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ARTICLE

CRANIAL KINESIS IN DINOSAURS: INTRACRANIAL JOINTS, PROTRACTOR MUSCLES, AND THEIR SIGNIFICANCE FOR CRANIAL EVOLUTION AND FUNCTION IN DIAPSIDS

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ABSTRACT—Different forms of intracranial mobility, including streptostyly, pleurokinesis, and prokinesis, have been postulated for many dinosaurs. The basis for inferring kinesis typically has included the presence of presumably synovial intracranial joints (otic and basal joints) and various ad hoc 'sliding joints' (many without modern parallels), whereas the protractor musculature that would have powered movement at these joints has received little attention. No study has reviewed the evidence underlying these inferences, and the functional mechanisms and evolution of kinesis among dinosaurs have remained unclear. We analyzed the relevant musculoskeletal structures in extant diapsids and extinct dinosaurs to evaluate in general the morphological support for inferences of cranial kinesis in dinosaurs. Four criteria (synovial otic joints, synovial basal joints, protractor muscles, and permissive kinematic linkages) were considered necessary but individually insufficient for the inference of kinesis. Assessing these criteria across dinosaurs reveals that synovial otic and basal joints are almost universally present (even in widely acknowledged akinetic taxa), and most taxa retained protractor musculature. However, unlike fully kinetic extant birds and squamates, almost all dinosaurs lacked the kinematic linkages that would have permitted movement (reduced palatal and temporal articulations, additional flexion zones). Thus, synovial basal and otic joints and protractor musculature are diapsid plesiomorphies, and, in the absence of permissive kinematic linkages, most formulations of nonavian dinosaur kinesis are currently problematic. Alternatively, persistent synovial joints may simply be cartilaginous sites that facilitate cranial growth during ontogeny.

INTRODUCTION

Cranial kinesis (the presence of relative movement of portions of the skull at intracranial joints) has been a subject of considerable interest among vertebrate paleontologists. Versluys (1910, 1912, 1936) classified types of cranial kinesis based on the location of the joint in the dorsal part of the skull, being either between the dermatocranium and occipital segment (metakinesis) or one more rostral in the skull (mesokinesis; Fig. 1A). Hofer (1949) further partitioned mesokinesis into mesokinesis proper, which occurs within the braincase (the frontoparietal joint) in many lizards, and prokinesis, which occurs between the braincase and facial skeleton (the nasofrontal joint, or within the nasals), as in birds (Fig. 1A). Streptostyly is the fore-aft movement of the quadrate about the otic joint (quadratosquamosal joint), although transverse movements may also be possible. Many hypothesized types of kinesis require basal joint kinesis (neurokinesis of Iordansky, 1990), that is, movement between the braincase and palate at the basipterygopterygoid joint (Fig. 1A, C).

Functional hypotheses of dinosaur feeding have often incorporated inferences of cranial kinesis, including streptostylic quadrate movement (ankylosaurs and theropods [Versluys, 1910]; *Massospondylus* [Gow et al., 1990]; *Coelophysis* (= *Syntarsus*) [Raath, 1985]; *Allosaurus* [McClelland, 1990; Rayfield, 2005]; *Tyrannosaurus* [Molnar, 1991]), mesokinesis (*Dromaeosaurus* [Colbert and Russell, 1969]; *Hypsilophodon* [Galton, 1974]), pleurokinesis (ornithopods [Norman, 1984; Weishampel, 1984; Ohashi, 2006]), streptostyly and prokinesis (*Shuvuuia* [Chiappe et al., 1998]), and widespread mobility among facial and palatal sutures (*Ceratosaurus* [Bakker, 1986]; *Carnotaurus* [Mazzetta et al., 1998]; *Tyrannosaurus* [Rayfield, 2004]). On the other hand, sauropods (Haas, 1963; Upchurch and Barrett, 2000; Barrett and Upchurch, 2007), ankylosaurs (Haas, 1969; Barrett, 2001; Rybczinski and Vickaryous, 2001), ceratopsians (Haas, 1955; Ostrom, 1964; Dodson, 1996), and sometimes hadrosaurs (e.g., Ostrom, 1961) have been considered to have possessed akinetic skulls. However, the anatomical basis for many of these inferences has yet to be reviewed, particularly in light of new data from in vivo experiments with squamates and birds that should raise concerns regarding cranial kinesis in dinosaurs.

Early hypotheses of cranial kinesis in extant diapsids were formulated largely through the manual manipulation of dead specimens rather than in vivo testing (e.g., Versluys, 1910; Frazzetta, 1962; Bock, 1964; Rieppel, 1978; Bühler, 1981; Weishampel, 1984; Iordansky, 1990; Arnold, 1998; Gussekloo and Bout, 2005). For obvious reasons, inferences of cranial kinesis in extinct dinosaurs have also typically relied on simple skeletal manipulations. These analyses have focused on the presence (and presumed mobility) of synovial joints and smooth, non-interdigitate sutures (e.g., Mazzetta et al., 1998; Rayfield, 2005) as primary indicators of kinesis. Although data from relevant soft tissues, such as muscles, are often incorporated in studies of extant taxa, (e.g., Ostrom, 1962; Herrel et al., 1999, 2000), only a few studies (e.g., Galton, 1974; Norman, 1984; Weishampel, 1984) have incorporated soft-tissue data (e.g., the protractor musculature) in analyses of cranial kinesis in fossil taxa.

Actual mobility at intracranial joints (e.g., streptostyly, mesokinesis, prokinesis) has been clearly documented in some extant

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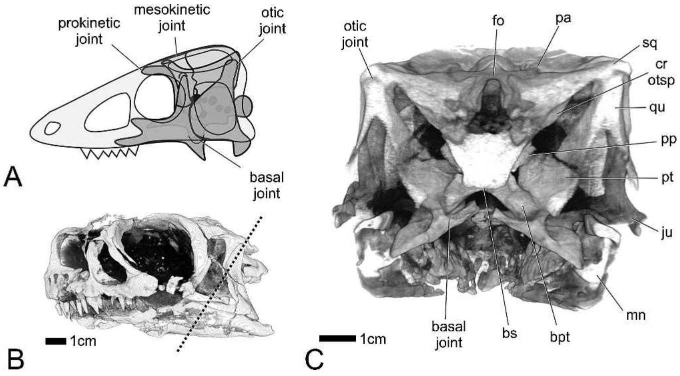

FIGURE 1. Major structures associated with cranial kinesis in diapsids. **A**, schematic of a generalized archosaur indicating hypothesized mobile intracranial joints; **B**, inset of the skull of the basal sauropod dinosaur *Massospondylus carinatus* (BP/1/4779) based on CT data, denoting the plane of section in C in left lateral view; **C**, caudal view of a section through the skull at the plane indicated in B, illustrating the synovial basal and otic joints, as well as other relevant anatomical structures.

taxa (e.g., geckos, *Uromastyx*, snakes, varanids, birds; Herrel et al., 2000; Schwenk, 2000; Bout and Zweers, 2001; Metzger, 2002). However, other analyses have identified a number of taxa (e.g., *Sphenodon*, *Heloderma*, *Iguana*, skinks) that do not express intracranial mobility in naturalistic settings, despite features suggestive of movement (i.e., protractor muscles, synovial basal and otic joints) or phylogenetic relationships that might have predicted mobility (e.g., among iguanids, *Agama* is akinetic but *Uromastyx* is kinetic; Gorniak et al., 1982; Herrel et al., 2000; Schwenk, 2000; Metzger, 2002; Wu, 2003). Therefore, an animal may exhibit morphological features suggestive of intracranial mobility but not necessarily demonstrate functionally significant mobility in vivo.

The functional significance of the protractor musculature and its relationship to powered movements of these intracranial joints also remains inconclusive. Electromyographic studies of geckos suggest that M. protractor pterygoideus indeed plays a role in elevating the snout at the mesokinetic joint during the opening phase of the gape cycle (Herrel et al., 1999). Neornithine birds also have synovial basal and otic joints and protractor muscles, and similar studies (e.g., Bout and Zeigler, 1994) have shown that M. protractor pterygoideus likewise actively powers prokinesis in some birds by protracting the palate and elevating the bill. However, Gussekloo and Bout (2005) found no evidence of powered rotation about these joints in ratite birds, but rather passive, incidental flexion of the bill (rhynchokinesis). Therefore, to what extent protractor musculature actively promotes kinetic movements (i.e., powered cranial kinesis) or perhaps modulates (via eccentric contraction) or resists feeding-induced intracranial movement by being activated with the adductor musculature remains unclear among extant taxa. This paper primarily addresses typical cranial kinesis as displayed in modern birds and (at least some) lizards in which intracranial mobility is grossly visible and measurable (and often powered by muscles), because this is the sort of kinesis usually postulated for extinct dinosaurs. Thus, we distinguish kinesis from the very slight and subtle movements that occur at many (if not all) patent sutures and that allow slight accommodation of bones and dissipation of mechanical stresses.

Interpretations of cranial kinesis have introduced a complicated and often confused nomenclature that muddles our understanding of the phenomenon. Relevant joints may be described based on their structure, such as synovial (versus synchondrodial), finished or smooth (versus roughened), interdigitate (i.e., serrate), or lamellar (i.e., squamous; Soames, 1999). However, some terms also carry functional connotation suggesting mobility, (e.g., streptostylic or diarthrodial) or immobility (e.g., fixed, fused, ankylosed, sutured). Use of these latter terms invokes a functional correspondence to a particular morphology, often without adequate functional evidence. Even classifying a fossilized joint as synovial assumes that soft tissues such as hyaline cartilage, synovial fluid, and a ligamentous capsule were once present, inferences that require characteristic osteological correlates (Witmer, 1995). In general, arthrological nomenclature suffers from the bias of mammalian skeletal biology in which the vast majority of synovial joints (which are classified as 'diarthroses') are indeed freely mobile. On the other hand, it is evident that sauropsids exhibit a different spectrum of articular functional morphology in which 'synovial' joints (i.e., non-interdigitate, finished, smooth joints with a synovial capsule) are not necessarily mobile or diarthrodial.

In sum, cranial kinesis in extant tetrapods is rare, being restricted to just two major clades (squamates and birds), and, although these clades tend to exhibit fairly clear morphological specializations, experimental studies have sometimes cast doubt on the significance of some of these attributes. Given these uncertainties regarding kinesis in the extant realm, our understanding of cranial kinesis in nonavian dinosaurs necessarily starts with a fairly shaky foundation. We here seek to shore up this analytical foundation by proposing clear criteria on which to base inferences of kinesis in extinct taxa, and thus bring paleontological inferences in line with modern experimental functional morphology. We recognize minimally four criteria that are necessary for inferences of powered cranial kinesis in fossil (and extant) taxa: (1) a synovial basal (basipterygopterygoid) joint; (2) a synovial otic (quadratosquamosal) joint; (3) protractor musculature; and (4) permissive kinematic linkages. Clearly, intracranial synovial joints such as the otic and basal joints are necessary to allow kinetic movement, and protractor muscles would help drive the system. Additionally, the connections between bones (kinematic linkages) must permit and not obstruct movement.

The fourth criterion (permissive kinematic linkages) may be the most crucial element for positive inferences of cranial kinesis. Extant taxa that clearly express functionally relevant intracranial movement have eliminated or modified a number of bony elements that would otherwise hinder mobility. Squamates lack a lower temporal bar, have developed synovial epipterygopterygoid and pterygoquadrate joints, and some developed a mesokinetic joint in the skull roof (Metzger, 2002; Evans, 2003). Birds, most of which are unequivocally kinetic, also evolved new synovial joints (e.g., pterygoquadrate, quadratoquadratojugal), eliminated bones (e.g., postorbital, ectopterygoid, and epipterygoid) such that both the upper temporal and postorbital bars were lost, and developed a series of flexion zones (i.e., thin, flat, bendable bony lamellae; Bühler, 1981). The breakdown of these bony connections permits significant mobility between the braincase and facial skeleton. However, not all squamates that have these features exhibit cranial kinesis *in vivo* (e.g., *Uromastyx*, Herrel et al., 1998), and thus inferences of cranial kinesis in fossil taxa should probably always be viewed with a measure of caution.

With that said, some extinct dinosaurs nevertheless may have been kinetic. However, it is not our intent here to evaluate the kinetic status of individual taxa or clades, because that would require full anatomical analyses, as well as potentially biomechanical modeling and three-dimensional animation. Rather, our intent is to establish a set of rigorous criteria by which such hypotheses can be judged and tested, or, in other words, simply to 'raise the bar' on what it takes to make the claim of cranial kinesis. The criteria set forth here are themselves hypotheses that are amenable to testing. Because extant crocodylians are completely akinetic, cranial kinesis in any dinosaur is at best a Level II inference (in the scheme of Witmer, 1995), and in many cases, inferences of kinesis will be Level III inferences, drawing no support from extant relatives—that is, such inferences would represent anatomical and functional novelty. Certainly, many dinosaurs were novel animals with presumably novel structures and functions. However, novelty nevertheless needs to be addressed in a context that is grounded in the reality provided by the study of extant taxa that still have soft tissues and functions that can be observed directly. Thus, we review the distribution and morphology of the protractor musculature, arthrological structures, and linkages among bones in not just dinosaurs but also their extant relatives, gathering data from x-ray computed tomography (CT scanning), and observations of well over 100 fossil archosaur taxa (Holliday, 2006).

