

## ACOUSTIC TRANSFORMER FUNCTION OF THE POSTDENTARY BONES AND QUADRATE OF A NONMAMMALIAN CYNODONT

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**ABSTRACT**—The theory that the reduced postdentary bones and quadrate of non-mammalian cynodonts were not only the morphological homologues, but also the functional equivalents of the mammalian tympanic bone and ear ossicles is tested on the basis of detailed new information of a specimen of *Chiniquodon*. The anatomy is shown to be a compromise between the respective requirements for a persistent, though reduced, stress transmission function of a jaw articulation, and an acoustic transformation function of a middle ear. There was a sound pressure level transformer ratio of about 30, but the mass and compliances of the elements restricted sensitivity to low frequencies, up to perhaps 2 kHz. Neither an air-filled tympanic cavity, nor a dedicated tympanic membrane were present, and snakes and other modern reptiles lacking a tympanic cavity offer a better mechanical analogy than mammals for the ear function of a cynodont. The fully mammalian acoustic transformer system, with tympanic cavity and tympanic membrane, could only have evolved after the origin of the dentary-squamosal jaw articulation, and was correlated with miniaturisation in the lineage leading to basal mammaliaforms.

### INTRODUCTION

The most celebrated case of the discovery of a wholly unexpected homology is surely that of the accessory ear ossicles of mammals with the jaw hinge bones of reptiles, a theory conceived by Reichert in 1837 and subsequently confirmed and elaborated upon by Gaupp (1913; see Maier, 1990 for a brief review). With the exception of Jarvik (1980), no serious worker has since doubted the relationship.

With the discovery of reduced jaw hinge bones in the non-mammalian cynodonts, attention turned to how the implied evolutionary transition occurred. Early work by Westoll (1945), Parrington (1946; 1949), Watson (1953; 1956), and Tumarkin (1955) defined the basic question of whether cynodonts lacked a tympanic membrane, possessed one in the modern reptilian postquadrate position behind the jaw articulation, or possessed one in the homologue of the mammalian position attached to the postdentary bones of the lower jaw. The culmination of the view that they possessed a postquadrate tympanic membrane was reached by Hopson (1966), who showed how such a tympanic membrane might have grown forward and become associated with the posterior jaw bones.

Allin (1975) presented the culmination of the alternative view that cynodonts had a tympanic cavity and tympanic membrane associated with the lower jaw, and that the hearing mechanism was essentially mammalian already, with sound conducted from this tympanic membrane via the articular and quadrate to the stapes and fenestra ovalis. He proposed that the transition to the modern mammalian condition consisted only of improving the performance of the system by reducing the mass of the bones and eventually freeing them of the damping effect of their attachment to the dentary. Allin's theory was soon accepted (eg, Crompton and Parker, 1978; Kemp, 1979; Kermack et al., 1981), although there was a lingering suspicion on the part of some that a postquadrate tympanic membrane may have existed in addition to the mandibular tympanic membrane (Kemp, 1979; Allin, 1986; Allin and Hopson, 1992).

The earlier demonstration by Parrington (1971) and Kermack

and colleagues (1973) that the mammaliaform *Morganucodon* possessed a cynodont-like arrangement of the postdentary bones and quadrate had not only added considerably to the argument in favor of Allin's (1975) theory on comparative anatomical grounds, but also offered an opportunity for a functional analysis of how such a sound conducting system might have operated. Kermack and colleagues (1981) concluded that *Morganucodon* did indeed hear by means of a mandibular tympanic membrane coupled to articular, quadrate and stapes, but that reception was limited to low frequencies, up to about 1kHz. In contrast, Rosowski and Graybeal (1991; Rosowski, 1992) estimated values for area of the tympanic membrane, area of the stapes footplate, and length of the basilar membrane of the cochlea in *Morganucodon*, from which they concluded that its hearing resembled that of small modern mammals, with sensitivity to frequencies of over 10 kHz.

A simple extrapolation of the mechanism of hearing in mammals, even *Morganucodon*, to a non-mammalian cynodont is of doubtful validity because the latter did not possess the secondary jaw articulation between the dentary and squamosal. Therefore the postdentary bones and quadrate must have retained their hinge function and at least a reduced stress transmission function, whether or not an auditory function was present. The present paper considers the possible role of the postdentary bones and quadrate as an acoustic impedance matching system in the non-mammalian eucynodont genus *Chiniquodon*, based on new information from a particularly well-preserved and completely prepared specimen.

**Institutional Abbreviations**—**GPIT**, Institut und Museum für Geologie und Paläontologie der Universität Tübingen; **MCZ**, The Museum of Comparative Zoology, Harvard; **NHM**, The Natural History Museum, London.

### MATERIAL

The main subject of this study is the almost complete skull NHM R8430. It was prepared by bisecting it just to the side of

the sagittal plane with a 'Lastec' diamond wire saw, and the matrix then completely removed mechanically from the internal and external regions. The posterior half of both lower jaws were detached; the right side was separated cleanly between articular and quadrate, and the postdentary rod posterior to the dentary subsequently detached. The left side separated equally cleanly between quadrate and squamosal. Neither quadratojugal nor stapes is present, but the middle ear region of the left side is very well preserved.

A second specimen is an isolated fragment consisting of the left postdentary bones lacking the angular, MCZ 4002. Little further preparation was necessary.

#### SYSTEMATIC PALEONTOLOGY

CYNODONTIA Owen, 1861

EUCYNODONTIA Kemp, 1982

PROBAINOGNATHIA Hopson, 1990

CHINIQUODONTIDAE von Huene, 1935-42

*CHINIQUODON THEOTENICUS* von Huene, 1935-42

#### Holotype—Partial skull, GPIT 1050.

**Type Locality and Age**—Chiniqua, Rio Grande do Sul State, Brazil. Ladinian, Middle Triassic.

**Referred Material**—A complete skull, NMH R8430, from the Chañares River, Campo de Talapaya, La Rioja Province, Argentina. This specimen was originally referred to as *Probesodon lewisi* Romer, but Abdala and Giannini (2002) have revised the family Chiniquodontidae and shown that *P. lewisi* is a junior synonym of *Chiniquodon theotenicus*. A second specimen is an isolated fragment consisting of the left postdentary bones lacking the angular. It is part of a disarticulated skeleton of *Chiniquodon theotenicus*, No. MCZ 4002. Romer and Lewis (1973) described the postcranial skeleton, but did not mention this fragment of the jaw.

