, because the posterior portion of the braincase is fused as tightly as in modern neognaths. In *Enaliornis* the frontals and parietals had a loose, buttressing contact, and there is little development of postorbital projections. These structures are fully developed in *Parahesperornis*, where the frontoparietal juncture is formed by a posterior ridge on the frontals fitting into an anterior groove along the parietals. In *Hesperornis* (Fig. 2a, d; Fig. 3a, b) the posterior portion of the frontals is roughly triangular and forms

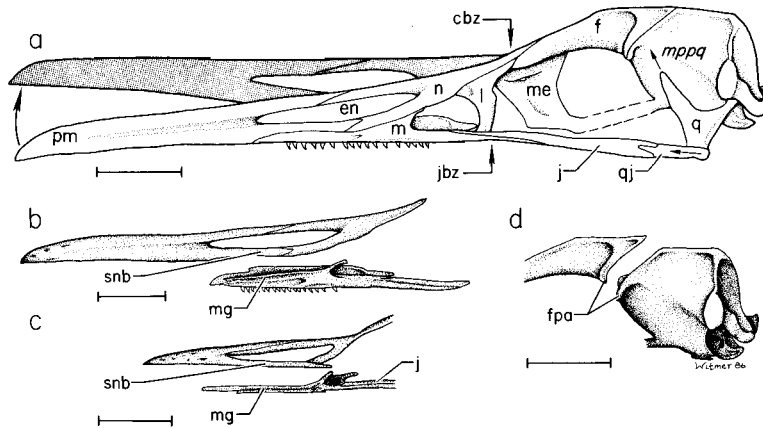


Fig. 2. Prokinesis in *Hesperornis regalis*. (a) Skull of *H. regalis* in left lateral view. The shaded premaxilla and nasal represents movement of the upper jaw resulting from protraction of the palate during prokinesis. (b) Partially exploded upper jaw of *H. regalis* in left lateral view showing the tongue-and-groove suture between the maxilla and the premaxilla/nasal complex. (c) The same in a modern loon, *Gavia immer*. (d) Partially exploded braincase and frontal of *H. regalis* in left lateral view showing the jointlike frontoparietal contact. The frontal overlies the parietal when connected. Scale bars equal 3 cm. Abbreviations: cbz = craniofacial bending zone within the premaxilla and nasal, en = holorrhinal external naris, f = frontal bone, fpc = frontoparietal contact, j = jugal bone, jbz = jugal bar bending zone within the maxilla and jugal, l = lacrimal bone, m = maxilla, me = mesethmoid, mg = maxillary groove in maxilla to receive the subnarial bar, mppq = *M. protractor pterygoidei et quadrati* originating on the braincase and inserting on the orbital process of the quadrate, n = nasal bone, pm = premaxilla, q = quadrate bone, qj = quadratojugal bone, snb = subnarial bar formed by processes from the premaxilla and nasal and fitting into the maxillary groove of the maxilla.

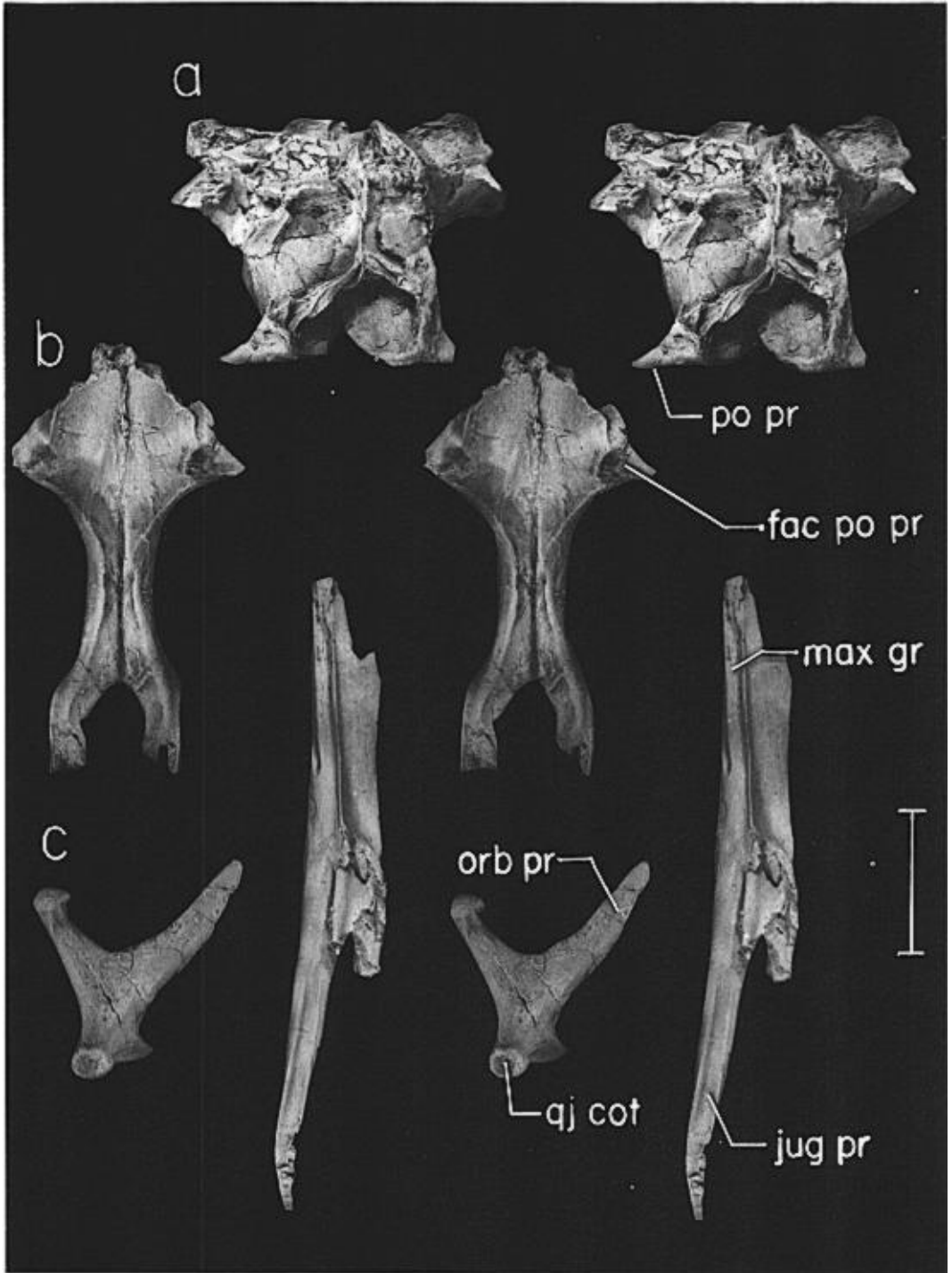
an interdigitating suture with the parietal, while the rest of the contact is a loose squamous one with the frontals overlying the parietals.