Anatomical Abbreviations—aCI, internal carotid artery; **ar**, articular bone; **arp**, articular process of quadrate bone; **asp**, ascending process of pterygoid bone; **bpt**, basipterygoid process; **bs**, basisphenoid bone; **cr otsp**, otosphenoidal crest; **cup**, cultriform process; **dtf**, dorsotemporal fossa; **ept**, epipterygoid bone; **ept cot**, epipterygoid cotyle; **eus**, Eustachian groove; **f V**, trigeminal foramen; **f $\mathbf{V_1}$**, ophthalmic foramen; **f $\mathbf{V_{2,3}}$**, maxillomandibular foramen; **f aCI**, internal carotid foramen; **fc**, fibrous capsule of joint; **fo**, fontanelle; **fr**, frontal bone; **g nCID**, groove for motor nerve to constrictor internus dorsalis muscles; **g $\mathbf{V_1}$**, ophthalmic groove; **hc**, hyaline (articular) cartilage of joint; **ju**, jugal bone; **ls**, laterosphenoid bone of archosaurs; **"ls"**, 'laterosphenoid' bone of snakes; **mAMEP**, musculus adductor mandibulae externus profundus; **mAMP**, musculus adductor mandibulae posterior; **mLPt**, musculus levator pterygoideus; **mn**, mandible; **mPPt**, musculus protractor pterygoideus; **mPPt 2°**, musculus protractor pterygoideus (secondary); **mPSTp**, musculus pseudotemporalis profundus; **mPSTs**, musculus pseudotemporalis superficialis; **mPTd**, musculus pterygoideus dorsalis; **mx**, maxilla bone; **na**, nasal bone; **nCID**, motor branch to constrictor internus dorsalis muscles; **occ**, occipital condyle; **otp**, otic process of quadrate bone; **pa**, parietal bone; **pal**, palatine bone; **po**, postorbital bone; **pp**, preotic pendant; **pr**, prootic bone; **pt**, pterygoid bone; **qj**, quadratojugal bone; **qu**, quadrate bone; **scl**, sclerotic ring; **sq**, squamosal bone; **tr**, trachea; **$\mathbf{V_1}$**, ophthalmic nerve; **$\mathbf{V_2}$**, maxillary nerve.

RESULTS

Osteological Correlates of Synovial Joints—The soft tissues of the synovial joints of extant taxa produce bony signatures that can be assessed in fossil taxa. In general, these joints include a convex bony element and a complementary concave element. Although specific bony features, such as the articular surface, can be identified in the concave portion of these joints, the convex portion typically offers additional data. Figures 2 and 3 illustrate common osteological correlates of synovial joints (e.g., laterosphenoid-postorbital, otic, and basal joints) in representative extant (e.g., crocodylian and squamate) and fossil (e.g., theropod and hadrosaur) diapsids. A smooth patina characterizes the surface of the joint where articular (hyaline) cartilage was once present, whereas a zone of relatively parallel striations distal to the articular surface typically indicates the attachment region of the fibrous capsule of the joint (Figs. 2, 3). Occasionally, large pits are present near the boundary of the fibrous capsule suggesting the possibility of ligamentous attachments (e.g., 3B, J). In most cases, the osteological correlates of these synovial joints are virtually identical to those found in the jaw joints (i.e., quadrate-articular; e.g., Figs. 3C, F) or appendicular skeleton of extant diapsids.

Basal Joint—Synovial joints between the pterygoid bone and the basipterygoid process of the basisphenoid bone are widespread among diapsids (Fig. 4), fulfilling one of the necessary criteria for cranial kinesis in most, if not all, dinosaurs. Among nonavian theropods, the peg-shaped basipterygoid processes ar-

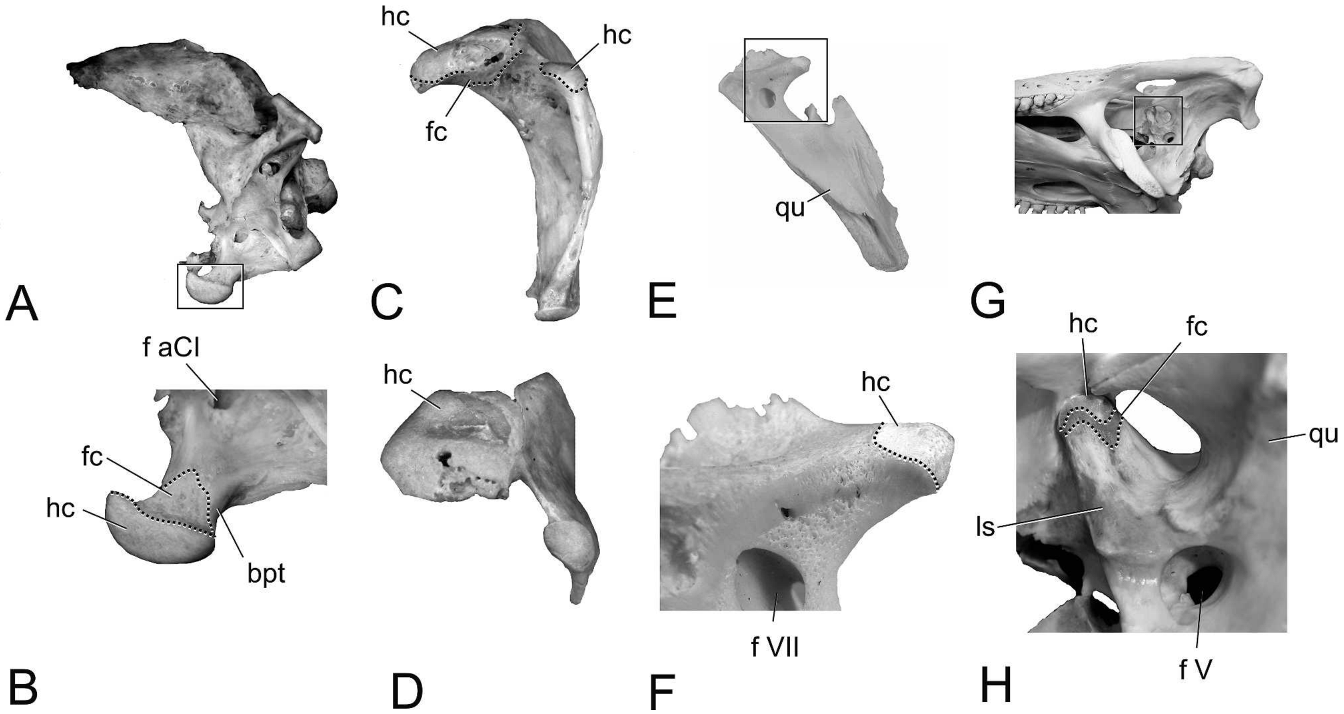

FIGURE 2. Osteological correlates of synovial joints in extant diapsids. Dotted lines indicate the extent of the articular cartilage and fibrous capsule. **A**, braincase of *Iguana iguana*, in left lateral view; **B**, close-up of the basipterygoid process from inset in A, showing the braincase portion of the basal joint; **C**, left quadrate of *I. iguana* in left lateral view; **D**, otic process of the left quadrate of *I. iguana* in left dorsal oblique view; **E**, quadrate of *Alligator mississippiensis* in left lateral view; **F**, close-up of the otic process of alligator quadrate from inset in E, showing the quadrate portion of the otic joint; **G**, *A. mississippiensis* adductor chamber in left ventrolateral view; **H**, close-up of the laterosphenoid-postorbital joint from inset in G.

ticulated with complementary slots on the medial surface of the pterygoid (Fig. 4I). On the other hand, in taxa such as the sauropod *Diplodocus* (Fig. 5) and the basal ceratopsian *Psittacosaurus* (Figs. 4G, 6A–D), the basipterygoid processes are long, slender, and directed rostrally. In these taxa, the pterygoids form more of a cup, giving the joint a mortar-and-pestle morphology. Ceratopsids (e.g., *Triceratops*) reduced the size of the basipterygoid process to a short, slender, vertical strut that articulated with the medial surface of the pterygoid, dorsal to the 'Eustachian groove' (Hatcher et al., 1907; Fig. 6E). The basipterygoid processes in basal ornithopods, such as *Zephyrosaurus* and *Dryosaurus*, are relatively short and oriented diagonally, whereas in more derived ornithopods (e.g., hadrosaurs), the basipterygoid processes are relatively long, oriented horizontally, and fit into an equally long, horizontal slot in the pterygoid (Ostrom, 1961; Heaton, 1972; Weishampel, 1984;) (Figs. 3G, HF). Surprisingly, the basipterygoid processes in most thyreophorans (e.g., *Scelidosaurus*, BMNH R1111; *Stegosaurus*, DMNH 6645; *Panoplosaurus*, ROM 1215; Fig. 7) are also smooth, finished, and articulated to a complementary socket on the pterygoid. Thus, despite the increased coossification of the skull in general, the basal joints in thyreophorans also remained covered by cartilage and unsutured to the pterygoids. Therefore, although a synovial basal joint may be necessary for an inference of cranial kinesis, given that all nonavian dinosaurs—including the obviously akinetic armored dinosaurs—plesiomorphically retained synovial basal joints, it clearly is not sufficient.

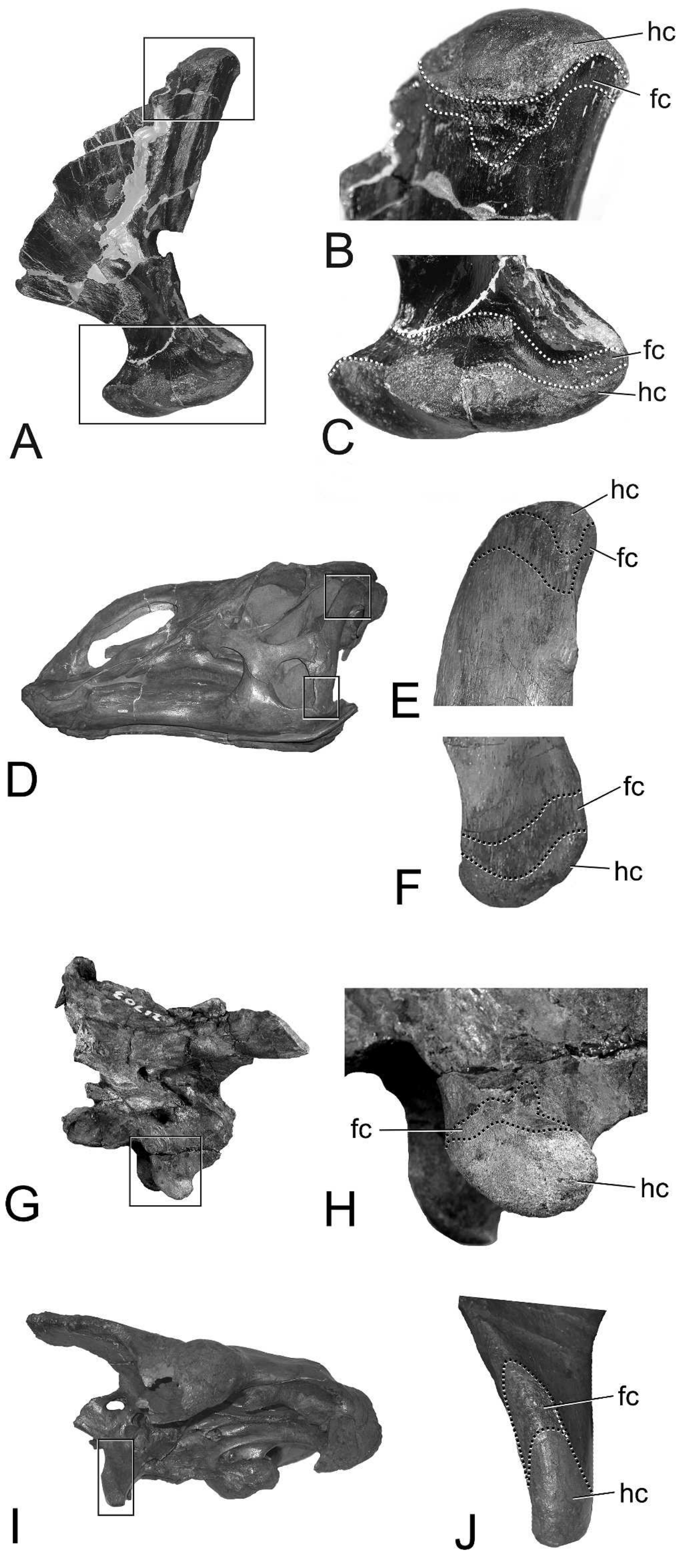

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FIGURE 3. Osteological correlates of synovial joints in fossil dinosaurs. Dotted lines indicate the extent of the articular cartilage and fibrous capsule. **A**, quadrate of *Allosaurus fragilis* (UMNH VP 18054 [UUVP 4642]) in left lateral view; **B**, close-up of the otic process of quadrate from inset in A, showing the quadrate portion of the otic joint; **C**, close-up of the articular process of the quadrate from inset in A; **D**, skull of *Brachylophosaurus canadensis* (MOR 1071) in left lateral view; **E**, close-up of the otic process of quadrate from inset in D, showing the quadrate portion of the otic joint; **F**, close-up of the articular process of the quadrate from inset in D; **G**, braincase of *A. fragilis* (CM 21703) in left lateral view; **H**, close-up of the basipterygoid process from inset in G in left lateral view, showing the braincase portion of the basal joint; **I**, braincase of *Edmontosaurus regalis* (CMN 2289) in left lateral view; **J**, close-up of the basipterygoid process from inset in I in left ventral view, showing the braincase portion of the basal joint.

Otic Joint—The otic process of the quadrate forms a synovial joint with the squamosal (and usually the paroccipital process) in almost all fossil archosaurs, including dinosaurs. The joint surfaces of these articulations are smooth in basal archosauriforms (e.g., *Chanaresuchus*; Romer, 1971), basal suchians (e.g., *Gracilisuchus*), phytosaurs, and basal dinosaur taxa including *Scelidosaurus*, *Massospondylus* (Fig. 1C), and *Herrerasaurus*, indicating that a synovial otic joint is likely a plesiomorphic feature of archosaurs. Synovial otic joints persist in pachycephalosaurs, ceratopsians, ornithopods, sauropods (Figs. 8A, B), and virtually all theropods. In ankylosaurs, the quadrates generally appear to be firmly sutured to the squamosal. However, in *Stegosaurus*, the quadratosquamosal joint is open in some individuals (e.g., DNMH 2818) but completely sutured in others (e.g., CM 106). This kind of variation demonstrates that these joints had the potential to become sutured during ontogeny in some taxa. The ubiquity of synovial otic joints among demonstrably kinetic and likely akinetic taxa suggests that (1) synovial otic joints are widespread among archosaurs (indeed among diapsids); and (2) although these joint morphologies are necessary for inferences of cranial kinesis, they are not sufficient. Metzger (2002) and Evans (2003) hypothesized that the origin of streptostyly occurred during the origin of Squamata and that streptostyly was subsequently lost in certain clades. These inferences were based on the ubiquity of synovial otic joints in Lepidosauria and in vivo data. However, synovial otic joints are ubiquitous among archosauriforms and lepidosaurs, and thus this character is more likely to be a plesiomorphy of Diapsida (Fig. 9).