#### DESCRIPTION

The postdentary rod (Fig. 1) consists of the surangular, angular, prearticular, and articular forming an integral unit, with no evidence of possible movement between any of the individual bones. Although sutures are present, and therefore the bones are not fused to one another, there has not been any post-mortem disarticulation at all. This is in marked contrast to the relationship of the postdentary rod as a whole to the dentary, where the appearance of a gap indicates that the connection had only been by soft tissues rather than by tight suture, and where the postdentary rod has indeed been somewhat displaced after death. The isolated fragment, MCZ 4002, confirms this interpretation, because loss of the angular has revealed the ridged and grooved sutural surfaces on the more medial bones that are characteristic of immoveable sutural connections (Fig. 1I).

**Surangular**—The surangular constitutes the dorsal surface of the postdentary rod. At the posterior end it expands dorsally and laterally like an asymmetrical trumpet horn. The saddle-shaped surface so created (Fig. 1C–H: bear.) fits closely against the underside of the hindmost 0.5-1 cm of the postdentary trough of the

dentary. The lateral part of the expansion is the surangular boss (sa. boss) of Crompton (1972). In posterior view (Fig. 1G and H) the surangular is seen to consist of three surfaces. The dorsal one is concave, faces posteriorly and slightly dorsally, and bears fine striations radiating toward the margins. The second surface (sa.lig.) is on the posterolateral side of the bone, and has a finely rugose surface indicating a ligamentous or tendinous attachment. It is positioned close to, but not in direct contact with the squamosal and, as discussed later, is interpreted as a region of connective tissue attachment of the surangular to the squamosal. The third surangular surface is ventral (sa.gl.), and is a lateral continuation of the glenoid of the articular bone. Like the latter, it lacks a periosteal finish and has the fine texturing characteristic of bone covered by synovial joint cartilage.

The medial surface of the surangular (Fig. 1B and C) is exposed above the prearticular, in the form of a horizontal trough that is limited ventrally by a sharp edge that presumably marks the upper limit of Meckel's cartilage. It ends anteriorly as a small forwardly directed point. The isolated postdentary rod of MCZ 4002 (Fig. 1I) is missing the angular, so the lateral face of the surangular is exposed as a thin, vertical sheet extending as far as the ventral margin of the postdentary rod. It is slightly concave from top to bottom and, as evident from NMH R8430, its lateral face was tightly sutured to the thin, sheet-like angular bone.

As it extends forward internal to the dentary, the surangular becomes a narrow rod, free of any direct contact with other bones, and shortly terminates. Its dorsal surface (Fig. 1D), anterior to the bearing surface, is finely sculptured into striations characteristic of bone covered only by tight periosteum. These commence along the posterolateral edge of the bone, run anteromedially, then turn to run longitudinally for the remaining length of the bone.

**Angular**—The angular is a thin, vertical sheet of bone, forming most of the lateral surface of the postdentary rod, and continued forward as a ventrally positioned rod within the postdentary trough of the dentary. A fine, very sharp ridge (Fig. 1E: ang.ri.) lies close to the upper margin, and turns ventrally parallel to the hind edge of the dentary. The lateral surface of the angular, as bounded by this ridge above and by the rounded ventral margin of the bone below, is perfectly smooth and lacks striations or rugosities. The limited exposure of the medial face between the surangular and the prearticular is also smooth and featureless.

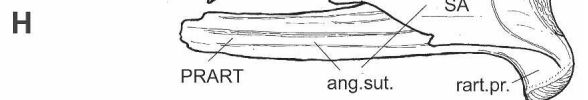
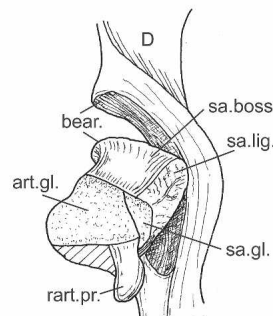
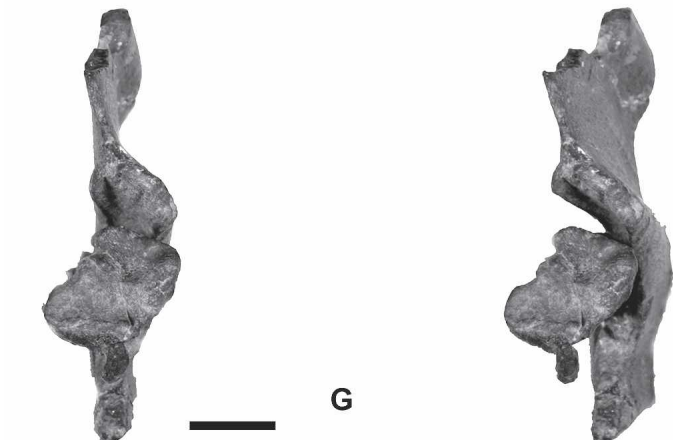
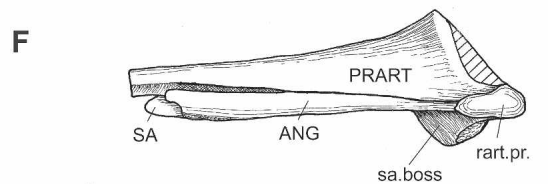
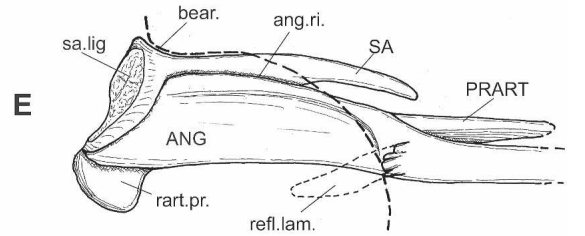
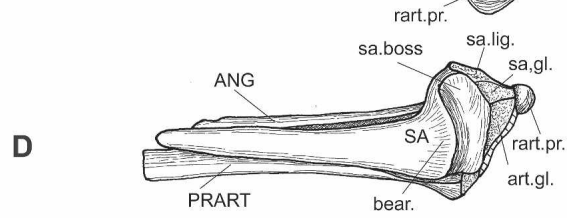
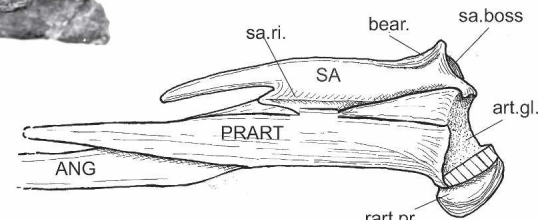
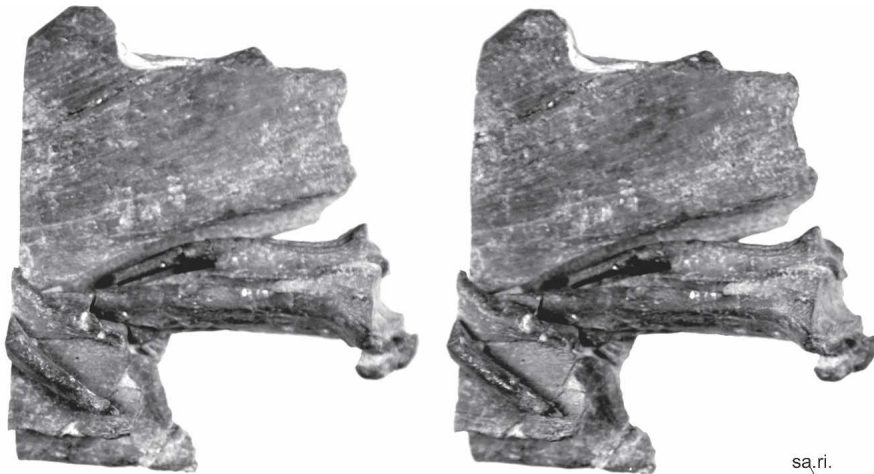
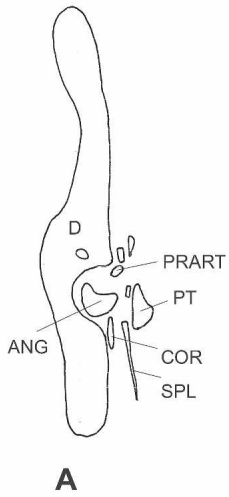
As it extends forward medial to the dentary, the angular gradually changes in cross-sectional shape from a vertical sheet to a hemicylindrical rod with a broad trough occupying the upper surface. This is seen in the transverse section (Fig. 1A), where it lies in the semicircular dentary trough. The latter is much greater in diameter than the angular rod, and so the two must have been separated by a significant space, occupied in life by soft tissues.