If there were a frontoparietal joint in *Hesperornis*, it is difficult to understand how the joint functioned. As mentioned, in some lizards an anterior cranial segment rotates dorsally around a transverse horizontal axis within the dermal skull roof (the frontoparietal or mesokinetic hinge). The frontals in *Hesperornis* overlap the parietals (Fig. 2d), however, and the only possible position of the axis of rotation is ventral to the dermal skull roof (that is, within the braincase). This overlap would inhibit the mesokinetic movement found in other vertebrates but would permit the frontals to rotate ventrally about the frontoparietal articulation. This movement, strictly speaking, could not be

termed "mesokinesis" because mesokinesis involves dorsal, not ventral, rotation of the frontals about the frontoparietal joint. But the frontals of *Hesperornis* lie on the mesethmoid, which is firmly connected to the parasphenoid rostrum and hence the cranium (Fig. 2a). This relationship, which is preserved in YPM 1206, would seem to disallow significant ventral rotation of the frontals in the adult.

The hesperornithid frontoparietal "joint," therefore, is a problematical structure. The frontals could not be elevated because of their overlap on the parietals, nor could they be depressed because of resistance from the ossified mesethmoid-rostrum-braincase assemblage. There are several hypotheses that may account for the incongruity. One hypothesis is that the juncture is a nonfunctional feature inherited from an

Fig. 3. Stereophotographs of cranial elements of *Hesperornis regalis* (KUV 71012). (a) Braincase unit in dorsal view (anterior is toward the bottom of the page) showing the cylindrical postorbital process of the parietal. (b) Frontal bones in ventral view (anterior is toward the bottom) showing the facet receiving the postorbital process of the parietal. (c) Right quadrate in lateral view (anterior is toward the right). (d) Left maxilla in dorsolateral view (anterior is toward the top) showing the maxillary groove that receives the



subnarial processes of the premaxilla and nasal. Abbreviations: fac po pr = facet on the frontal bone for the postorbital process of the parietal; jug pr = dorsoventrally flattened jugal process of maxilla; max gr = maxillary groove; orb pr = orbital process of quadrate; po pr = postorbital process of the parietal bone; qj cot = cotyle for quadratojugal. Scale bar equals 2 cm.

ancestor in which the joint was functional. At present, however, none of the proposed sister taxa of birds are known to have the peculiar hesperornithid frontoparietal contact. Another hypothesis is that the suture between the frontals and parietals is a growing zone with no kinematic function. Comparable junctures or sutures between growing skull bones are widely distributed (though not as highly developed) in reptiles and amphibians. The hesperornithid frontoparietal juncture may have provided increased strength; the broad contact surfaces served to prevent breakage within the braincase. The adductor musculature originated immediately posterior to the frontoparietal suture. During biting activity of the elongate hesperornithid jaw apparatus, stress on this suture would have been significant. We believe the frontoparietal suture in hesperornithiform birds had no kinematic function in adults and is a primitive feature that is obliterated through pneumatization in most modern birds.

Mesokinesis was reported in an early Tertiary paleognath by Houde and Olson (1981). They noted that the "frontals and parietals are not merely unfused, but actually form an articulating joint, as may also be true of certain Hesperornithiformes . . ." We now can rule out a kinetic frontoparietal articulation in *Archaeopteryx*, hesperornithids, and all other known birds. Until the cranial kinematics of these early paleognaths are analyzed in detail, it is better to regard these birds as simply retaining the sutured skull roof observed in nonavian archosaurs, *Archaeopteryx*, tinamous, some ratites, and young neognaths.