Protractor Musculature—All current evidence indicates that the protractor and levator pterygoideus muscles were typically present in most dinosaur clades, and their osteological correlates (preotic and levator pendants, respectively) usually lend themselves to relatively robust inferences of the size, direction, and

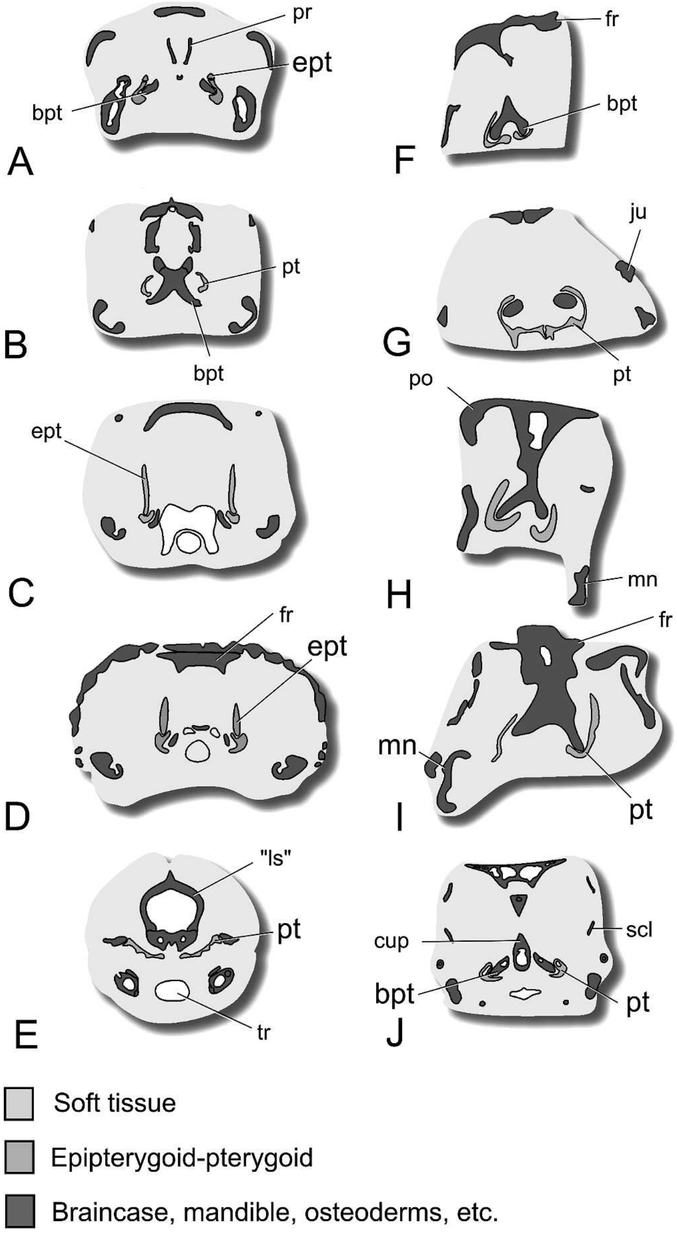


FIGURE 4. Synovial basal joints are widespread among diapsids, as shown by axial (coronal) sections through the orbitotemporal regions of lepidosaurs and dinosaurs. **A**, *Sphenodon punctatus*; **B**, *Ctenosaura pectinata*; **C**, *Varanus gouldi*; **D**, *Heloderma suspectum*; **E**, *Python molurus*; **F**, *Dryosaurus altus* (CM 3392); **G**, *Psittacosaurus mongoliensis* (IGM 100/1132); **H**, *Camarasaurus lentus* (CM 11338); **I**, *Tyrannosaurus rex* (FMNH PR2081); **J**, *Struthio camelus*. B–E adapted from data from www.digimorph.org.

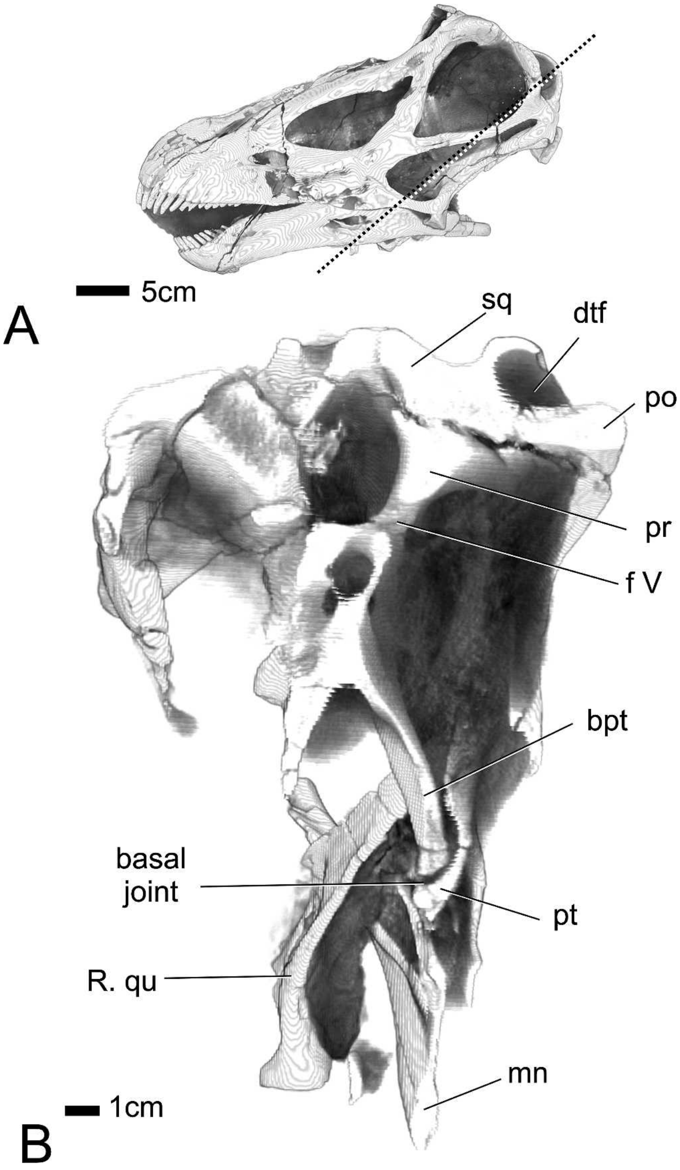


FIGURE 5. Basal joint in *Diplodocus longus* (CM 3452), based on CT data. **A**, skull in left lateral view depicting location of section; **B**, caudal view of a section at the plane indicated in A, illustrating the elongated basipterygoid process and synovial basal joint.

potentially gross architecture of the muscles (Holliday, 2006; Fig. 10). Both muscles cross and act upon the basal, otic, and, when present, the epipterygolaterosphenoid joints (Fig. 11). As in most lepidosaurs, the levator pterygoideus muscle in virtually all of the dinosaurs studied maintained a position parallel with the basipterygoid process, epipterygoid, and quadrate and attached dorsal to the basipterygoid articulation. Therefore, the muscle maintained a primarily vertical component of force on these joints among all taxa.

On the other hand, the protractor pterygoideus muscle appears to have evolved several different angulations relative to the palate. Among most theropod dinosaurs, for example, the protractor pterygoideus maintains an angulation of approximately 30–45° relative to the long axis (z-axis) of the skull, or orthogonal to the coronal planes formed by the basipterygoid process, epipterygoid, and quadrate otic process, crossing diagonally and ventrally toward the medial surface of the pterygoquadrate suture (Figs. 11I–L). This angulation is perpendicular to the primary force vector of the temporal muscles and parallel with that of the pterygoideus muscles (e.g., Haas, 1955; Ostrom, 1964; Schwenk, 2000). Some theropods, such as *Tyrannosaurus* (Fig. 10C) and *Masiakasaurus* (Carrano et al., 2002), apparently modified this angulation by shifting part of the palatal attachment of protractor pterygoideus rostrally to a position more similar to that of levator pterygoideus, although in *Tyrannosaurus* the dorsal part of the muscle maintained the plesiomorphic angulation. *Psittacosaurus*, *Diplodocus*, and hadrosaurs (Fig. 11E, F) had protractor pterygoideus muscles that, in addition to

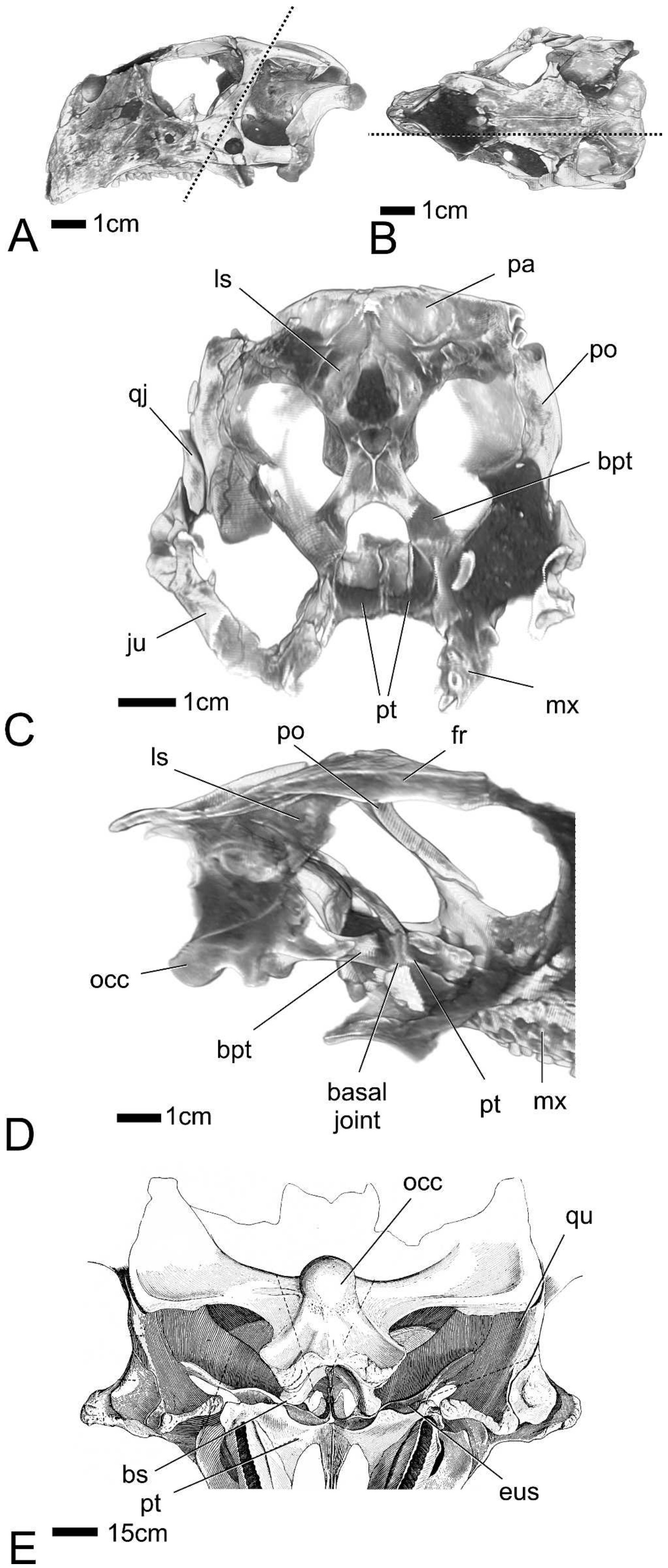


FIGURE 6. Basal joints in ceratopsians. **A**, skull of *Psittacosaurus mongoliensis* (IGM 100/1132) in left lateral view based on CT data, depicting the location of the avail (coronal) section in C; **B**, skull in dorsal view depicting the location of the parasagittal section in D; **C**, rostral view of a section through orbitotemporal region at the plane indicated in A, illustrating the synovial basal joints; **D**, parasagittal section of skull in right lateral view at the plane indicated in B, illustrating a medial view of the left basal joint; **E**, skull of *Triceratops horridus* in ventral view illustrating its unconstrained basal joints (modified from Hatcher et al., 1907).

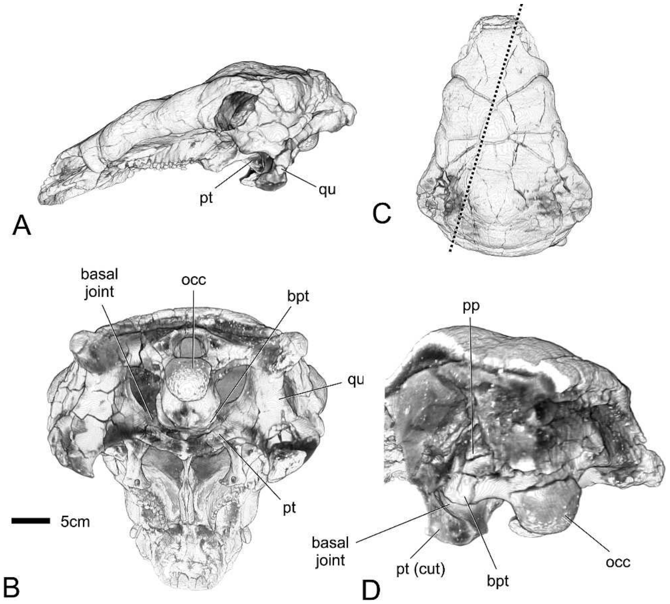


FIGURE 7. Basal joint in *Panoplosaurus mirus* (ROM 1215). **A**, skull in left lateral view based on CT data; **B**, skull in caudoventral view illustrating the basal joints; **C**, skull in dorsal view depicting the location of the oblique parasagittal section in D; **D**, left, caudolateral view of the oblique parasagittal section at the plane indicated in C, illustrating the synovial basal joint.

having had caudodorsally-oriented fibers, also appear to have had fibers that maintained angulations essentially parallel to the basipterygoid process and quadrate rather than being orthogonal to them (Holliday, 2006). In most nonavian dinosaurs (except hadrosaurs), there appears to have been little mediolateral (x-axis) to the apparent muscle forces (Fig. 11). Hadrosaurs maintained the primitive orthogonal angulation of the dorsal portion of the protractor pterygoideus muscle. However, in addition to a rather ligamentous levator pterygoideus (Holliday, 2006), hadrosaurs also expanded the muscle's angulation with the addition of rostrally- and laterally-oriented fibers (mPPt2°; Figs. 10B, 11E, F), greatly increasing the mediolateral component of the protractor musculature.