Only the damaged root of the small reflected lamina of the angular (refl.lam.) is preserved (Fig. 1B). It consists of three or four short, finger-like fragments of bone, suggesting that originally it was corrugated.

**Prearticular**—The ventral surface of the prearticular (Fig. 1F) expands posteriorly, and sheaths the medial and ventral faces of

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FIGURE 1. The right postdentary rod of *Chiniquodon theotenicus* NHM R8430. **A**, transverse section, as exposed in the posterior section of the right jaw; **B**, stereophotograph of the posterior section of the right jaw in medial view showing the postdentary rod as slightly displaced from the dentary trough; **C**, the right postdentary rod in medial view; **D**, stereophotograph and interpretive diagram of the right postdentary rod in dorsal view; **E**, the same in lateral view; **F**, the same in ventral view; **G**, stereophotograph of the right postdentary rod and dentary in posterior view; **H**, interpretive diagram of the right postdentary rod and dentary trough in posterior view. **I**, Fragment of left postdentary rod of MCZ 4004 in lateral view. **Abbreviations:** **ANG**, angular; **ang.ri.**, angular ridge; **ang.su.**, sutural surface for angular; **ART**, articular; **art.gl.**, glenoid surface of articular; **bear.**, bearing surface of surangular against the dentary; **COR**, coronoid; **D**, dentary; **PRART**, prearticular; **refl.lam.**, reflected lamina of the angular; **ra.r.p.**, retroarticular process; **SA**, surangular; **sa.boss**, surangular boss; **sa.gl.**, glenoid surface of surangular; **sa.lig.**, ligamentous attachment of surangular to squamosal; **sa.ri.**, surangular ridge; **SPL**, splenial. Scale bars on the photographs equal 1 cm.



the articular bone. The surface of the bone lacks any markings that might indicate the attachment of muscle or tendon. Anteriorly, the prearticular attenuates to a slender rod, extending forward and getting finer and finer. By the time it is exposed in the transverse section (Fig. 1A), the diameter is less than 1 mm and it is well separated from the angular.

Specimen MCZ 4002 reveals that the hind part of the prearticular curves ventrally and contributes much of the retroarticular process (Fig. 1I: *rart.pr.*). This specimen also shows the grooved sutural surface (*ang.sut.*) to which the angular was firmly attached.

**Articular**—The articulating surface (*art.gl.*) of the articular bone is continuous with that of the surangular (*sa.gl.*). Together they form an approximately transversely aligned trough with a mid-dorsal extension, the whole facing backward (Fig. 1G and H). The capping surangular boss (*sa.boss*) contributes a small but definite lip bounding the dorsal edge of the glenoid. Due to a strip of damaged bone, the ventral edge of the glenoid of specimen NMH R8430 is not visible, but MCZ 4002 is undamaged in this region and possesses a slight lip separating the articulating surface of the articular from the retroarticular process below.

The retroarticular process (*rart.pr.*) is also best preserved in the latter specimen (Fig. 1I). It is transversely compressed and curves ventrally forward in the plane of the angular bone. The ventral edge is thickened, creating a curving edge, while the anterior edge is fairly sharp.

The only part of the articular bone anterior to the articulating surface that is exposed is on the medial side of the postdentary rod (Fig. 1B and C). Here it is seen to be tightly wedged between the surangular above and the prearticular below. It lacks a periosteal finish, and was presumably continued forward as a persistent Meckel's cartilage.

**Postdentary Trough of the Dentary**—At the level of the transverse section (Fig. 1A), the postdentary trough of the dentary is semicircular in cross-section, and within it lies the anterior extension of the angular bone as described above. As it extends backward, the lower edge of the trough remains horizontal all the way to the hind border of the dentary. The upper edge, however, rises gradually and then more steeply. By its posteriormost region, the trough has become effectively a transversely concave roof over the postdentary rod (Fig. 1B). The diameter of the concavity matches the transverse convexity of the posterodorsal surface of the surangular (Fig. 1H: *bear.*), and it is only at this point that the two bones appear to have made direct osteological contact with one another in life.

**Quadrate**—The quadrate (Fig. 2) is generally similar to that of *Massetognathus* and *Probainognathus* as described by Luo and Crompton (1994).

The front face of the quadrate is virtually flat and featureless (Fig. 2E and F). In shape it attenuates asymmetrically dorsally, ending in a blunt apex toward the lateral side. There is a prominent posterior process (Fig. 2C and D: *p.pr.q.*) whose lateral face (*l.sq.*) abuts against the delicate vertical process of the squamosal that separates the quadrate recess from the narrow, parasagittal slit (Fig. 2E and F: *qj.re.sq.*) that housed the missing quadratojugal. The medial face of the posterior process of the quadrate (*m.sq.*) fits conformably against the quadrate recess of the squamosal plus its antero-medial extension, so that the quadrate is strongly supported postero-medially. There is a fine, vertical groove (Fig. 2E and F: *q.ra.con.*) close to the antero-medial edge, which marks the point where the quadrate ramus of the pterygoid made contact (Fig. 2C). The actual contact is visible on the left side of the skull (Fig. 3D). The contact surface of the quadrate for the stapes is not well-preserved; its position is assumed to be a damaged, roughened area close to the medial termination of the condyle (Fig. 2D: *sta.*).