MAXILLOKINESIS

The main systems of cranial kinesis in modern birds, prokinesis and rynchokinesis, were rejected for *Hesperornis* by Gingerich (1973, 1976), although he was a little more cautious regarding prokinesis in his 1976 paper. Alternatively, he postulated a new type of cranial kinesis that he termed maxillokinesis. Maxillokinesis, as formulated by Gingerich, is not found in birds or any other living vertebrates. In *Hesperornis* a distinct groove is situated obliquely on the dorsolateral surface of the maxilla into which the corresponding processes of the premaxilla and nasal fit (Fig. 2b: mg). The premaxilla and nasal are joined by a vertical squamous suture below the external naris. Ac-

ording to the maxillokinesis hypothesis (Gingerich 1973), this "subnarial bar" (Fig. 2a, b: snb), fitting into the maxillary groove, served to guide the maxilla in fore-aft movements associated with protraction and retraction of the palate. Gingerich (1976) later suggested that the "only possible functional advantage of having the kind of maxillary kinesis postulated here would be in moving each side independently," perhaps as in snakes (Albright and Nelson 1959). As additional evidence for gliding maxillae, Gingerich (1973) cited the disarticulated nature of the specimens, in which the maxillae were found separated from the other skull bones on the slab.

Disarticulation of the facial bones, however, is not unique to *Hesperornis*. Maceration of the skulls of many modern birds often results in disarticulation of the premaxilla, maxillae, nasals, and palatines. None of these birds is maxillokinetic. Thus, disarticulation is not strong evidence for maxillokinesis. Gingerich's major line of evidence, the presence of a maxillary groove, also is not unique to *Hesperornis*. Similar grooves to receive the premaxillonasal bar can be found on the maxillae of modern birds (at least while they are still growing). This premaxilla-nasal-maxilla assembly is fused in the adults of most modern birds, but in some ratites (e.g. *Struthio*) and some basal neognaths (e.g. loons [Fig. 2c], penguins, chickens) the maxillary groove is retained in the postnestling stage. There is no independent movement of the maxilla (maxillokinesis) in any modern bird, however. Therefore, the presence of a maxillary groove and subnarial bar in *Hesperornis* is considered primitive and is in itself insufficient to demonstrate maxillokinesis.

AVIAN CRANIAL KINESIS

Within modern birds two forms of cranial kinesis are dominant, prokinesis and rynchokinesis (Bock 1964, Bühler 1981). Amphikinesis (found only in rails) may represent a third system (Zusi 1984). These kinematic systems share certain features not found in nonavian kinesis. The skulls of all birds may be divided into four kinematical units: (1) the upper jaw (or a portion thereof); (2) the palate, including the quadrates, pterygoids, jugal bars, and palatovomer complex; (3) the braincase; and (4) the lower jaw (Bock 1964, Bühler 1981). Hesperornithids also possess these four kine-

matic units. We excluded the lower jaw from our discussion of cranial kinesis in hesperornithids because it may itself represent as many as five kinematic units because of the presence of a prementary bone (Martin 1987) and an intramandibular articulation (Gregory 1951). The omission of the complex relationship of the hesperornithid lower jaw to cranial kinesis as a whole does not affect the identification of prokinesis in these birds.

Prokinesis is common in modern birds, with rhynchokinesis being restricted to certain taxa (primarily the Gruiformes, Charadriiformes, Columbiformes, Apodiformes, and "Paleognathae"; Bühler 1981, Zusi 1984). Despite the great morphological differences between the functional extremes (for example, the prokinetic parrots and rhynchokinetic woodcocks), these two types of kinesis are very similar (Bock 1964). The fundamental difference lies in where bending occurs between kinematic units 1 and 2, that is, between the upper jaw and braincase. In prokinetic birds (Fig. 1b) bending occurs posterior to the upper jaw, while in rhynchokinetic birds (Fig. 1c) bending also occurs within the upper jaw. There are various types of rhynchokinesis that are differentiated by the position of the bending zone within the upper jaw. Bühler (1981) and Zusi (1984) discussed rhynchokinesis in some detail, and we consider here only the rhynchokinetic features that contrast the prokinetic features of hesperornithids.

In avian cranial kinesis, in contrast to the other forms of dermal skull roof kinesis ("prokinesis" of snakes, mesokinesis, and metakinesis), there are usually no true diarthroses or syndesmoses formed, only bending zones within bone. Morphologists generally speak of "hinges," "bending zones," or "plate-spring articulations" and not "joints." Note that some prokinetic birds (for example, large parrots), but no rhynchokinetic birds, develop synovial joints between the upper jaw and braincase (Bühler 1981).

Some features are shared by all forms of avian cranial kinesis and establish that hesperornithids possessed some form of avian kinesis. Among these are streptostyly, the disposition of certain flexion zones, and a gap in the nasal-interorbital septum.