The osteological correlates of the protractor musculature (Figs. 1, 10) suggest that the muscles either hypertrophied or disappeared during the evolution of certain clades of dinosaurs. If cranial kinesis were indeed possible in those taxa that most commonly are regarded as kinetic, one would expect that relatively larger muscles would be necessary to move relatively larger and heavier bones. Among nonavian theropods, the preotic pendant in tyrannosaurs is greatly enlarged relative to braincase size compared to other coelurosaurs (Fig. 10C). *Allosaurus* appears to have greatly enlarged levator and protractor pterygoideus muscles compared to other basal theropods. This potentially suggests that the muscles hypertrophied to compensate for the enlarged adductor muscles and increased bite force characteristic of these predatory dinosaurs (e.g., Erickson et al., 1996; Hurum and Currie, 2000; Rayfield et al., 2001; Meers, 2002). There appears to have been a marked expansion in the size of protractor pterygoideus during the evolution of ornithopod dinosaurs. *Hypsilophodon* merely has a small spur for a preotic pendant, *Dryosaurus* has a larger, rectangular pendant, and hadrosaurs (e.g., *Brachylophosaurus*) have greatly expanded tripartite preotic pendants reflective of greatly modified and enlarged protractor pterygoideus muscles (Figs. 10B, 11E, F).

On the other hand, sauropod evolution is characterized by the reduction of protractor pterygoideus. *Plateosaurus* and *Masso-*

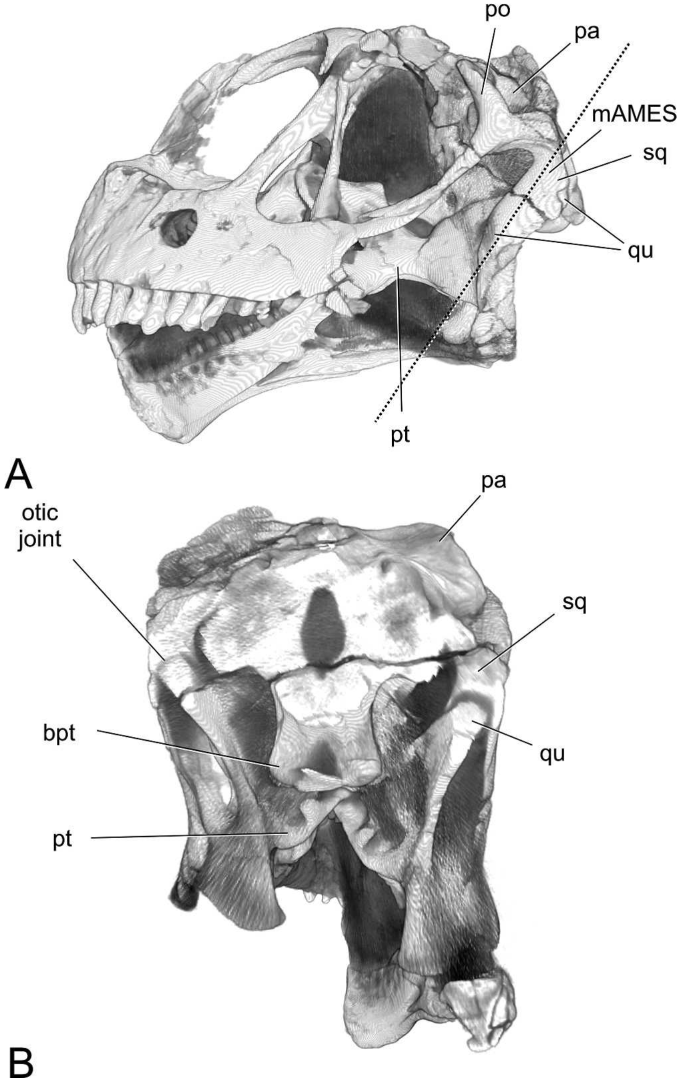


FIGURE 8. Otic joints in the sauropod *Camarasaurus lentus* (CM 11338). **A**, skull based on CT data in left lateral view illustrating the otic (quadratosquamosal) joint and the location of the section in B; **B**, caudal view of the section at the plane indicated in A, illustrating the otic joints.

spondylus have relatively large, rectangular preotic pendants, whereas the pendants in *Shunosaurus* and *Camarasaurus* are more slender and triangular, as well as being relatively smaller compared to head size. However, the preotic pendant is long, thin, tapering, and compressed against the basipterygoid process in *Diplodocus* and *Nigersaurus*, and is apparently absent in the titanosaur *Rapetosaurus* (Curry et al., 2004), suggesting protractor pterygoideus was generally small, if not completely absent in these long-snouted sauropods. Protractor musculature was well developed in ornithopods, ceratopsians, and theropods, and rudimentary in sauropods and thyreophorans. However, save a proper scaling analysis, it remains to be determined how protractor muscle size relates to braincase or overall head size in non-avian dinosaurs. Although protractor muscles are necessary for inferences of powered cranial kinesis, they are not sufficient, because they were still present in dinosaurs that have been widely accepted to be akinetic (most notably ceratopsids, in which the muscles were very well developed). Moreover, protractor muscles are present in *Sphenodon* and other akinetic lepidosaur taxa (Schwenk, 2000; Metzger, 2002), further indicating that protractor muscles are not sufficient to infer powered cranial kinesis.

DISCUSSION

Inferences of Cranial Kinesis in Dinosaurs

Based on the four criteria discussed above that are necessary but not individually sufficient for inferences of powered cranial kinesis, we propose three different categories of inferred kinetic state (Table): (1) partially kinetically competent (i.e., possessing key synovial joints and protractor muscles, but lacking bony gaps permitting movement); (2) fully kinetically competent (i.e., possessing the joints and muscles as well as permissive bony linkages, but lacking demonstrable movement in vivo); (3) kinetic (i.e., possessing the necessary joints, muscles, and kinematic linkages, as well as in vivo movement). Akinesis perhaps represents a fourth category, but broadly overlaps with the first category and even overlaps with some examples in the second category (e.g., those extant lizards that lack in vivo movement). Almost all dinosaur clades pass three of the four criteria necessary for inferences of powered cranial kinesis, including the persistence of synovial basal and otic joints and the spanning of the joints by levator and protractor pterygoideus muscles. These factors alone might seem to suggest the potential for intracranial mobility (Versluys, 1910; Iordansky, 1990; Metzger, 2002). Nonetheless, despite being partially kinetically competent (i.e., some but not all of the requisite components are in place), there is reason to be cautious about inferring cranial kinesis in most nonavian dinosaurs (Fig. 9).

First, not all intracranial synovial joints are necessarily mobile. The laterosphenoid is an apomorphic ossification in the braincase of archosauriforms (Clark et al., 1993) that forms a synovial joint with the ventral surface of the frontal and/or postorbital bones (Fig. 2F). Despite the presence of a synovial sac and hyaline cartilage on the articular surfaces of the joint, the element is tightly sutured to other neighboring elements among dinosaurs, including the prootic, parietal, basisphenoid, and even the frontal. Moreover, this synovial joint, as well as a patent otic joint (Fig. 2), persist in extant crocodylians, which have clearly eliminated any possibility of cranial kinesis by firmly suturing the pterygoid and quadrate to the braincase.

Second, some of the same features often cited as indicative of kinesis in some taxa are found in taxa that are universally regarded as akinetic, reflecting an inconsistency in the application of criteria. For example, osteological correlates such as the basal and otic joints, which typically have smooth, finished articular surfaces, have been the most commonly cited criteria suggestive of cranial kinesis in some dinosaurs (e.g., ornithopods and theropods). However, the fact that these joint morphologies are ubiquitous among archosaurs (Figs. 3G, H), including dinosaurs, should thus require similar inferences of intracranial mobility in sauropods, ceratopsians, and even some thyreophorans, despite the extensive suturing of most other cranial elements in the latter two groups.

Third, some putatively mobile joint types have no modern counterparts. Many of the synarthrodial cranial sutures (e.g., postorbitojugal, quadratoquadratojugal, postorbitosquamosal, and pterygoquadrate) have smooth or grooved articular surfaces, and these have been used as indicators of a sliding manner of mobility (e.g., Galton, 1974; Weishampel, 1984; Rayfield, 2005). However, no evidence of such function has been reported in similar sutures (e.g., the postorbitosquamosal joint in squamates) in extant reptiles or birds, and thus no comparable functional basis for these inferences exists. For example, Gingerich (1973) suggested that the Cretaceous bird *Hesperornis* exhibited 'maxillokinesis' in which a dorsal groove in the maxilla allowed its fore-aft movement relative to a 'rail' formed by the subnarial processes of the premaxilla and nasal. Bühler et al. (1988), however, showed that the joint structure of hesperornithid upper jaws was virtually identical to that of loons and other holorhinal, prokinetic birds, which completely lack any relative movement of these bones.

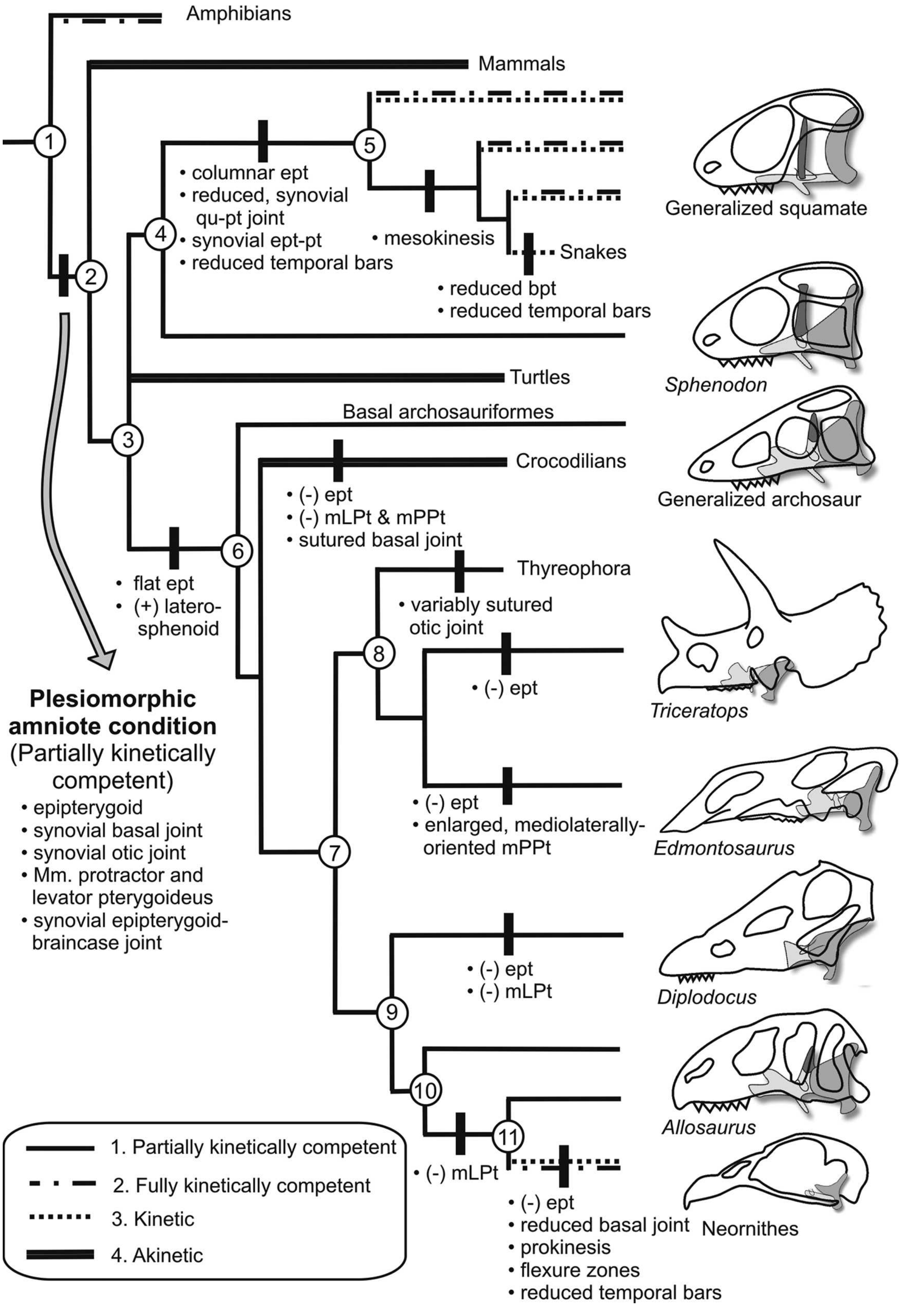
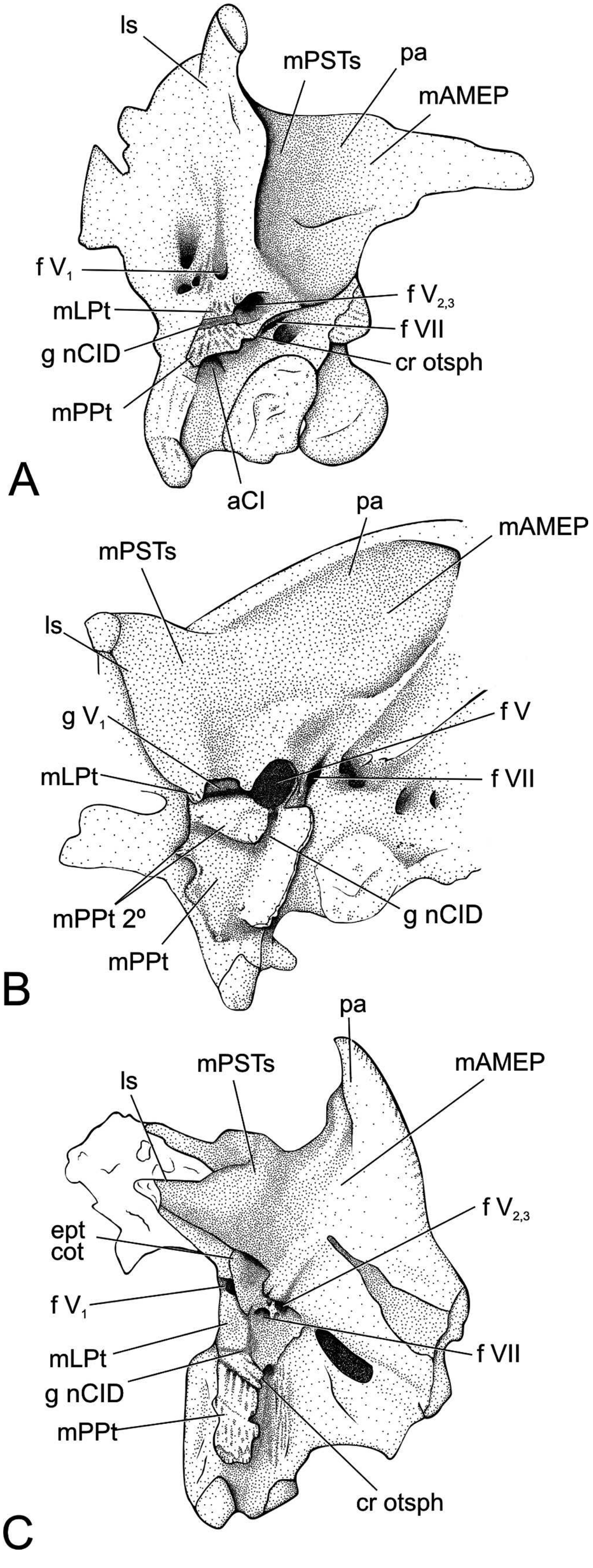


FIGURE 9. Evolutionary history of the morphological correlates of cranial kinesis in amniotes with special emphasis on dinosaurs. Nodes: 1, Tetrapoda; 2, Amniota; 3, Sauropsida; 4, Lepidosauria; 5, Squamata; 6, Archosauria; 7, Dinosauria; 8, Ornithischia; 9, Saurischia 10, Theropoda; 11, Maniraptora.