The form of the condylar surface of the quadrate (Fig. 2C) closely matches that of the articular-surangular glenoid surface.

It faces anteriorly to anteroventrally, and is hemicylindrical in form; its central region is extended dorsally above the level of the medial and lateral parts. The condyle extends laterally to the body of the quadrate, where its dorsal surface would have supported the quadratojugal.

**Squamosal**—The left quadrate is slightly displaced from its recess in the squamosal (Fig. 2E and F), revealing the latter to correspond in shape to the posterior face of the body of the quadrate. The roof of the recess is demarcated by a sharp edge that would approximate the dorsal margin of the quadrate if the latter were in its natural position. The recess is extended antero-medially as a vertical wing that caps the end of the paroccipital process, and is overlapped laterally by the slender quadrate ramus of the pterygoid (Fig. 3C and D: *q.ra.pt.*).

Lateral to the narrow recess for the quadratojugal (*qj.re.sq.*), the squamosal curves anterolaterally and extends ventrally (Fig. 2E and F). This region forms the articular flange of the squamosal (*art.fl.sq.*), which lies anterolateral to and at a somewhat higher level than the quadrate condyles. It faces toward the surangular boss, but the two are separated by a few millimeters. The surface of the articular flange is marked by fine striations that indicate the attachment of collagenous tissue, such as ligament or tendon, and not articular cartilage.

**Fenestra Ovalis**—The fenestra ovalis is perfectly preserved on the left side of the skull (Fig. 3C), where it faces directly laterally toward the quadrate. In shape the fenestra is indeed oval, with the major axis inclined anterodorsally to posterior-ventrally. Its approximate dimensions are 5 mm by 3 mm, giving a surface area of about 12 mm<sup>2</sup>. A thickened rim around the fenestra presumably supported an annular ligament for attachment of the footplate of the stapes. Neither stapes is preserved in the specimen.

## FUNCTIONAL INTERPRETATION

Notwithstanding the seductive morphological homologies, and the eventual evolution of the mammalian acoustic transformer system from them, the postdentary bones and quadrate of a eucynodont cannot have functioned in a manner closely similar to that found in modern mammals. In the absence of a secondary, dentary-squamosal articulation, these bones were substantially larger, both relatively and absolutely, because they had necessarily retained a significant mandibular function of stress transmission and control of jaw movements. The question to be addressed is the extent to which the structure can be interpreted as a compromise between the requirements for the two respective functions, stress transmission and acoustic transformation.

### Mandibular Function

The demonstration that the geometrical reorganization of the adductor musculature of eucynodonts greatly reduced the reaction forces at the jaw articulation is of critical importance for understanding the function of the postdentary rod and quadrate (Crompton, 1963; Kemp, 1972; Bramble, 1978; Kemp, 1980; Crompton and Hylander, 1986). However, in the absence of a direct contact between the dentary and the squamosal, it is inevitable that at times stresses would have been generated between the dentary and cranium that had to be transmitted via the jaw articulation.

By inference this would have been particularly the case during jaw opening, although the anatomy of the jaw opening musculature of cynodonts is not well understood. The retroarticular process of the articular (Fig. 3A and B: *rart.pr.*) is far too small and feebly attached via the postdentary rod to the dentary for it to be considered the point of insertion of a large, standard amniote depressor mandibuli muscle. Kemp (1979, 1980) interpreted narrow grooves on the medial side of the angular process of the dentary as the major site of insertion of jaw opening musculature in both the basal cynodont *Procynosuchus* and the