Streptostyly.—The terms streptostyly and monimostyly were proposed to describe whether or not the quadrate bone was capable of moving relative to the braincase (Stannius 1856). A

streptostyly quadrate has some mobility relative to the braincase, while a monimostyly quadrate lacks relative movement. Streptostyly has been considered by some as a synonym for kinesis, but Versluys (1912) correctly noted that metakinetic forms may be monimostyly. While streptostyly does not necessarily indicate kinesis, it remains a constant feature of avian cranial kinesis. All modern birds are streptostyly (Bock 1964).

Hesperornis and *Parahesperornis* both have streptostyly quadrates (Fig. 2a: q, Fig. 3c) that exhibit (1) a diarthrotic articulation between the condyle of its otic process and the corresponding cotyle on the braincase; (2) an elongate orbital process (Fig. 3c: orb pr) for insertion of *M. protractor pterygoidei et quadrati* and for origin of *M. pseudotemporalis profundus*; (3) a probably diarthrotic articulation with the pterygoid bone; and (4) a lateral cotyle articulating by diarthrosis or syndesmosis with a corresponding condyle from the quadratojugal (Fig. 3c: qj cot). Thus, hesperornithids have typically avian quadrates with surprisingly modern features.

Three types of flexion zones at the posterior end of the upper jaw.—In birds the upper jaw connects kinematically to the rest of the skull by three types of bending zones: one dorsally (the craniofacial hinge; modified in rhynchokinetic birds), a pair laterally in the jugal bars, and a pair ventrally in the palatal bars. These bending zones are characterized by flattening and thinning of the bone. In some cases, especially in large-skulled forms, a multilayered condition is developed in which the bones building the flexion zone lose their pneumaticity and form, with the intervening connective tissue, a structure that permits deformation despite a sometimes considerable thickness (see Bühler 1980, 1981). These features are fully developed in hesperornithids.

In *Hesperornis* and *Parahesperornis* the craniofacial bending zone is within the posterodorsal processes of the premaxilla and nasals anterior to their juncture with the frontals and dorsal to the anterior end of the mesethmoid (Fig. 2a: cbz). Although Gingerich (1976) considered these posterodorsal processes to be too thick for bending, the processes are complete on KUVV 71012 (*Hesperornis*) and KUVV 2287 (*Parahesperornis*) and are very thin and flattened dorsoventrally as in modern prokinetic birds.

The bending zone within the jugal bar is typically avian in hesperornithids (Fig. 2a: jbz). The

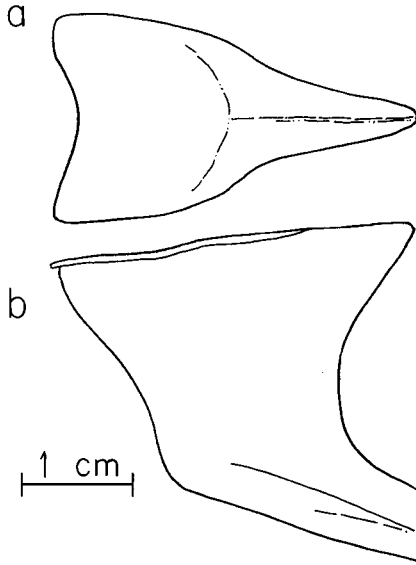


Fig. 4. Mesethmoid of *Hesperornis regalis* (KUV 71012) in (a) dorsal and (b) left lateral views. The anterior margin of the mesethmoid resembles prokinetic birds in being transversely truncate rather than protruding anteriorly as in rhynchokinetic birds.

processes by which the maxilla and jugal articulate are dorsoventrally flattened and very thin, together forming a multilayered structure. Figure 3d shows the thin jugal process of the maxilla and the broad groove for the jugal that overlies it.

The hesperornithid palatal bending zone is developed, as in modern birds, within the palatine bones. Witmer and Martin (1987: fig. 4) described and figured the palate of *Hesperornis*. The anterior end of the palatine is extremely thin at its contact with the maxilla, and deformation would have occurred within the palatine posterior to this juncture.

Gap in the nasal-interorbital septum.—In hesperornithids, as in most modern birds, the interorbital septum (which ossifies primarily as the mesethmoid) is not continuous with the nasal septum. This results in a hiatus in the nasal-interorbital septum (Fig. 1b and Fig. 2a: me). The nasal septum is not preserved in any of the fossils. KUV 71012 (*Hesperornis*) includes a complete mesethmoid (Fig. 4); the anterior edge of the bone is finished, indicating that a hiatus was present. This hiatus in the nasal-interorbital septum is characteristic of all modern prokinetic birds and also many neognathine rhynchokinetic birds such as gulls. Paleognaths have

a continuous nasal-interorbital septum; this is probably an apomorphic condition. Most workers (Bock 1964, Bühler 1981, Zusi 1984) have considered paleognathine rhynchokinesis to have been acquired independently of neognathine rhynchokinesis.

PROKINESIS IN HESPERORNITHIDS

In modern birds the main type of cranial kinesis is prokinesis, in which the whole upper jaw is elevated relative to the braincase upon protraction of the palate. The unit construction of the upper jaw, the position of the holorhinal nostril, the relative thickness (oval in cross section) of the bony bars surrounding the nostril, and the shape of the anterior end of the mesethmoid suggest that hesperornithids were prokinetic.