Fourth, many of the cranial sutures in dinosaurs are broad overlapping articular surfaces (e.g., pterygoquadrate and epipterygopterygoid joints) that should limit potential mobility rather than facilitate it (Fig. 12A). In extant taxa that exhibit true kinesis (e.g., varanids, geckos, snakes, birds), joint mobility is conferred by (a) reduction in contact area between bones, (b) development of demonstrably synovial joint capsules (e.g., the pterygoquadrate and epipterygopterygoid joints in squamates, the pterygoquadrate and quadratoquadratojugal joints in birds), (c) formation of thinned flexion zones (e.g., the craniofacial hinge of birds), and/or (d) loss and/or replacement of bones with ligamentous connections that are more adapted to the tensile environments experienced during kinesis (e.g., quadratojugal ligament in squamates, postorbital ligaments in geckos and birds; Herrel et al., 1999; Bout and Zweers, 2001; Figs. 12B, D). These attributes that constitute our 'permissive kinematic linkages' are generally absent in the nonavian dinosaur clades most typically regarded as kinetic. In fact, members of these clades typically have very broad contact surfaces with no clear evidence of synovial structure. Likewise, the inferred presence of suborbital ligaments in many theropod dinosaurs, including *Tyrannosaurus*, *Carnotaurus*, *Majungasaurus*, and *Acrocanthosaurus* (Chure, 1998; Sampson and Witmer, 2007), would further tie the skull together and suggests the need for additional stability and thus less potential for mobility. Indeed, a variety of workers have pointed to precisely these kinds of firm contacts between bones as evidence for the absence of kinesis (e.g., Ostrom, 1961; Galton, 1985; Chatterjee, 1991; Rayfield, 2005; Barrett and Upchurch, 2007).

Importantly, hadrosaurs and ceratopsids appear to have convergently replaced the bony epipterygoid with either a ligament or hypertrophied M. levator pterygoideus (Holliday, 2006; Fig. 12C). If true, the presence of soft tissues conferring a more tensile environment between the braincase and palate may support a stronger inference of intracranial mobility in these taxa compared to other taxa that retain a bony epipterygoid linking the palate and braincase. However, it remains unclear where mobility would actually occur in the temporal regions of the skulls of hadrosaurs, let alone ceratopsians due to the other constraints noted above. Alternative and equally plausible hypotheses include that the epipterygoid was lost simply to increase space for the temporal musculature (e.g., M. pseudotemporalis and M. adductor mandibulae externus profundus) or as a consequence of the wholesale reorganization of the palate and suspensorium in these highly apomorphic clades. With these criteria, we can reevaluate previous hypotheses of cranial kinesis in dinosaurs.

Pleurokinesis in Ornithopods—Ornithopods are an excellent example of partially kinetically competent dinosaurs. These dinosaurs possess synovial basal and otic joints as well as protractor musculature. The primary issue centers on the status of the requisite permissive kinematic linkages. Ostrom (1961:163) concluded that the skulls of hadrosaurs were akinetic based on his interpretations of the sutures and joints, leading him to argue that "at every junction of the neurocranial and maxillary segments, there exists a completely coalesced or very strong sutural union which appears to have been completely or very largely inflexible." He regarded the protractor musculature as absent, instead inferring an enlarged M. levator bulbi muscle attaching on the lateral surface of the basisphenoid. However, Norman (1984), Weishampel (1984), and Norman and Weishampel (1985;

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FIGURE 10. Braincases of dinosaurs in left lateral view illustrating the osteological correlates of the levator and protractor pterygoideus muscles and other relevant structures in the adductor chambers. **A**, *Triceratops horridus* (MOR 699); **B**, *Brachylophosaurus canadensis* (MOR 1071); **C**, *Tyrannosaurus rex* (AMNH 5117).

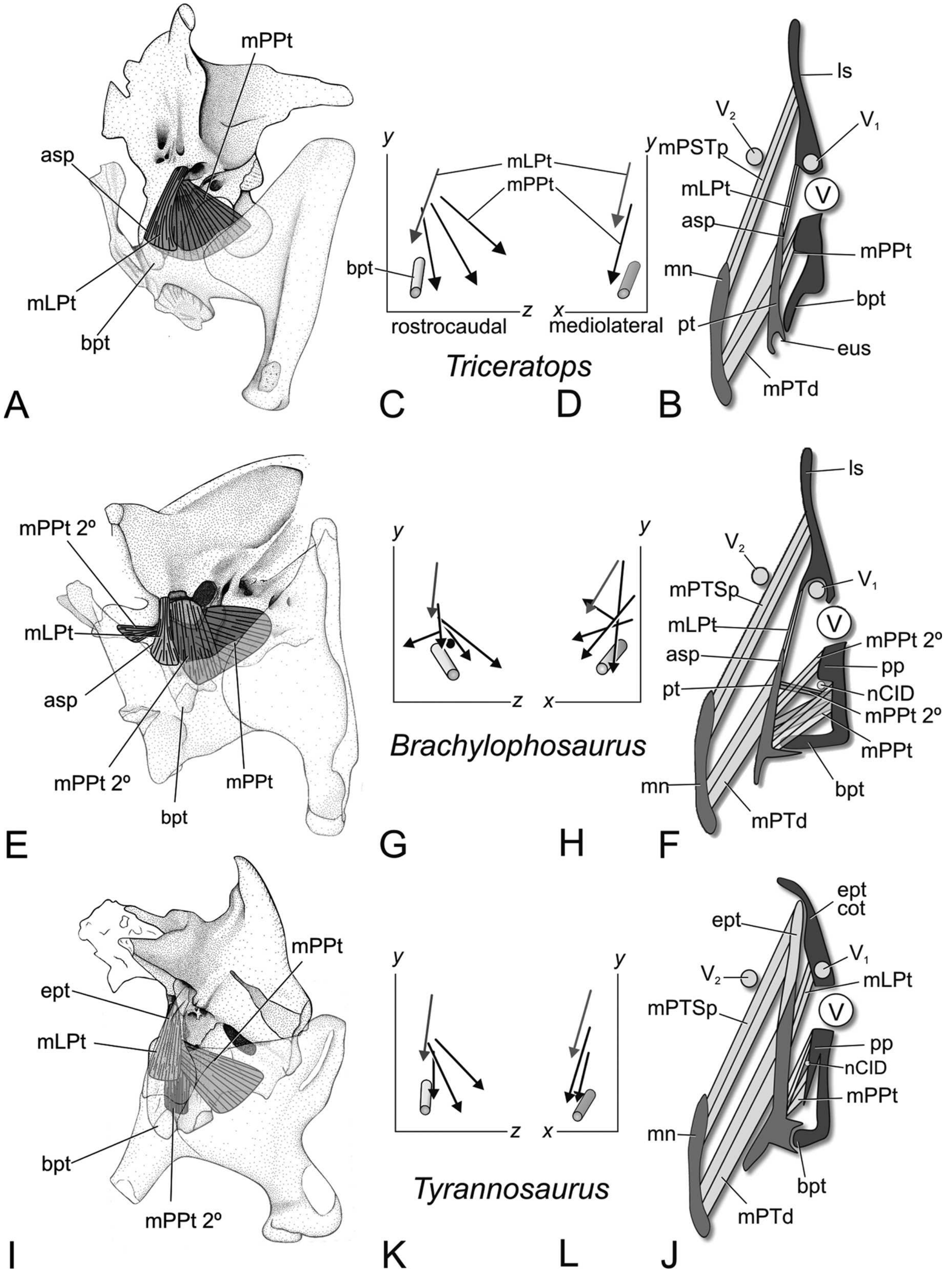

FIGURE 11. The protractor and levator pterygoideus muscles of *Triceratops horridus* (A–D), *Brachylophosaurus canadensis* (E–H), and *Tyrannosaurus rex* (I–L) illustrating the muscle attachments and generalized angulations. **Far left (A, E, I)**, braincase and palate (translucent) with musculature in left lateral view; **Far right (B, F, L)**, orbitotemporal region in left axial (coronal) section illustrating relevant anatomical structures; **left middle (C, G, J)**, **right middle (D, H, K)**, schematics of general angulations of different bellies of the left-side levator and protractor pterygoideus muscles in lateral and caudal views, respectively. Cylinder, basipterygoid process; grey arrows, mLPt; black arrows, mPPt.

TABLE 1. Inferences of cranial kinesis in various diapsids (i.e., dinosaurs and lepidosaurs) based on morphological and functional criteria.

Criteria necessary but not sufficient for inferences of cranial kinesis
1. A synovial basal (basipterygopterygoid) joint
2. A synovial otic (quadratosquamosal) joint
3. Protractor musculature
4. Kinematically permissive linkages

Inferred kinetic state	Description	Examples
1. Partially kinetically competent	Some or all of criteria 1–3, but not 4; no in vivo validation	nonavian theropods, sauropods, ornithopods, ceratopsians, pachycephalosaurs
2. Fully kinetically competent	Criteria 1–4, but no in vivo validation	*Sphenodon, Uromastix, Heloderma, Struthio*
3. Kinetic	Criteria 1–4, in vivo validation	snakes, geckos, some varanids, most neoavians

see also Weishampel and Norman, 1985) reinterpreted the arthrology and protractor myology in ornithopods and concluded that they were not only kinetic, but had evolved a novel form of cranial kinesis termed pleurokinesis whereby the maxillary segment rotated laterally relative to the upper portion of the facial skeleton, effecting a transverse power stroke. Pleurokinesis not only requires mobility at the basal joint but also transverse movements about the otic joint (somewhat different from classic streptostyly) and novel rotation within sutures in the facial and maxillary skeletal units. Norman's and Weishampel's interpretations of sutural functional morphology were not fully consistent throughout their analyses. Whereas Weishampel (1984) and Norman (1984) inferred mobility between the maxillopalatal segment and neighboring segments via the broad overlapping sutures of the premaxillomaxillary and quadratoquadratojugal joints, they inferred immobility in the similarly shaped contacts within the maxillopalatal segment including the pterygopalatine, pterygoquadrate, and ectopterygomaxillary joints.

Cuthbertson (2006) re-evaluated the evidence for the 'dynamic streptostyly mechanism' (i.e., pleurokinesis) based on detailed analysis of a well-preserved skull of the hadrosaurid *Brachylophosaurus.* His findings largely agree with ours, suggesting that the evidence currently advanced for mobility at the requisite 'pleurokinetic joints' is not sufficiently robust to support the inference of kinesis. On the contrary, the broad contact areas between bones and the apparent lack of permissive kinematic linkages or other strategies for conferring mobility (see above) would tend to falsify the hypothesis of pleurokinesis and support Ostrom's (1961) original assessment. Additionally, new 3D kinematic modeling of pleurokinetic movements in the hadrosaurid *Edmontosaurus* has identified unexpectedly large and unrealistic intracranial deformations (Rybczynski et al., 2006, in press), suggesting that indeed hadrosaur kinematic linkages apparently do not permit pleurokinesis. Weishampel and Cheney (2007), on the other hand, reported in an abstract that they performed similar 3D animation analyses that did affirm pleurokinesis. Their model, however, omitted the palate and thus probably was not a valid test given that palatal articulations comprise key linkages.

Ohashi's (2006) finite element analysis of the hadrosaurid *Hypacrosaurus* examined the mechanical effects of pleurokinesis, revealing that pleurokinesis would have been beneficial by dispersing potentially dangerous stress concentrations. Ohashi's analysis, however, took pleurokinesis as an assumption, and did not comprise a true test of the kinematic model. In fact, in some respects, his study may simply be reflecting the presence of sutures, which are well known to dissipate and/or absorb mechanical strains (Herring et al, 2001; Rafferty et al., 2003; Rayfield, 2004, 2005; Metzger et al., 2005), and thus his non-pleurokinetic model (a fully rigid analysis without sutures) would be expected to exhibit high stress concentrations.