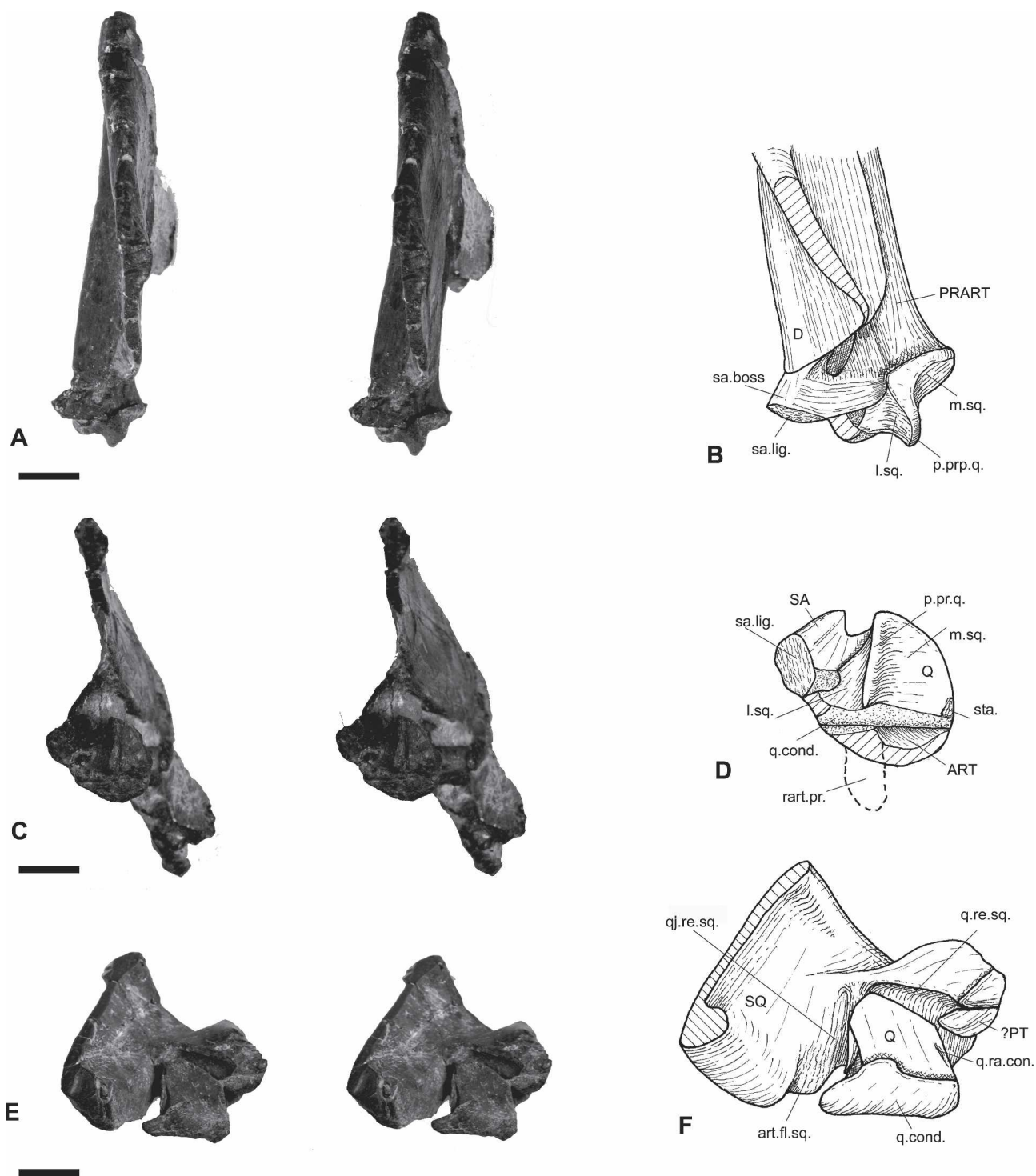


FIGURE 2. The left quadrate and adjacent structures of *Chiniquodon theotonicus*, NMH R8430. **A**, stereophotograph of the left quadrate and hind end of the jaw in dorsal view; **B**, interpretive diagram of **A**. **C**, stereophotograph of the left quadrate and hind end of the lower jaw in posterior view; **D**, interpretive diagram of **C**; **E**, stereophotograph of the right quadrate and squamosal in anterior view; **F**, interpretive diagram of **E**. Abbreviations: **ART**, articular; **art.fl.sq.**, articular flange of the squamosal; **D**, dentary; **l.sq.**, lateral contact surface with squamosal; **m.sq.**, medial contact surface with squamosal; **p.pr.q.**, posterior process of quadrate; **PT**, pterygoid; **Q**, quadrate; **q.cond.**, quadrate condyle; **qj.re.sq.**, quadratojugal recess of the squamosal; **rart.pr.**, retroarticular process; **SA**, surangular; **sa.boss**, surangular boss; **sa.lig.**, area of attachment of surangular-squamosal ligament; **SQ**, squamosal; **sta.**, contact point for stapes. Scale bars on photographs equal 1 cm.

eucynodont *Luangwa*. This presumed muscle complex can only have been associated with the fascia of the intermandibular and throat regions, perhaps acting via a hyoid. To open the jaws, the force generated would have had a posteriorly directed compo-

nent that would have generated an anteroposterior compressive reaction at the dentary-postdentary, articular-quadrate, and quadrate-squamosal contacts. At times of vigorous jaw activity the magnitude of this stress would necessarily have been signifi-