Upper jaw segment operating as a rigid unit.—In modern prokinetic birds the bones of the upper jaw (the premaxilla, maxillae, and nasals) are firmly united, if not completely fused, such that the unit (Fig. 1b) is separated kinematically from the rest of the skull. Deformation within the upper jaw unit is not possible. This situation contrasts with rhynchokinetic birds, in which parts of the upper jaw (Fig. 1c) are flexible and the anterior portion can be moved separately. Deformation typically occurs in the dorsal, ventral, and nasal bars of the upper jaw (although in ratites the last is accomplished by interruption of the nasal bar).

The upper jaw bones of hesperornithids (Fig. 2a) are not co-ossified (the primitive condition) but are tightly united and exhibit the rigid unit-construction characteristic of other prokinetic birds. Hesperornithids lack bending zones within the upper jaw. Gingerich rejected rhynchokinesis for *Hesperornis*, but his restoration (Gingerich 1973: fig. 1, 1976: fig. 4) does not preclude rhynchokinetic bending in the dorsal and ventral bars immediately posterior to the anterior margin of the external naris. Our analysis (Fig. 2a) differs from Gingerich's restoration, and it must be remembered that the latter is a composite of two genera and could not incorporate data from the newly discovered University of Kansas specimen (KUV 71012). Bending in the dorsal bar (the dorsal process of the premaxilla) is precluded in *Hesperornis* by its considerable thickness (approximately 3 mm) and its oval shape. The presence of teeth along the ventral bar would prevent rhynchokinesis

and amphikinesis but not prokinesis (Zusi 1984). Gingerich (1973, 1976) reconstructed a ventral bar that is rather thin and edentulous anteriorly. In KUVV 71012, however, the teeth extended further anteriorly (Fig. 2a, b) than indicated by Gingerich (1973, 1976). Furthermore, the maxillae are broad, vaulted plates of bone that when united with the premaxilla are too thick to permit deformation in the ventral bar. Thus, the upper jaw of hesperornithids is a rigidly constructed unit with no internal bending zones.

The lacrimals of hesperornithids traveled with the upper jaw during protraction and retraction. This is not common in modern birds, where the lacrimal is usually associated with the braincase segment and not with the upper jaw segment. It developed convergently within several groups of birds, however, such as nightjars (Bühler 1980) and penguins (Zusi 1975).

Holorhinal nostril situated anterior to craniofacial hinge.—The rigidity of the upper jaw is correlated with the shape and position of the nostril (Bock and McEvey 1969, Bühler 1981, Zusi 1984). In modern prokinetic birds (Fig. 1b) the external naris is oval posteriorly and situated anterior to the craniofacial bending zone (holorhiny), disallowing bending in the nasal bar. The upper jaw must act as a single unit. In rhynchokinetic birds (Fig. 1c) the external naris is usually slitlike posteriorly, always extends posterior to the craniofacial bending zone (schizorhiny), and permits functional separation of the dorsal and nasal bars and deformation of the nasal bar (Zusi 1984). Elevation and depression of only the anterior part of the upper jaw is possible. Zusi (1984: 10) noted that among modern taxa "no bird is both rhynchokinetic and holorhinal." In hesperornithids the nostril is oval posteriorly and is 20–30 mm anterior to the craniofacial bending zone (Fig. 2a: en), preventing deformation within the upper jaw. Thus, a typically prokinetic holorhinal nostril occurs in *Hesperornis* and *Parahesperornis*.

Mesethmoid truncate anteriorly.—Among birds exhibiting a hiatus in the nasal-interorbital septum, the shape of the anterodorsal margin of the mesethmoid reflects the type of kinesis (Bühler 1981, Zusi 1984). In prokinetic birds the anterodorsal margin of the mesethmoid is truncate or transversely squared off. In rhynchokinetic birds the median portion of the mesethmoid protrudes anterior to the cranial attachment of the nasal bars (Fig. 1c) and thus effects division of the craniofacial hinge and

separation of the dorsal and nasal bars (Zusi 1984). The mesethmoids of hesperornithids (Fig. 4) resemble those of modern prokinetic birds in lacking any median protrusion and being squared off transversely. The mesethmoid (along with the frontal) acts as a fulcrum for dorsal rotation of the upper jaw about the craniofacial hinge.

A related matter is the presence or absence of a distinct hinge line in dorsal view (Zusi 1984). In most prokinetic birds with highly pneumatic skulls there is a single well-defined band where pneumaticity is lacking; this band represents the craniofacial bending zone. A few rhynchokinetic birds such as skimmers (*Rhynchops*) develop this single straight hinge line. But this hinge line is not developed in any of the long-skulled diving birds such as grebes (*Podiceps*), guillemots (*Uria*), mergansers (*Mergus*), emperor penguins (*Aptenodytes*), cormorants (*Phalacrocorax*), or loons (*Gavia*) despite the well-developed upper jaw mobility of these birds. This results because, as a whole, the skull bones of these divers are poorly or not pneumatized. It is therefore not surprising that such a distinct line is lacking in hesperornithids as well.