Thus, although ornithopod dinosaurs do meet three criteria necessary for inferences of powered cranial kinesis (i.e., synovial basal and otic joints, protractor muscles), based on our analysis and those of others, we regard the lack of permissive kinematic linkages as significant. Apart from the normal slight movements at sutures (measured in microstrain magnitudes; Herring et al., 2001) that dissipate mechanical stress and strain, we are reluctant to accept the multiple requisite and supposedly extensive 'sliding contacts' and 'hinges' between bones that have no modern counterparts. That said, Weishampel's (1984) finding of transverse striations on the teeth of hadrosaurs offers some support for the hypothesis in this clade. Indeed, these are the kinds of data that provide reasonable tests of kinematic hypotheses in extinct taxa. Although we are not in a position to evaluate these findings directly, it is worth noting that other explanations for the striations have been offered, such as mediolateral movements of the mandible at the jaw joint, with compensatory movements at the

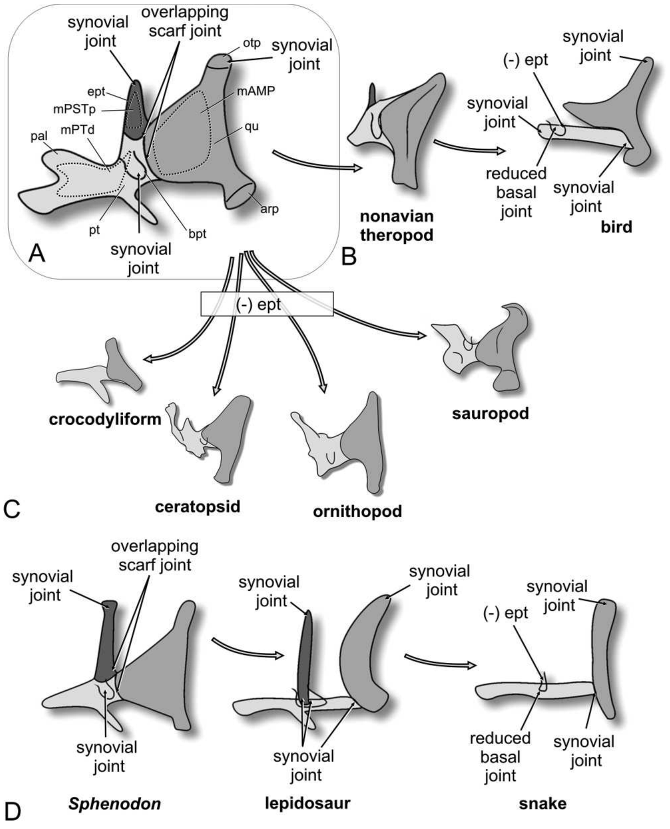

FIGURE 12. Evolution and breakdown of kinematic linkages in the palates in diapsids, using schematic images of elements in left lateral view. **A**, basal archosaur condition; **B**, evolution of the avian condition; **C**, the epipterygoid was eliminated in several archosaur and dinosaur lineages but overlapping scarf joints were not; **D**, evolution of the palate among lepidosaurs.

predentary-dentary contact (Cuthbertson, 2006, 2007; see also Weishampel [1984] and Crompton and Attridge [1986] for comparable mandibular mechanisms in *Heterodontosaurus*). Moreover, White (1958) and Calvo (1994) reported transverse dental striations in the sauropod *Camarasaurus*, invoking similar mediolateral movements at the jaw joint. We would emphasize, however, that these mandibular mechanisms require the same scrutiny as we advocate for the cranium proper. Finally, ornithopods were novel animals, and it is certainly possible that they evolved a novel feeding mechanism. However, despite the popularity of pleurokinesis and its impact on notions of dinosaur herbivory, further evidence needs to be advanced to substantiate the hypothesis and counter the evidence suggesting that ornithopod skulls lack permissive kinematic linkages.

Cranial Kinesis in Nonavian Theropods—Despite their close ties to birds, which are demonstrably kinetic, functional hypotheses in nonavian theropod dinosaurs must be supported by features necessary and sufficient for positive inferences of cranial kinesis. Since the time of Versluys (1910, 1912), the idea of kinetic theropod skulls has been a widespread assumption, although, somewhat surprisingly, neither widely documented nor critically analyzed (at least formally: some unpublished theses and conference presentations have dealt with theropod kinesis). More recently, using finite element modeling, Rayfield et al. (2001) interpreted *Allosaurus* to be overbuilt and to have evolved a novel feeding mechanism. Frazzetta and Kardong (2002), however, countered, arguing that because *Allosaurus* had synovial basal joints, it would have had a kinetic skull, which would affect the initial interpretations of the finite element model. As discussed above, however, movement in the basal joint is only one of several criteria necessary for inferences of powered cranial kinesis. Rayfield (2005) subsequently interpreted the postorbitosquamosal joint in *Allosaurus* to be mobile based on its smooth, moderately interdigitate morphology and the nasofrontal joint to be mobile based on its overlapping, beveled morphology. However, Rayfield (2004) suggested that the nasofrontal joint in *Tyrannosaurus*, which also has a moderately interdigitate morphology similar to that of the nasofrontal joint in *Allosaurus*, was immobile. Thus, as noted for ornithopods, inferences of mobility have not been based on consistently applied criteria. Moreover, 'looseness' of the joints serving to dissipate strains or absorb shocks (e.g., Russell, 1970; Rayfield, 2005; see above) is not always distinguished in the theropod literature from the kind of gross movements typically invoked for cranial kinesis.

Most non-maniraptoran theropod dinosaurs, which are well represented by *Allosaurus* and *Tyrannosaurus,* only meet three of the four criteria necessary for inferences of powered cranial kinesis (i.e., having synovial otic and basal joints and protractor muscles) yet lack permissive kinematic linkages. Thus, nonavian theropods were only partially kinetically competent and were not functionally kinetic.

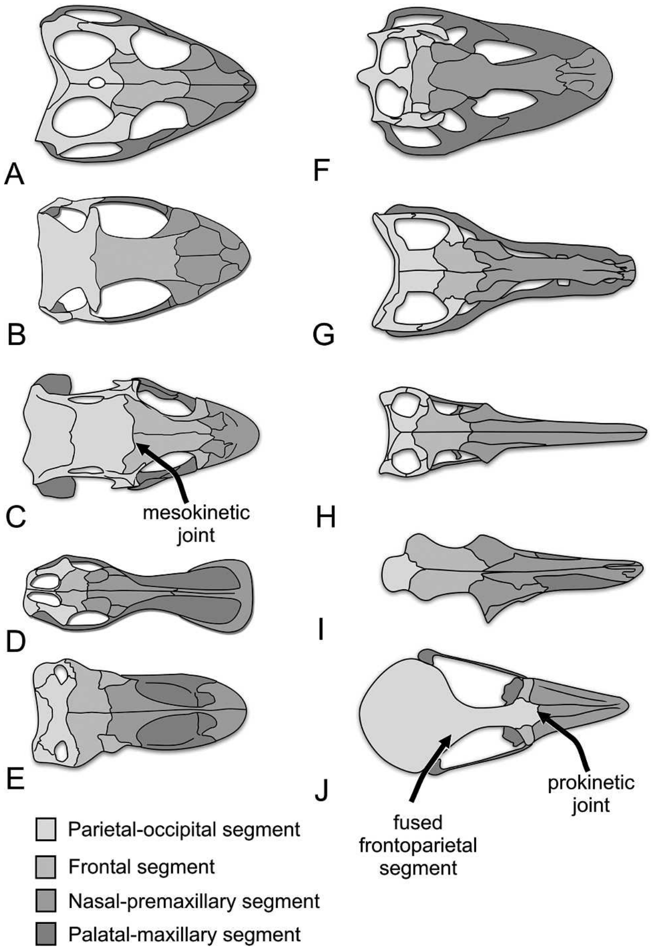

FIGURE 13. Skull roof diversity among lepidosaurs and dinosaurs illustrating the position of flexible hinge joints in extant taxa. Nonavian dinosaurs do not possess the cranial architecture and kinematic linkages permitting kinesis. **A**, *Sphenodon punctatus*; **B**, *Iguana iguana* (an iguanian); **C**, *Gymnophthalmus sp.* (a derived scleroglossan); **D**, *Edmontosaurus regalis*; **E**, *Camarasaurus lentus*; **F**, *Majungasaurus crenatissimus*; **G**, *Gorgosaurus libratus*; **H**, *Troodon formosus*; **I**, *Shuvuuia deserti*; **J**, *Eudromia elegans*.

The Evolution of Avian Kinesis—When among maniraptorans avian-style prokinesis evolved remains unclear. It is well beyond the scope of this paper to present a full analysis of the evolution of kinesis in birds, and the subject has been explored many times before from different perspectives (e.g., Bock, 1964, 2002; Bühler, 1981, 1985; Bühler et al., 1988; Chatterjee, 1991, 1997; Zusi, 1984, 1993; Zweers et al., 1997; Zweers and Vanden Berge, 1998; Meekangvan et al., 2006). Our intent here is simply to apply the criteria set forth above to a few select taxa. The data presented above indicate that most nonavian Maniraptoriformes (e.g., deinonychosaurs, oviraptorosaurs) were partially kinetically competent (e.g., they had synovial basal and otic joints and protractor muscles; see Table), yet were still probably not kinetic because they lacked permissive kinematic linkages. For example, these taxa generally retain the plesiomorphic complement of bones (e.g., postorbital, ectopterygoid) and connections (e.g., postorbitojugal) that would effectively disallow movement. Some maniraptorans (e.g., *Saurornithoides*, *Byronosaurus* [Makovicky et al., 2003]; *Buitreraptor* [Makovicky et al., 2005]) do indeed appear to have relatively thin nasal bones, suggesting the potential for a flexion zone within the nasals. However, Bühler (1981; see also Zusi, 1984, 1993) recognized that avian kinesis requires more than just the single flexion zone in the face (i.e., the craniofacial or frontonasal hinge), but also flexion zones in the rostral portion of the palate and jugal bars. Moreover, the nasofrontal suture is beveled and broadly overlapping as well as sutured to the lacrimal bone in most nonavian theropod taxa (Figs. 13G, H). Therefore, without additional morphological evidence, any inference of kinetically meaningful flexion in these bones is weak.

Some nonavian maniraptorans show some breakdown of the otherwise constraining diapsid arches, potentially raising the possibility of the presence of permissive kinematic linkages and achievement of our 'fully kinetically competent' category. For example, the peculiar Cretaceous Mongolian theropod *Avimimus* lacks contact between the quadratojugal and squamosal and also between the jugal and postorbital, which would effectively give it a very birdlike 'jugal bar' (Kurzanov, 1985, 1987). However, despite this seemingly giant step towards kinesis, the quadrate is fused to the quadratojugal, braincase, and pterygoid (Kurzanov, 1985; Norman, 1990). Thus, *Avimimus* reveals that even having permissive kinematic linkages—the absence of which is the major obstacle for most inferences of dinosaur kinesis—is not individually sufficient, because *Avimimus* lacks the necessary criteria of synovial otic and basal joints.

Likewise, the alvarezsaurid *Shuvuuia* has a delicate skull with reduced articulations of the temporal bars and quadrate resulting from loss of the postorbital process of the jugal and of the squamosal process of the quadratojugal, leading Chiappe et al. (1998, 2002) to the inference of prokinesis. Indeed, the formation of a 'jugal bar' in *Shuvuuia*—but without the movement-prohibitive fusions of *Avimimus*—does suggest the potential for kinematically permissive quadrate mobility (Chiappe et al., 1998, 2002). However, the nasofrontal region in MGI 100/977 is composed of a complex arrangement of broad articulations between the frontal, nasal, and prefrontal (Sereno, 2001; Fig. 13I), seemingly precluding any significant flexion about the joint regardless of mobility of other intracranial joints. Moreover, it is neither clear whether alvarezsaurids had the maxillojugal and palatal flexion zones that must be present to allow prokinesis (Bühler, 1981) nor whether they had lost the ectopterygoid. Nevertheless, the temporal region of alvarezsaurids displays some of the key elements of the avian kinetic system, and additional material may shed light on their kinetic status.

Interpreting the significance of alvarezsaurid morphology is hampered by the fact that the relationships of alvarezsaurids are controversial, which influences subsequent transformational hypotheses regarding the evolution of kinesis. Placement of alvarezsaurids near the ancestry of birds (Perle et al., 1993, 1994; Forster et al., 1998; Chiappe et al., 1998, 2002) not only makes the inference of alvarezsaurid kinesis more likely (i.e., potentially homologous to avian kinesis) but also suggests that kinesis may have evolved prior to the diversification of birds (i.e., Aves/Avialae) and further implies that confuciusornithids (e.g., *Confuciusornis*), which have complete temporal bars, but unclear nasofrontal joint morphology, likely lost the potential for prokinesis, suggesting an evolutionary reversal (Chiappe et al., 1999). However, other analyses concluded that alvarezsaurids were either basal maniraptorans (Norell et al., 2001; Clark et al., 2002; Novas and Pol, 2002; Makovicky et al., 2005) or even more basal theropods (e.g., near Ornithomimosauria; Sereno, 2001). A more basal position would make any alvarezsaurid kinesis independently derived from avian kinesis, suggesting that avian-style kinesis in general and the prokinetic hinge in particular are probably avian apomorphies (Fig. 13J) that did not evolve until after *Archaeopteryx* and confuciusornithids.

Archaeopteryx, of course, has always been central to any analysis of the evolution of avian kinesis (Bühler, 1985; Chatterjee, 1991, 1997; Zweers et al., 1997; Zweers and Vanden Berge, 1998; Elzanowski, 2002; Paul, 2002), and again our intent is not provide a full analysis, but rather address the criteria set out here. The available fossils of *Archaeopteryx* do not allow detailed assessment of all of the criteria, but it seems clear that it had basal and otic joints (Elzanowski and Wellnhofer, 1996, fig. 2; Elzanowski, 2002) that were basically similar to those of other theropods in which the synovial nature of these joints is not controversial. The presence of protractor musculature is harder to assess directly although Elzanowski and Wellnhofer (1996) illustrated a structure that may be best interpreted as a preotic pendant (their "rostroventral wing of the prootic"). Much more contentious is the question of whether *Archaeopteryx* had permissive kinematic linkages. Paul (2002) reconstructed *Archaeopteryx* with a slender epipterygoid based on the Eichstätt specimen. Some workers have doubted that a postorbital bone was present (Bühler, 1985; Martin and Zhou, 1997), but most workers accept that it was indeed present (Chatterjee, 1991; Elzanowski and Wellnhofer, 1996; Chiappe et al., 1999; Elzanowski, 2001, 2002; Witmer, 2002; Paul, 2002; Mayr et al., 2007). Less certain is whether the peculiarly shaped jugal contacted the postorbital (Witmer, 2002), although Paul (2002) made a well-reasoned case for a compete postorbitojugal bar. New relevant information on the palate (Mayr et al., 2007; see also Elzanowski and Wellnhofer, 1996; Elzanowski, 2001, 2002; Paul, 2002), however, confirms a very nonavian maniraptoran structure to the palate, with well-developed ectopterygoids, very dromaeosaur-like palatines, and elongate pterygoids. The picture that emerges is of a skull that kinematically is maniraptoran in form with few compelling reasons to suggest that there were bony linkages that permitted any significant mobility.