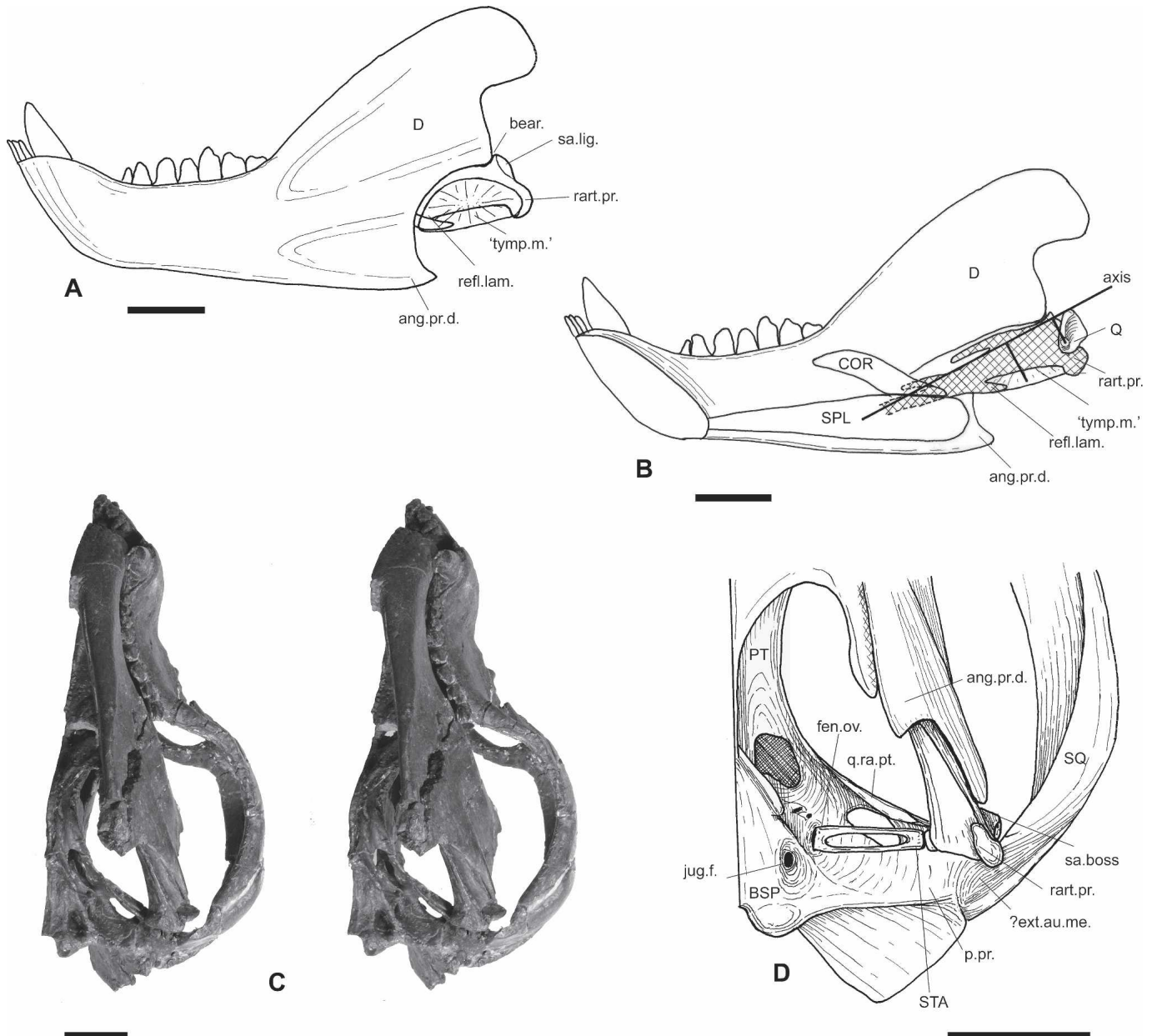


FIGURE 3. Reconstruction of the lower jaw of *Chiniquodon* in **A**, lateral view showing reconstructed putative tympanic membrane; **B**, medial view showing the postdentary rod cross-hatched, and the position of the hypothetical axis of vibration. **C**, stereophotograph of the left half of the skull in ventral and slightly lateral view; **D**, reconstruction of the left ear region in ventral view. **Abbreviations:** *ang.pr.d.*, angular process of the dentary; *BSP*, basisphenoid; *COR*, coronoid; *?ext.au.me.*, alleged groove for external auditory meatus; *fen.ov.*, fenestra ovalis; *jug.f.*, jugular foramen; *Q*, quadrate; *q.ra.pt.*, quadrate ramus of the pterygoid; *rart.pr.*, retroarticular process; *refl.lam.*, reflected lamina of the angular; *sa.boss*, surangular boss; *sa.lig.*, area of attachment of surangular-squamosal ligament; *SQ*, squamosal; *SPL*, splenial; *STA*, stapes; *tym.p.m.*, tympanic membrane. Scale bars equal 2 cm.

cant. Other circumstances generating a hinge reaction of some magnitude must have included sudden changes in the stress pattern due to rapid and unexpected changes in the resistance to jaw movements when food between the teeth yielded, and in the case of a presumed predator such as *Chiniquodon*, struggling prey tending to disarticulate the mandible.

The nature of the contacts between the dentary and the postdentary rod supports the interpretation that modest compression was the main stress to be resisted here. At the front there is the manifestly loose association between the rodlike anterior extension of the angular and the much broader dentary trough. The soft tissue filling the considerable space between them can have

provided little of the strength or stiffness required to resist stresses of any kind. However, the saddle-shaped posterior contact between the bearing surface of the surangular, and the hind end of the dentary trough (Fig. 3D: bear.) would have provided resistance to a longitudinal compressive force between them, and also perhaps a degree of dorso-ventral compression. Little resistance would have been offered to any longitudinal tension tending to pull the dentary forward. The orientation of the articulating surfaces of the mandibular glenoid and the quadrate condyle in an approximately transverse plane is also clearly designed for transmission of a mainly longitudinally oriented compressive stress. Similarly, the direct osteological support of the quadrate

behind and medially by the squamosal recess appears to be designed primarily for resistance to such compression between these elements.

The relationship between the surangular boss and the articular flange of the squamosal is problematic. Crompton (1972; Luo and Crompton, 1994) ascribed to it the function of reducing the loading on the quadrate, and Allin (1975) specifically suggested that it reduced the compressive load on that bone. An important part of the reasoning was that it is the forerunner of the dentary-squamosal jaw articulation of mammals, which in primitive forms demonstrably does have a significant compression resisting function (Crompton and Hylander, 1986). In *Chiniquodon*, however, there is no direct contact between the two bones; the squamosal flange lies several millimeters posterolateral to the surangular boss. Furthermore, the surfaces of both are marked by fine rugosities indicating connective tissue attachment, rather than the cartilage covering expected of a synovial joint. It must have been either elastic ligament or muscle that spanned the gap, because the distance between the flange and the boss would have varied with angle of gape. The only stress that might have been effectively transmitted by this arrangement is tension, an interpretation incongruent with the evidence for lack of significant tensile resistance between the postdentary rod and the dentary. Another function must be sought, as discussed later.

Thus it is concluded that the postdentary rod and quadrate had greatly reduced stress resistance, as predicted from their reduced size and the familiar reorganization of the cynodont adductor jaw musculature. Nevertheless, they retained a mechanical function associated with mandibular action, primarily in the form of offering significant resistance to a longitudinally oriented compression stress, particularly in relation to the forces generated in jaw opening, but also at other times when brief stresses were generated at the hinge.

### Acoustic Function

For the postdentary rod and quadrate to function in essence as a mammalian acoustic transformer, it would require a combination of acoustic isolation, which is defined as a low percentage of transfer of energy from a vibrating element to an attached element, and acoustic linkage, which is defined as a high percentage transfer of energy from a vibrating element to an attached element, in the following pattern: (i) acoustic isolation of the postdentary rod from the dentary; (ii) acoustic linkage between the articular (malleus) and the quadrate (incus); (iii) acoustic isolation of the quadrate (incus) from the cranium; (iv) acoustic linkage between the quadrate (incus) and the stapes. There must also be (v) significant impedance matching by means of a transformer pressure ratio between the air-borne sound receiving surface and the fenestra ovalis; (vi) masses and compliances of the elements within acceptable limits.

**(i) Acoustic Isolation of the Postdentary Rod**—The anterior support of the postdentary rod consists of the rodlike anterior section of the angular lying within the larger diameter, hemicylindrical dentary trough. The presumed loose connective tissue between them would have offered insignificant constraint to rotational vibration about a longitudinal axis (Fig. 3B:axis). The only other attachment of the postdentary rod to the dentary is the contact between the posterior end of the dorsal surface of the surangular and the posteriormost part of the roof of the dentary trough (Fig. 3A: *bear*). Both are approximately semicircular in transverse section, and their surfaces are slightly rugose, indicating a syndesmotic attachment. Assuming a non-restraining, collagenous connection between them, this arrangement would also have permitted angular vibration of the postdentary rod about a longitudinal axis, at a level immediately below the contact.

The loose, syndesmotic connection between the surangular boss and the articular flange of the squamosal lies approximately

along the line of the axis, as defined by the two attachment points of the postdentary rod to the dentary. It is therefore positioned in the predictable place to act as a non-rigid suspension point for the vibrating postdentary rod that is independent of the dentary (Fig. 3A:sa.lig.). This is likely to have been the primary, if not the sole function of the otherwise difficult to explain relationship between the surangular and the squamosal in cynodonts.

These three contacts therefore define a potentially vibrating postdentary rod that is acoustically isolated from the jaw and cranium.

**(ii) Acoustic Linkage Between Articular and Quadrate**—When the lower jaw is placed in the closed position, the posterior-facing glenoid receives the matching hemicylindrical quadrate condyle along its transverse width, and the slight supraglenoid and subglenoid ridges tighten the contact. Even under the constraint that the articular and quadrate acted as a jaw articulation, with this geometrical arrangement vibration of the articular about a longitudinal axis would have been efficiently transmitted as vibration of the quadrate also about a longitudinal axis.