DISCUSSION

Recent studies of *Archaeopteryx*, Hesperornithiformes, and modern birds indicate that birds were never metakinetic because in all birds the occipital region is fused with the dermal skull roof. Several groups of birds have been described as mesokinetic, including hesperornithids. We suggest that no known birds have ever had a true mesokinetic hinge of saurian morphology. Likewise, maxillokinesis, as proposed by Gingerich (1973) for *Hesperornis*, is probably not found in any vertebrates. Thus, prokinesis and rhynchokinesis remain the only forms of cranial kinesis observed in birds.

The identification of prokinesis in hesperornithiform birds supports the suggestion (Bock 1964, Zusi 1984) that prokinesis is primitive for post-*Archaeopteryx* birds. Bühler (1985) suggested that *Archaeopteryx* also may have had kinesis of a form resembling prokinesis. Although the existing *Archaeopteryx* material does not permit the identification of all of the correlated features seen in hesperornithids and modern prokinetic birds, Bühler's hypothesis raises the possibility that prokinesis may be a

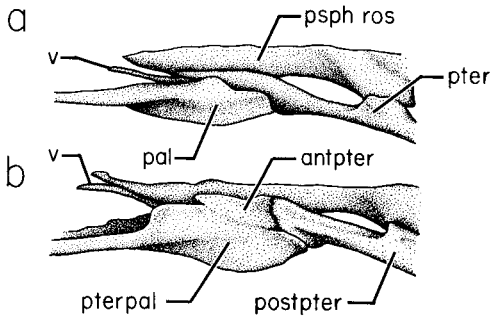


Fig. 5. Neognath pterygoid segmentation in *Stearntornis caripensis*. Left lateral view with anterior toward the left. (a) Nestling showing a true palatine and an unsegmented (unit) pterygoid that contacts the vomer. (b) Adult showing the results of pterygoid segmentation. Abbreviations: antpter = anteropterygoid (or hemipterygoid), representing the anterior portion of the segmented pterygoid; pal = true palatine bone before pterygoid segmentation; postpter = posteropterygoid ("pterygoid" of most workers), representing the free posterior portion of the segmented pterygoid; psph ros = parasphenoid rostrum; pter = true unit pterygoid before segmentation; pterpal = pterygopalatine ("palatine" of most workers), representing the fusion of the true palatine and the anteropterygoid; v = vomer. (Redrawn from Pycraft 1901.)

primitive feature of the Aves. Paleognath and neognath rhynchokinesis are regarded as independent specializations (Bock 1964, Zusi 1984).

We describe here all the requisite features of prokinesis in a nonneognath bird. As discussed by Witmer and Martin (1987), the palatal morphology of hesperornithids is unique and is neither "paleognathous" (Gingerich 1973) nor "neognathous" (Balouet 1982). The detailed similarities between hesperornithid and neognath prokinesis suggest that they are indeed homologous. Hesperornithids, however, lack the typical neognath palatal specializations.

Most modern prokinetic birds have a peculiar palatal ontogeny (Fig. 5). The dermal pterygoid bone of nestlings segments during ontogeny. Its anterior portion fuses to the palatine bone, and the posterior portion remains free. A (usually) diarthrotic *intrapterygoid* joint forms between anterior and posterior segments of an initially single bone (Fig. 5; Pycraft 1901). Jollie (1957) referred to the anterior segment as the anteropterygoid (hemipterygoid of Pycraft 1901) and the posterior segment as the posteropterygoid. The fused anteropterygoid-palatine as-

sembly is the pterygopalatine. This pterygoid segmentation may be the principal factor shaping the neognath palate (Witmer MS). None of the so-called "paleognathous" birds exhibit pterygoid segmentation. It appears to be a synapomorphy of the Neognathae (Pycraft 1900, Balouet 1982). Some neognaths (anatids, for example) secondarily suppress segmentation and have a true unit pterygoid. Nevertheless, modern birds show a positive correlation of pterygoid segmentation and prokinesis. (Recall that neognath rhynchokinesis is considered an apomorphic modification from prokinetic ancestors.) No paleognath has either segmented pterygoids or a prokinetic skull.

There is no evidence of pterygoid segmentation in hesperornithids (contrary to Balouet 1982). Therefore, the identification of prokinesis in hesperornithids represents a positive demonstration of prokinesis in a bird with plesiomorphically unsegmented pterygoids. The correlation between pterygoid segmentation and prokinesis observed in modern birds is thus misleading. Prokinesis was present in birds before the evolution of pterygoid segmentation. It often has been assumed that the rhynchokinetic paleognaths evolved from prokinetic ancestors. This assumption seemed problematical in light of the positive correlation of prokinesis and pterygoid segmentation. This can now be seen to be an entirely plausible hypothesis because, as indicated by the hesperornithids, prokinesis is possible in birds with primitively unsegmented pterygoids.