Cranial Growth, Kinesis, and Exaptation

The above discussion reveals that almost all dinosaurs—indeed almost all archosaurs—were at least partially kinetically competent in that they possessed synovial basal and otic joints, yet potentially only birds evolved true cranial kinesis. What, then, was the role of the synovial joints in the vast majority of archosaurs that lacked kinesis? We suggest that there may be a link between these joints and growth. Intramembranous skull growth occurs at the periosteal surface of dermal bones, whereas endochondral growth maintains the presence of a cartilaginous growth plate between elements (e.g., sphenoccipital synchondrosis in mammals) throughout most of ontogeny (e.g., Martin et al., 1998; Opperman, 2000). Although endochondral growth plates are primarily regulated by genes that cause them to eventually fuse during ontogeny, recent evidence suggests that mechanical stimuli can also upregulate the growing cartilage and delay ossification (e.g., Wang and Mao, 2002). The synovial joints relevant to cranial kinesis in the skulls of diapsids occur at the junctions of endochondral elements (e.g., basisphenoid, laterosphenoid, and quadrate) and intramembranous elements (pterygoid, frontal, squamosal). The surface textures of the joints suggest that cartilage was present (as in birds and squamates), and the high level of joint congruence in some taxa suggests that the cartilage was likely very thin. Articular cartilage persists in loading environments that exert hydrostatic pressures (which result in a change in volume but not shape) but exert low shear stresses (which change shape but not volume; Carter et al., 1998; Carter and Beaupré, 2001). The morphology and anatomical position of the synovial joints in the skulls of dinosaurs, particularly the basal and laterosphenoid joints, suggests that these joints would experience large shear stresses associated with torque and asymmetrical loading during biting. Therefore, the minimal amount of cartilage covering the ends of particular joints suggests that these synovial joints were simply growth zones rather than the articular surfaces of mobile joints. This hypothesis is supported by the maintenance of patent synovial joints in not only the laterosphenoid and otic joints in large, mature crocodylians (e.g., Fig. 2) but also the basal and laterosphenoid joints of ankylosaurs, which otherwise coossify and fuse virtually every element in the skull, including the two pterygoids.

Because cartilage-covered, synovial growth zones are probably structurally weaker joints than other cranial joints (e.g., interdigitate sutures), they may be subjected to potentially damaging loading during feeding. Therefore, rather than actively promoting intracranial movement, the role of the protractor musculature may have been to protect these growth zones and the braincase from shear and tensile forces conducted through the facial skeleton and mandible. This hypothesis is supported by the mixed angulation of protractor musculature and the highly constrained basal joints of most nonavian theropods, which likely experienced a variety of forces associated with predatory behaviors including unilateral biting, twisting, and neck movements. Ornithopods exhibit characteristics similar to theropods in that their hypertrophied and mediolaterally-oriented protractor muscles suggest that the palate experienced increased mediolateral forces compared to other dinosaur taxa. These force components may be the result of the inset, anisognathic tooth rows that may redistribute vertical forces incurred during the power stroke laterally (e.g., Heaton, 1972; Norman, 1984; Weishampel, 1984; Fig. 11).

Thus, if indeed synovial basal and otic joints (as well as the synovial laterosphenoid joint) and protractor muscles evolved as a mechanical consequence of growth dynamics and not in the context of intracranial mobility, then it becomes apparent that these attributes are exaptations, not adaptations, for cranial kinesis. Only *after* certain mechanical constraints were released by the loss of bones or bony processes—thus enabling the requisite permissive kinematic linkages—was it even possible for mobility to occur. The already-present synovial joints and protractor muscles were then available to be co-opted for movement, leading to the attainment of the 'fully kinetically competent' state and powered kinesis. This suite of coordinated changes apparently has evolved as few as only two times, once in squamates and once in birds. Moreover, the large number of lizard taxa that are fully kinetically competent yet still lack demonstrable kinesis attests to the rarity of cranial kinesis. Thus, in this light, it is perhaps not surprising that the inference of cranial kinesis in nonavian dinosaurs is tenuous at best.

CONCLUSIONS

Although it is clear that almost all nonavian dinosaurs had myology and arthrology evocative of intracranial mobility (Fig. 9), it is unwarranted to suggest that they displayed cranial kinesis. Protractor musculature and intracranial synovial joints are plesiomorphic features of diapsids and may be primarily adaptations for growth rather than feeding. In general, nonavian dinosaurs have complete temporal arcades, overlapping sutures in the palate (including the epipterygopterygoid joint), and highly congruent basal joints—features shared with *Sphenodon*, which is demonstrably akinetic (Gorniak et al., 1982; Schwenk, 2000). Many of the morphological characteristics of functionally kinetic diapsids are squamate or avian apomorphies that result in kinematically permissive linkage systems including synovial epipterygopterygoid and pterygoquadrate joints, loss of one or more temporal bars, and less-constrained basal joints. Many extant taxa that exhibit unequivocal kinesis (e.g., birds and snakes; see Table) have also eliminated the epipterygoid and have evolved specialized hinges in the dermatocranium (e.g., mesokinesis and prokinesis). Without compelling morphological evidence that is both sufficient and necessary for unequivocal positive inferences of cranial kinesis in fossil taxa, it is unlikely most fossil dinosaurs displayed functionally relevant, powered cranial kinesis, although they may have exhibited very slight movements at sutural junctures that would have served to dissipate or redistribute mechanical stresses and strains.

Inferring kinesis in extinct taxa, such as in nonavian dinosaurs, may be extremely difficult without compelling morphological evidence that suggests otherwise. The functional and adaptive significance of the intracranial synovial joints in diapsids remains to be reviewed thoroughly in extant taxa (e.g., histology, CT; Schwenk, 2000) and full understanding of the system may never be known in extinct ones (e.g., Lauder, 1995). What remains to be determined is how much intracranial movement is necessary to be considered functionally relevant 'cranial kinesis' and to what extent these movements are actually adaptive. To what extent the protractor system initiates kinesis, as in birds, or more passively modulates intracranial joints, also remains to be determined in many taxa. Certainly, typically immobile, cartilaginous growth zones can be shifted due to particular loads. However, these may or may not be detrimental to animals such as squamates and dinosaurs. Moreover, it appears that ontogeny may influence the relative mobility of certain joints over time (e.g., *Stegosaurus*, *Varanus* [Schwenk, 2000]). Given these data, inferences of cranial kinesis (i.e., mobility about intracranial joints) in nonavian dinosaurs are problematic without compelling, unequivocal morphological evidence that these joints are mobile and adaptive to feeding.

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LITERATURE CITED

Arnold, E. N. 1998. Cranial kinesis in lizards: variations, uses, and origins; pp. 323–357 in M. Hech, R. Macintyre, and M. Clegg (eds.) Evolutionary Biology Volume 30. Plenum Press, New York.

Bakker, R. 1986. The Dinosaur Heresies: new theories unlocking the mystery of the dinosaurs and their extinction. William Morrow and Company, New York. 481 pp.

Barrett, P. M. 2001. Tooth wear and possible jaw action of *Scelidosaurus harrisonii* Owen and a review of feeding mechanisms in other thyreophoran dinosaurs; pp. 25–52 in K. Carpenter, (ed.) The Armored Dinosaurs. Indiana University Press, Bloomington and Indianapolis.

Barrett, P. M., and P. Upchurch. 2007. The evolution of herbivory in sauropodomorph dinosaurs; pp. 91–112 in P. M. Barrett and D. J. Batten (eds.), Evolution and Palaeobiology of Early Sauropodomorph Dinosaurs. Special Papers in Palaeontology 77.

Bock, W. J. 1964. Kinetics of the avian skull. Journal of Morphology 114:1–42.

Bock, W. J. 2002. The evolution of avian cranial kinesis; pp. 191–201 in Z. Zhou and F. Zhang (eds.) Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1–4 June 2000. Science Press, Beijing.

Bout, R. G., and H. P. Zeigler 1994. Jaw muscle (EMG) activity and amplitude scaling of jaw movements during eating in pigeon (*Columba livia*). Journal of Comparative Physiology A 174:433–442.

Bout, R. G., and G. A. Zweers 2001. The role of cranial kinesis in birds. Comparative Biochemistry and Physiology A: Molecular & Integrative Physiology 131(1):197–205.

Bühler, P. 1981. Functional anatomy of the avian jaw apparatus; pp. 439–468 in A. S. King and B. K. McClelland (eds.) Form and Function in Birds, Volume 2. Academic Press, London.

Bühler, P. 1985. On the morphology of the skull of *Archaeopteryx*; pp. 135–147 in M. K. Hecht, J. H. Ostrom, F. Viohl, and P. Wellnhofer (eds.) The Beginnings of Birds, Proceedings of the International *Archaeopteryx* Conference Eichstätt. Freunde des Jura-Museums Eichstätt, Eichstätt.

Bühler, P., L. D. Martin, and L. M. Witmer, 1988. Cranial kinesis in the Late Cretaceous birds *Hesperornis* and *Parahesperornis*. Auk 105(1):111–122.

Calvo, J. 1994. Jaw mechanics in sauropod dinosaurs; pp. 183–194 in M. G. Lockley, V. F. dos Santos, C. A. Meyer, and A. Hunt (eds.), Aspects of Sauropod Paleobiology. Gaia 10.

Carrano, M. T., S. D. Sampson, and C. A. Forster, 2002. The osteology of *Masiakasaurus knopfleri*, a small abelisauroid (Dinosauria: Theropoda) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 22(3):510–534.

Carter, D. R., and G. S. Beaupré, 2001. Skeletal Function and Form: Mechanobiology of skeletal development, aging, and regeneration. Cambridge University Press, New York. 318 pp.

Carter, D. R., B. Mikić, and K.Padian. 1998. Epigenetic mechanical factors in the evolution of long bone epiphyses. Zoological Journal of the Linnean Society 123:163–178.

Chatterjee, S. 1991. Cranial anatomy and relationships of a new Triassic bird from Texas. Philosophical Transactions of the Royal Society of London B 332:277–342.

Chatterjee, S. 1997. The Rise of Birds. Johns Hopkins University Press, Baltimore. 312 pp.

Chiappe, L. M., M. A., Norell, and J. M. Clark, 1998. The skull of a relative of the stem-group bird *Mononykus*. Nature 392:275–278.

Chiappe, L. M., S. Ji, Q. Ji, and M. A. Norell. 1999. Anatomy and systematics of the Confuciusornithidae (Aves) from the late Mesozoic of northeastern China. Bulletin of the American Museum 242:1–89.

Chiappe, L. M., M. A. Norell, and J. M. Clark. 2002. The Cretaceous, Short-armed Alvarezsauridae: *Mononykus* and its kin; pp. 87–120 in L. M. Chiappe and L. M. Witmer (eds.) Mesozoic Birds: above the heads of dinosaurs. University of California Press, Berkeley.

Chure, D. J. 1998. On the orbit of theropod dinosaurs. Gaia 15:233–240.

Clark, J. M., J. Welman, J. A. Gauthier, and J. M Parrish. 1993. The laterosphenoid bone of early archosauriforms. Journal of Vertebrate Paleontology 13(1):48–57.

Clark, J. M., M. A. Norell, and P. J. Makovicky. 2002. Cladistic approaches to the relationships of birds to other theropod dinosaurs; pp. 31–61 in L. M. Chiappe and L. M. Witmer (eds.) Mesozoic Birds: above the heads of dinosaurs. University of California Press, Berkeley.

Colbert, E. H., and D. A. Russell. 1969. The small Cretaceous dinosaur *Dromaeosaurus*. American Museum Novitates 2380:1–49.

Crompton, A. W., and J. Attridge. 1986. Masticatory apparatus of the larger herbivores during Late Triassic and Early Jurassic times; pp. 223–236 in K. Padian (ed.), The Beginning of the Age of Dinosaurs. Cambridge University Press, New York.

Curry Rogers, K. and C. A. Forster. 2004. The skull of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 24(1):121–144.

Cuthbertson, R. S. 2006. A redescription of the holotype of *Brachylophosaurus canadensis* (Dinosauria: Hadrosauridae), with a discussion of chewing in hadrosaurs. M. S. thesis, Carleton University, Ottawa, Ontario, Canada, 128 pp.

Cuthbertson, R. S. 2007. Pleurokinesis revisited. Kinetic limitations of cranial joints in hadrosaurine dinosaurs. Journal of Vertebrate Paleontology 27(Supplement to 3):64A.

Dodson, P. 1996. The Horned Dinosaurs: a natural history. Princeton University Press, New Jersey. 360pp.

Elzanowski, A. 2001. A novel reconstruction of the skull of *Archaeopteryx*. Netherlands Journal of Zoology 51:207–215.

Elzanowski, A. 2002. Archaeopterygidae (Upper Jurassic of Germany); pp. 129–159 in L. M. Chiappe and L. M. Witmer (eds.) Mesozoic Birds: above the heads of dinosaurs. University of California Press, Berkeley.

Elzanowski, A., and P. Wellnhofer. 1996. Cranial morphology of *Archaeopteryx*: evidence from the seventh skeleton. Journal of Vertebrate Paleontology 16:81–94.

Erickson, G. M., S. D. van Kirk, J. Su, M. E. Levenston, W. E. Caler, and D. R. Carter 1996. Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones. Nature 382:706–708.

Evans, S. E. 2003. At the feet of the dinosaurs: the origin, evolution and early diversification of squamate reptiles (Lepidosauria: Diapsida). Biological Reviews 78(4):513–555.

Forster, C. A., S. D. Sampson, L. M. Chiappe, and D. W. Krause. 1998. The theropodan ancestry of birds: new evidence from the Late Cretaceous of Madagascar. Science 279:1915–1919.