**(iii) Acoustic Isolation of the Quadrate**—Kemp (1979) for the more basal cynodont *Procynosuchus*, and Luo and Crompton (1994) for the more progressive cynodont *Probainognathus* concluded that the quadrate was syndesmotically rather than suturally attached to the squamosal, and that rotational vibration about a longitudinal axis running through the point of contact between the medial edge of the bone and the quadrate ramus of the pterygoid would have been relatively unconstrained. The same is evidently the case here for *Chiniquodon*. Neither quadratojugal is preserved in this specimen, but if it were similar to that of *Probainognathus*, it would have been free to move dorso-ventrally in its narrow recess in the squamosal (Fig. 2F: qj.re.sq.) and therefore would not have restricted the proposed vibration of the quadrate to which it was attached.

**(iv) Acoustic Linkage Between the Quadrate and the Stapes**—Neither stapes is preserved in this specimen, but its form is fairly constant among cynodonts (Fig. 3D). It would have contacted the medial side of the quadrate at or slightly above the level of the condyle; a more dorsal contact would not have been possible because of the limit imposed by the horizontal level of the quadrate ramus of the pterygoid. This proposed orientation of the stapes is supported by the fact that the fenestra ovalis faces directly toward the lower part of the quadrate. The vibration of the quadrate about a longitudinal axis was transformed into a piston action of the stapes, which vibrated directly in and out of the fenestra ovalis.

**(v) Impedance Matching**—The amniote middle ear acts as an impedance matching system by transforming the low sound pressure of the airborne sound waves meeting the tympanic membrane ( $P_T$ ) into higher sound pressure waves ( $P_{FO}$ ) at the stapes footplate where they enter the aqueous medium of the cochlea (for description of middle ear function see, for example, Møller, 1974; Relkin, 1988; Rosowski, 1994; 1996). The principal means of achieving this in modern mammals is referred to as the 'ideal transformer,' which consists of two linked acoustic transformers, the ratio of tympanic membrane area ( $A_T$ ) to fenestra ovalis area ( $A_{FO}$ ), and the ratio of the effective lever arm of the manubrium of the malleus ( $L_M$ ) to the length of the crus brevis of the incus ( $L_I$ ), such that:

$$P_{FO}/P_T = A_T/A_{FO} \cdot L_M/L_I \gg 1$$

Following Allin (1975), the reconstruction of airborne sound receiving soft tissue covering the lateral surface of the postdentary rod and acting as a tympanic membrane (Fig. 3A) assumes that its boundary is marked by the ridge along the anterior and dorsal parts of the exposed angular, the curved edge of the retroarticular process, and a ventral margin supported at the front by the reduced reflected lamina of the angular. As such, it has a surface area of about 240 mm<sup>2</sup>. The area of the fenestra ovalis is about

12 mm<sup>2</sup>. This gives an area ratio  $A_T/A_{FO}$  of about 20, which is well within the modern mammalian range of 10–40 (Rosowski and Graybeal, 1991; Rosowski, 1992). The length of the lever arm of the postdentary rod is taken to be the distance between its inferred axis and a point close to the ventral margin (Fig. 3B). This gives a figure for  $L_M$  of about 12 mm. The lever arm of the quadrate,  $L_I$ , is taken to be the distance from the presumed axis of rotation of the postdentary rod to the point of attachment of the stapes. It has a value of about 8 mm. The lever arm ratio  $L_M/L_I$  is therefore around 1.5, which again is comfortably within the modern mammalian range: Rosowski (1996) quotes figures of 2.5 for the cat and 1.2 for the guinea pig and human middle ears. Taken together, the two ratios therefore represent an ideal transformer ratio of 30.

Most modern amniotes have at least one additional device to increase the transformer ratio. The catenary effect in modern mammals results from different amplitudes of vibration, and therefore different pressures, at different parts of the tympanic membrane, and increases the ratio approximately twofold (Khanna and Tonndorf, 1972; Rosowski, 1996). However, it can only apply to a flexible tympanic membrane, not a stiff unit like the postdentary rod. Most mammals also possess an external pinna and external auditory meatus, which, in addition to providing directional sensitivity, can act as an acoustic horn (Rosowski, 1996). However, this effect is only significant at frequencies higher than what is argued shortly to have been the probable maximum to which the cynodont system was sensitive. In birds and lizards, the stapes is pivoted on the edge of the fenestra ovalis and it has a rocking rather than a linear motion, which creates a pressure transformation (Saunders et al., 2000). In the cynodont, the orientation of the quadrate, stapes and fenestra ovalis indicates that the movement of the stapes must have been piston-like, as in mammals, and that no such rocking action was possible.

**(vi) Masses and Compliances**—The performance of an acoustic transformer depends on the physical attributes of its constituent parts, particularly the masses, in so far as they are related to the moment of inertia of a vibrating system, and the compliances (reciprocals of stiffness) that affect the amplitude of movement under a given force. The relative effect of both is also related to the frequency of the sound being received (eg, Relkin, 1988; Rosowski, 1996). The greater the moment of inertia, the less the angular acceleration of a vibrating element under a given sound pressure level, and therefore the higher the impedance: this reduction in performance becomes more significant as frequency increases. The lower the compliance (the stiffer), the lower the amplitude of vibration under a given sound pressure level: this reduction in sensitivity becomes more significant as frequency decreases. Qualitative consideration of these properties gives an indication of the likely performance of the system.

The separated part of the postdentary rod of the *Chiniquodon* specimen has a measured volume of 1660 mm<sup>3</sup>, which, when multiplied by the density of normal bone of approximately 2000 kg.m<sup>-3</sup>, gives an estimated mass of about 0.33 g. To this must be added the mass of the anterior, unexposed part of the postdentary rod, the quadrate, and the stapes. These add roughly another 50%, bringing the overall mass of the postdentary rod, quadrate, and stapes to round about 0.5 g. Even ignoring additional mass due to unpreserved soft tissues, this figure is far in excess of the mass of modern mammalian ear ossicles; for example, Wever and Lawrence (1954) quote a mass of only 0.06 g for the malleus and incus, and a further 0.003 g for the stapes in humans. Given the greater effect of high inertia on higher frequency sound, an acoustic transformer of this mass and presumed inertia in the cynodont can only have been sensitive to low frequency sound, perhaps up to a maximum of 1–2 kHz.

There are several parts of the proposed cynodont acoustic transformer system where the value of the compliance would

have been particularly important: the tympanic cavity if present, where the larger the volume of air the greater the compliance; the tympanic membrane or equivalent airborne sound receiving area, where the stiffer the material the lower the compliance; and the stiffness of the ligamentous or muscular attachments of the vibrating elements to the fixed points of the rest of the cranium.