ACKNOWLEDGMENTS

We thank W. Hoffman, R. M. Mengel, R. L. Zusi, and an anonymous referee for their valuable comments on various drafts of this manuscript. For permission to examine specimens in their care we thank A. J. Charig, A. Milner, and C. A. Walker (British Museum [Natural History], London); H. Jaeger and H. Fischer (Humboldt Museum für Naturkunde, Berlin); G. Viohl (Jura Museum, Eichstätt); P. Wellenhofer (Bayerische Staatssammlung, Munich); S. L. Olson, R. L. Zusi, N. Hotton III, and A. Elzanowski (U.S. National Museum, Washington, D.C.); J. H. Ostrom and M. A. Turner (Yale Peabody Museum, New Haven); R. M. Mengel and M. A. Jenkinson (University of Kansas Museum of Natural History, Lawrence); and E. Wendt (private collection, Asperg, Württemberg). We thank O. Bonner for preparation of KUPV 71012 and M. A. Klotz for Fig. 3a. Funding for P. Bühler was provided by Deutsche Forschungsgemeinschaft (Bu 567/1-1). Funding for L. D. Martin was provided

by the University of Kansas (sabbatical leave) and General Research Grant 3251-5038, NSF DEB 7821432, and National Geographic 2228-80. Funding for L. M. Witmer was provided by the University of Kansas, the University of Kansas Museum of Natural History, and the American Ornithologists' Union Alexander Wetmore Fund.

LITERATURE CITED

- ALBRIGHT, R. G., & E. M. NELSON. 1959. Cranial kinetics of the generalized colubrid snake *Elaphe obsoleta quadrivittata*. II. Functional morphology. *J. Morphol.* 105: 214-292.
- BALOUET, J.-C. 1982. Les paleognathes (Aves) sont-ils primitifs? *J. Soc. Zool. France* 1982: 648-653.
- BOCK, W. J. 1964. Kinetics of the avian skull. *J. Morphol.* 114: 1-42.
- , & A. MCEVEY. 1969. Osteology of *Pedionomus torquatus* (Aves: Pedionomidae) and its allies. *R. Soc. Victoria Proc.* 82: 87-232.
- BÜHLER, P. 1980. Zur Methodik funktionsmorphologischer Untersuchungen. Pp. 185-189 in *Acta 17th Congr. Int. Ornithol.* (R. Nohring, Ed.). Berlin, Verlag der Deutschen Ornithologen.
- . 1981. Functional anatomy of the avian jaw apparatus. Pp. 439-468 in *Form and function in birds*, vol. 2 (A. S. King and J. McLelland, Eds.). New York, Academic Press.
- . 1985. On the morphology of the skull of *Archaeopteryx*. Pp. 135-140 in *The beginnings of birds* (M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer, Eds.). Eichstätt, Jura-Museum.
- BURTON, P. J. K. 1985. Skull. Pp. 549-551 in *A dictionary of birds* (B. Campbell and E. Lack, Eds.). Calton, England, Poyser.
- FRAZZETTA, T. H. 1962. A functional consideration of cranial kinesis in lizards. *J. Morphol.* 111: 287-319.
- . 1986. The origin of amphikinesis in lizards. Pp. 419-461 in *Evolutionary biology*, vol. 20 (M. K. Hecht, B. Wallace, and G. Prance, Eds.). New York, Plenum.
- GINGERICH, P. D. 1973. Skull of *Hesperornis* and early evolution of birds. *Nature* 243: 70-73.
- . 1976. Evolutionary significance of the Mesozoic toothed birds. *Smithsonian Contrib. Paleobiol.* 27: 23-33.
- GREGORY, J. T. 1951. Convergent evolution: the jaws of *Hesperornis* and the mosasaurs. *Evolution* 5: 345-354.
- HEILMANN, G. 1926. *The origin of birds*. London, Witherby.
- HÉRRISANT, M. 1748. *Observations anatomiques sur les mouvemens du bec des Oiseaux*. Mémoires de Mathématique et de Physique de L'Académie Royale des Sciences 1748: 345-386.
- HOFER, H. 1949. Die Gaumenlücken der Vögel. *Acta Zool.* 30: 209-248.
- . 1955. Neuere Untersuchungen zur Kopfmorphologie der Vögel. Pp. 104-137 in *Acta 11th Congr. Int. Ornithol.* 1954 (Experientia, Suppl. 3).
- . 1960. Vergleichende Untersuchungen am Schädel von *Tupinambis* und *Varanus* mit besonderer Berücksichtigung ihrer Kinetik. *Jahrb. Morphol. mikrosk. Anat.* (Abt. 1) 100: 706-746.
- HOUDE, P., & S. L. OLSON. 1981. Paleognathous carnates from the early Tertiary of North America. *Science* 214: 1236-1237.
- JOLLIE, M. T. 1957. The head skeleton of the chicken and remarks on the anatomy of this region in other birds. *J. Morphol.* 100: 389-436.
- LUCAS, F. A. 1903. Notes on the osteology and relationships of the fossil birds of the genera *Hesperornis*, *Hargeria*, *Baptornis* and *Diatryma*. *Proc. U.S. Natl. Mus.* 26: 545-556.
- MARSH, O. C. 1880. *Odontornithes: a monograph on the extinct toothed birds of North America*. *Mem. Peabody Mus. Nat. Hist.* 1: 1-201.
- MARTIN, L. D. 1980. The foot-propelled diving birds of the Mesozoic. Pp. 1237-1242 in *Acta 17th Congr. Int. Ornithol.* (R. Nöhrling, Ed.). Berlin, Verlag der Deutschen Ornithologen-Gesellschaft.
- . 1983. The origin and early radiation of birds. Pp. 291-338 in *Perspectives in ornithology* (A. H. Brush and G. A. Clark Jr., Eds.). New York, Cambridge Univ. Press.
- . 1984. A new hesperornithid and the relationships of the Mesozoic birds. *Trans. Kansas Acad. Sci.* 87: 141-150.
- . 1987. The beginning of the modern avian radiation. Pp. 9-19 in *Evolution des oiseaux d'après le témoignage des fossiles* (C. Mourer-Chauviré, Ed.). *Doc. Lab. Geol. Fac. Sci. Lyon* No. 99.
- , & J. TATE JR. 1976. The skeleton of *Baptornis advenus* from the Cretaceous of Kansas. *Smithsonian Contrib. Paleobiol.* 27: 35-66.
- NITZSCH, C. L. 1816-1817. Über die Bewegung des Oberkiefers der Vögel. *Deutsch. Arch. Physiol.* (Halle) 2: 361-380, 470; 3: 384-388.
- . 1822. Ueber die Bewegung des Oberkiefers der eidechsenartigen Amphibien. *Deutsch. Arch. Physiol.* (Halle) 7: 68-85.
- OSTROM, J. H. 1976. *Archaeopteryx* and the origin of birds. *Biol. J. Linn. Soc.* 8: 91-182.
- PYCRAFT, W. P. 1900. On the morphology and phylogeny of the Palaeognathae and Neognathae. *Trans. Zool. Soc. London* 15: 149-290.
- . 1901. Some points on the morphology of the palate of the Neognathae. *J. Linn. Soc. London* 28: 343-357.
- RIEPEL, O. 1978. Streptostyly and muscle function in lizards. *Experientia* 34: 776-777.
- . 1979. A functional interpretation of the varanid dentition (Reptilia, Lacertilia, Varanidae). *Gegenbaurs Morphol. Jahrb.* 125: 797-817.