Frazzetta, T. H. 1962. A functional consideration of cranial kinesis in lizards. Journal of Morphology 111:287–319.

Frazzetta, T. H., and K. V. Kardong. 2002. Prey attack by a large theropod dinosaur. Nature 416:387–388.

Galton, P. M. 1974. The ornithischian dinosaur *Hypsilophodon* form the Wealden of the Isle of Wight. Bulletin of the British Museum of Natural History 25(1):1–152.

Galton, P. M. 1985. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. II. All the cranial material and details of soft-part anatomy. Geologica et Palaeontologica 19:119–159.

Gingerich, P. D. 1973. Skull of *Hesperornis* and early evolution of birds. Nature 243:70–73.

Gorniak, G., H. Rosenberg, and C. Gans. 1982. Mastication in the tuatara, *Sphenodon punctatus* (Reptilia: Rynchocephalia): structure and activity of the motor system. Journal of Morphology 171: 312–353.

Gow, C. E., J. W. Kitching, and M. A. Raath. 1990. Skulls of the prosauropod dinosaur *Massospondylus carinatus* Owen in the collections of the Bernard Price Institute for Palaeontological Research. Palaeontologia Africana 27:45–58.

Gussekloo, W. S., and R. G. Bout, 2005. Cranial kinesis in palaeognathus birds. Journal of Experimental Biology 208:3409–3419.

Haas, G. 1955. The jaw musculature in *Protoceratops* and in other ceratopsians. American Museum Novitates 1729:1–24.

Haas, G. 1963. A proposed reconstruction of the jaw musculature of *Diplodocus*. Annals of the Carnegie Museum 36:139–157.

Haas, G. 1969. On the jaw musculature of *Ankylosaurus*. American Museum Novitates 2399:1–11.

Hatcher, J. B., O. C.Marsh, and R. S. Lull. 1907. The Ceratopsia. U.S. Geological Survey Monographs. 49:1–300.

Heaton, M. J. 1972. The palatal structure of some Canadian Hardrosauridae (Reptilia: Ornithischia) Canadian Journal of Earth Sciences 9(185):185–205.

Herrel, A., P. Aerts, and F. De Vree. 1998. Static biting in lizards: functional morphology of the temporal ligaments. Journal of Zoology London 244:135–143.

Herrel, A., F. De Vree, V. Delheusy, and C. Gans. 1999. Cranial kinesis in gekkonid lizards. Journal of Experimental Biology. 202: 3687–3698.

Herrel, A., J. Cleuren, and F. De Vree. 2000. Cranial kinesis in geckoes: functional implications. Journal of Experimental Biology 203: 1415–1423.

Herring, S. W., K. L. Rafferty, Z. J. Liu, and C. D. Marshall. 2001. Jaw muscles and the skull in mammals: the biomechanics of mastication. Comparative Biochemistry and Physiology Part A 131:207–219.

Hofer, H. 1949. Die Gaumenlücken der Vögel. Acta Zoologica 30: 209–248.

Holliday, C. M. 2006. Evolution and function of the jaw musculature and adductor chamber of archosaurs (crocodilians, dinosaurs, and birds). Ph. D. dissertation, Ohio University, Athens, Ohio, 325 pp.

Hurum, J. H., and P. J. Currie. 2000. The crushing bite of tyrannosaurids. Journal of Vertebrate Paleontology 20(4):619–621.

Iordansky, N. N. 1990. Evolution of cranial kinesis in lower tetrapods. Netherlands Journal of Zoology 40(1–2):32–54.

Kurzanov, S. M. 1985. The skull structure of the dinosaur *Avimimus*. Paleontological Journal 1985:92–99.

Kurzanov, S. M. 1987. Avimimidae and the problem of the origin of birds. (in Russian). Transactions of the Joint Soviet-Mongolian Paleontological Expedition 31:1–94.

Lauder, G. V. 1995. On the inference of function from structure; Pp. 1–18 In J. J. Thomason (ed.) Functional Morphology in Vertebrate Paleontology. Cambridge University Press, Massachusetts.

Makovicky, P. J., M. A. Norell, J. M. Clark, and T Rowe. 2003. Osteology and Relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae) American Museum Novitates 3402:1–32.

Makovicky, P. J., S. Apestguía, and F. L. Agnolín. 2005. The earliest dromaeosaurid theropod from South America. Nature 437: 1007–1011.

Martin, L. D., and Z. Zhou. 1997. *Archaeopteryx*-like skull in enantiornithine bird. Nature 389:556.

Martin, B. R., N. Sharkey, and D. Burr. 1998. Skeletal Tissue Mechanics. Springer-Verlag, New York. 460pp.

Mazzetta, G. V., R. A., Fariña, and S. F. Vizcaíno. 1998. On the paleobiology of the South American horned theropod *Carnotaurus sastrei* Bonaparte. Gaia 15:185–192.

Mayr, G., B. Pohl, S. Hartman, and D. S. Peters. 2007. The tenth skeletal specimen of *Archaeopteryx*. Zoological Journal of the Linnean Society 149:97–116.

McClelland, B. K. 1990. Anatomy and cranial kinesis of the *Allosaurus* skull. Master's thesis, University of Utah, Salt Lake City. 122 pp.

Meekangvan, P., A. A. Barhosrst, S. Chatterjee, and L. Schovanec. 2006.

Nonlinear dynamical model of avian cranial kinesis. Journal of Theoretical Biology 240:32–47.

Meers, M. B. 2002. Maximum bite force and prey size of *Tyrannosaurus rex* and their relationships to the inference of feeding behavior. Historical Biology 16(1):1–12.

Metzger, K. 2002. Cranial kinesis in lepidosaurs: skulls in motion; pp. 15–46in P. Aerts, K. D'Août, A. Herrel, and R. Van Damme (eds.) Topics in Functional and Ecological Vertebrate Morphology. Shaker Publishing, Maastricht.

Metzger, K. A, W. J. T. Daniel, and C. F. Ross. 2005. Comparison of beam theory and finite-element analysis with in vivo bone strain data from the alligator cranium. Anatomical Record 283A:331–348.

Molnar, R. E. 1991. The cranial morphology of *Tyrannosaurus rex*. Palaeontographica Abteilung A 217:137–176.

Norell, M. A., J. M. Clark, and P. J. Makovicky. 2001. Phylogenetic relationships among coelurosaurian dinosaurs; pp. 49–67 J. Gauthier and L. F. Gall (eds.) In New perspectives on the origin and early evolution of birds. Yale Peabody Museum, New Haven.

Norman, D. B. 1984. On the cranial morphology and evolution of ornithopod dinosaurs. Symposium of the Zoological Society of London 52:521–547.

Norman, D. B. 1990. Problematic Theropoda: "coelurosaurs."; pp. 280–305 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.) The Dinosauria. University of California Press, Berkeley.

Norman, D. B., and D. B. Weishampel. 1985. Ornithopod feeding mechanisms: their bearing on the evolution of herbivory. American Naturalist 126:151–164.

Novas, F. E., and D. Pol. 2002. Alvarezsaurid relationships reconsidered. pp. 121–125 in L. M. Chiappe and L. M. Witmer (eds.) Mesozoic Birds: above the heads of dinosaurs. University of California Press, Berkeley.

Ohashi, T. 2006. Structural analysis of derived ornithopod skull using 3D finite element method: reconsideration of their feeding method. Journal of Vertebrate Paleontology **26**(Supplement to 3), 107A.

Opperman, L. A. 2000. Cranial sutures as intramembranous bone growth sites. Developmental Dynamics 219:472–485.

Ostrom, J. H. 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. Bulletin of the American Museum of Natural History 122(2):39–186.

Ostrom, J. H. 1962. On the constrictor dorsalis muscles of *Sphenodon*. Copeia 1962:732–735.

Ostrom, J. H. 1964. A functional analysis of jaw mechanics in the dinosaur *Triceratops*. Postilla, Peabody Museum of Natural History, Yale University 88:1–35.

Paul, G. S. 2002. Dinosaurs of the Air. Johns Hopkins University Press, Baltimore, 460 pp.

Perle, A., M. A. Norell, L. M. Chiappe, and J. M. Clark. 1993. Flightless bird from the Cretaceous of Mongolia. Nature 362:623–626.

Perle, A., L. M. Chiappe, R. Barsbold, J. M. Clark, and M. A. Norell. 1994. Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. American Museum Novitates 3105:1–29.

Raath, M. A. 1985. The theropod *Syntarsus* and its bearing on the origin of birds; pp. 219–227 in M. K. Hecht, J. H. Ostrom, G. Viohl, and P. Wellnhofer (eds.), The Beginnings of Birds. Freunde des Jura-Museums, Eichstätt.

Rafferty K. L., S. W. Herring, and C. D. Marshall. 2003. Biomechanics of the rostrum and the role of facial sutures. Journal of Morphology 257:33–44.

Rayfield, E. J. 2004. Cranial mechanics and feeding in *Tyrannosaurus rex*. Proceedings of the Royal Society B 271:1451–1459.

Rayfield, E. J. 2005. Using finite-element analysis to investigate suture morphology: a case study using large carnivorous dinosaurs. The Anatomical Record 283A, 349–365.

Rayfield, E., D. Norman, C. Horner, J. Horner, P. Smith, J. Thomason, and P. Upchurch. 2001. Cranial design and function in a large theropod dinosaur. Nature 409:1033–1037.

Rieppel, O. 1978. Streptostyly and muscle function in lizards. Experientia 34:776–777.

Romer, A. S. 1971. The Chañares (Argentina) Triassic reptile fauna XI. Two new long-snouted thecodonts *Chanaresuchus* and *Gaulosuchus*. Breviora 379:1–22.

Russell, D. A. 1970. Tyrannosaurs from the Late Cretaceous of Western Canada. National Museum of Natural Sciences, Publications in Palaeontology 1:1–34.

Rybczynski, N. and M. K.Vickaryous. 2001. Evidence of complex jaw movement in the Late Cretaceous ankylosaurid *Euoplocephalus tutus* (Dinosauria: Thyreophora); pp. 299–317 in (K. Carpenter, ed.) The Armored Dinosaurs Indiana University Press, Bloomington and Indianapolis.

Rybczinski, N., A. Tirabasso, R. Cuthburtson, and C. M. Holliday. 2006. A 3D cranial animation of *Edmontosaurus* for testing feeding hypotheses. Journal of Vertebrate Paleontology 26 (Supplement to 3):117A.

Rybczinski, N., A. Tirabasso, P. Bloskie, R. Cuthburtson, and C. M. Holliday. In press. A three-dimensional animation model of *Edmontosaurus* (hadrosauridae) for testing chewing hypotheses. Paleontologica Electronica.

Sampson, S. D., and L. M. Witmer. 2007. Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 27 (Supplement to 2):32–102.

Schwenk, K. 2000. Feeding in lepidosaurs pp. 175–291 in K. Schwenk (ed.) Feeding: form, function, and evolution in vertebrates. Academic Press, New York.

Sereno, P. C. 2001. Alvarezsaurids: birds or ornithomimosaurs?; pp. 69–98 in J. Gauthier and L. F. Gall (eds.) New perspectives on the origin and early evolution of birds. Yale Peabody Museum, New Haven.

Soames, R. W. 1999. Skeletal system; pp. 425–736 in P. L. Williams, L. H. Bannister, M. M. Berry, P. Collins, M. Dyson, J. E. Dussek, M. W. J. Ferguson (eds.). Gray's Anatomy: The Anatomical Basis of Medicine and Surgery. Churchill Livingstone, London.

Upchurch, P. and P. M. Barrett. 2000. The evolution of sauropod feeding mechanisms; pp. 79–122 in H.D. Sues (ed.). Evolution of Herbivory in Terrestrial Vertebrates: perspectives from the fossil record. Cambridge University Press, Massachusetts.

Versluys, J. 1910. Streptostylie bei Dinosauriern, nebst Bemerkungen über die Verwandtschaft der Vögel und Dinosaurier. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 30: 175–260.

Versluys, J. 1912. Das Streptostylie-Problem und die Bewegung im Schädel bei Sauropsida. Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 2 (Suppl. 15):545–716.

Versluys, J. 1936. Kranium und Visceralskelett der Sauropsiden. 1. Reptilien; pp. 699–808 in L. Bolk, E. Göppert, E. Kallius, and W. Lubosch (eds.). Handbuch der vergleichenden Anatomie der Wirbeltiere, Volume 4. Urban and Schwarzenberg. Berlin.

Wang, X., and J. J. Mao. 2002. Chondrocyte proliferation of the cranial base cartilage upon in vivo mechanical stress. Journal of Dental Research 81(10):701–705.

Weishampel, D. B. 1984. Evolution of jaw mechanisms in ornithopod dinosaurs. Advances in Anatomy, Embryology, and Cell Biology 87:1–110.

Weishampel, D. B., and D. Cheney. 2007. Virtual hadrosauroid mastication. Journal of Vertebrate Paleontology 27(Supplement to 3): 164A.

White, T. E. 1958. The braincase of *Camarasaurus lentus* (Marsh). Journal of Paleontology 32(3):477–494.

Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils; pp. 19–33, in J. J. Thomason (ed.) Functional Morphology in Vertebrate Paleontology. Cambridge University Press, New York.

Witmer, L. M. 2002. The debate on avian ancestry: phylogeny, function, and fossils; pp. 3–30 in L. M. Chiappe and L. M. Witmer (eds.). Mesozoic Birds: Above the Heads of Dinosaurs. University of California Press, Berkeley.

Wu, X-C. 2003. Functional morphology of the temporal region in the Rhynchocephalia. Canadian Journal of Earth Sciences 40:589–607.

Zusi, R. L. 1984. A functional and evolutionary analysis of rhynchokinesis in birds. Smithsonian Contributions to Zoology 395:1–40.

Zusi, R. L. 1993. Patterns of diversity in the avian skull; pp. 391–438 in J. Hanken and B. K. Hall (eds.). The Skull, volume 2. University of Chicago Press, Chicago.

Zweers, G. A., J. C. Vanden Berge, and H. Berkhoudt. 1997. Evolutionary patterns of avian trophic diversification. Zoology 100:25–57.

Zweers, G. A. and J. C. Vanden Berge. 1998. Birds at biological boundaries. Zoology 100:183–202.

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