- RUSSELL, D. A. 1964. Intracranial mobility in mosasaurs. *Postilla, Peabody Mus. Nat. Hist.* 86: 1-19.
- SEELEY, H. G. 1876. On the British fossil Cretaceous birds. *Q. J. Geol. Soc.* 32: 496-512.
- SHUFELDT, R. W. 1915. On a restoration of the base of the cranium of *Hesperornis regalis*. *Bull. Am. Paleontol.* 5: 73-85.
- SIMONETTA, A. M. 1960. On the mechanical implications of the avian skull and their bearing on the evolution and classification of birds. *Q. Rev. Biol.* 35: 206-220.
- STANNIUS, H. 1856. Die Amphibien. Pp. 1-270 in *Handbuch der Zootomie. Zweiter Theil, Die Wirbelthiere (Handbuch der Anatomie der Wirbelthiere)*.
- VERSLUYS, J. 1910. Streptostylie bei Dinosauriern. *Zool. Jahrb. (Anat.)* 30: 177-258.
- . 1912. Das Streptostylie-Problem und die Bewegung im Schädel bei Sauropsida. *Zool. Jahrb., Suppl.* 15, 2: 545-716.
- . 1936. Kraniaum und Visceralskelett der Sauropsiden. 1. Reptilien. Pp. 699-808 in *Handbuch der vergleichenden Anatomie der Wirbeltiere*, vol. 4 (L. Bolk, E. Göppert, E. Kallius, and W. Lubosch, Eds.). Berlin and Vienna, Urban and Schwarzenberg.
- WELLNHOFER, P. 1974. Das fünfte Skelettexemplar von *Archaeopteryx*. *Palaeontogr. Abt. A* 147: 169-216.
- WHETSTONE, K. N. 1983. Braincase of Mesozoic birds: I. New preparation of the "London" *Archaeopteryx*. *J. Vertebr. Paleontol.* 2: 439-452.
- WHYBROW, P. J. 1982. Preparation of the cranium of the holotype of *Archaeopteryx lithographica* from the collections of the British Museum (Natural History). *Neues Jahrb. Geol. Palaeontol. Monatsch.* 1982: 184-192.
- WILLISTON, S. W. 1898. Birds. *Univ. Geol. Surv. Kansas* 4: 43-64.
- WITMER, L. M., & L. D. MARTIN. 1987. The primitive features of the avian palate with special reference to Mesozoic birds. Pp. 21-40 in *Proc. First International Roundtable on the Evolution of Birds* (C. Mourer-Chauviré, Ed.). Lyon, CNRS.
- ZUSI, R. L. 1975. An interpretation of the skull structure in penguins. In *The biology of penguins* (B. Stonehouse, Ed.). Bristol, Macmillan.
- . 1984. A functional and evolutionary analysis of rhynchokinesis in birds. *Smithsonian Contrib. Zool.* 395: 1-40.