Allin's (1975) model of the auditory function of the postdentary rod assumed that there was an air-filled cavity occupying the lateral face of the body of the angular, and that the tissues bounding the cavity externally, including the reduced reflected lamina of the angular, constituted a tympanic membrane. Acoustic vibrations of the latter were transmitted by the postdentary rod, via the quadrate, to the stapes. However there is a flaw in this proposed mechanism, because the reflected lamina and the body of the angular bone must have vibrated as part of a single unit. To act as a tympanic membrane, the whole postdentary rod as a unit would have to bound a tympanic cavity that lay entirely medially to, not contained within itself. Allin (1975) does not discuss whether there was indeed an air cavity internal to the whole postdentary rod. Allin and Hopson's (1992) reconstruction of the head of *Thrinaxodon* illustrates an air-filled 'mandibular recess' medial to the postdentary rod, but which also extends over the lateral surface of the angular. The authors do not comment on why this extension should have existed.

An air-filled tympanic cavity having the same topological relationships as in a mammal would lie internal to the entire postdentary rod and quadrate, and enclose the stapes (cf. Fig. 3D), and would therefore be relatively huge in volume. It would be unsupported ventrally, and there would be a large distortion to its shape as the jaw opened. Anatomically such a structure is entirely unrealistic. It would also be functionally superfluous. Given the limitations to hearing unavoidably imposed by the high mass of the bony elements of *Chiniquodon*, it is very doubtful that a large tympanic cavity would add much to the sensitivity. Among living amniotes, *Sphenodon*, several lizard taxa, and snakes lack or have only a vestigial tympanic cavity (Henson, 1974; Wever, 1978; Saunders et al., 2000). Nevertheless, all can hear airborne sound surprisingly well, although only in the low frequency range up to 1–2 kHz (Gans and Wever, 1976; Wever, 1978; Dooling et al., 2000). The details differ among the groups and are not well understood, but the basic mechanism consists of reception of airborne sound by acoustically partially isolated superficial tissues overlying the jaw or quadrate, the vibrations of which are transmitted to the stapes. Instead of occupying an air-filled tympanic cavity, the stapes is enclosed in diffuse, cellular connective tissue. It is assumed on phylogenetic grounds that in these modern forms the tympanic cavity has been secondarily lost, but an analogous mechanism in an unrelated group such as cynodonts, in whose ancestry a tympanic cavity need never have existed, is perfectly feasible.

Virtually by definition, a tympanic membrane bounds a tympanic cavity. In the absence of the latter, the former is simply an area of tissue that acts as an air-borne sound receiver. In the present case, it is inferred that the area of the postdentary rod exposed laterally behind the dentary constituted the acoustically isolated tissue (Fig. 3A). As such, its compliance would have been relatively low because of the stiffness of soft tissues lying medially to it in the animal's throat region, and surrounding the stapes below the paroccipital process. The threshold of sensitivity of *Chiniquodon* would therefore have been high but, again by analogy with those modern reptiles lacking a tympanic cavity, well within a biologically useful range.

Allin's (1975; see also Luo and Crompton, 1994) arguments against a postquadrate tympanic membrane in cynodonts, either alone (Hopson, 1966) or in addition to a mandibular one (Kemp, 1979; Allin and Hopson, 1992) hold *a fortiori* in the present interpretation of the *Chiniquodon* ear. The maximum realistic diameter of a postquadrate tympanic membrane would be about



6mm, giving an area of less than 30 mm<sup>2</sup> compared to the fenestra ovalis area of 12 mm<sup>2</sup>. This would have provided a trivially small transformer ratio. One argument offered in favor of the presence of a postquadrate tympanic membrane in cynodonts was the claim that the groove, or trough on the posterior face of the squamosal housed an air-filled external auditory meatus leading to it (Fig. 3C and D: ?ext.au.me.). First proposed by Gregory (1910), the view was endorsed by many authors including Watson (1953; 1956), Parrington (1949), and Hopson (1966). However Allin (1975) and Kermack and colleagues (1981) rejected this interpretation of the function of the groove on the grounds that such a meatus could not realistically have reached the postdentary tympanic membrane, which they believed to have been present. Furthermore, it may be noted that the distal termination of the stapes of cynodonts lies some distance antero-medially from the end of the presumed external auditory meatus, and therefore there would need to have been a long cartilaginous extrastapes, with an orientation making it difficult to see how the relatively massive stapes could have an effective sound pressure transformer function. An alternative explanation for the squamosal trough is that it reflects the cranial architecture of the skull, as related to the reorganization of the adductor musculature within the temporal fenestra. The basal cynodont *Procynosuchus* lacks the trough. In this form, the squamosal forms a relatively high, almost vertical posterior wall of the adductor fossa, which must have provided an area of origin for much of the temporalis muscle (Kemp, 1979). The muscle ran forward to insert on the relatively small and anteriorly situated coronoid process. In later cynodonts, the coronoid process became larger and more posteriorly placed. For the temporalis muscle to remain of adequate length, there had to be a corresponding posterior shift in its origin. It may have been this requirement that led to the reflection of the dorsal edge of the fossa backward, thereby creating incidentally the trough below it.

Another aspect of the proposed acoustic transformer system in which compliance is critical concerns the nature of the attachment of the postdentary rod. Both its anterior and posterior attachments to the dentary were evidently by relatively unconstraining connective tissue, as also was the inferred ligamentous connection between the surangular boss and the articular flange of the squamosal. Such a mode of suspension of the postdentary rod, relative to the dentary and the cranium, would have increased the compliance of the system, and therefore the amplitude of vibration of the postdentary rod under the influence of incoming air-borne sound waves. As noted earlier, this effect is particularly important for lower frequencies and is therefore functionally consistent with the inference already drawn that only low frequency sound could be detected. The similarly loose attachment of the quadrate to the squamosal, despite its stress transmission function, would have resulted in increased compliance at this joint too.

## CONCLUSIONS

### Anatomical and Functional Conclusions

The anatomy of the postdentary rod and quadrate of *Chiniquodon* indicates a compromise structure between that required of a reduced but still significant stress transmission function on the one hand, and that required of an acoustic transformer function a good deal less sophisticated than in mammals on the other. The principal stress at the jaw articulation consisted of longitudinal compression. It was resisted successively by the posterior part of the surangular forming a concave bearing against the convex posterior end of the dentary, by the near-vertical orientation of the articular glenoid and quadrate condyle surfaces, and by the nature of the quadrate-squamosal articulation. The acoustic transformation function was enhanced by the compliant na-

ture of the anterior and posterior attachments of the postdentary rod to the dentary, the latter again being a result of the specialized bearing surface of the surangular. In contrast to earlier proposals, the association between the surangular boss and the articular flange of the squamosal is interpreted as a ligamentous connection between the postdentary rod and cranium that constituted a compliant support allowing the postdentary rod to vibrate in acoustic isolation of the dentary.

There is no anatomic evidence for a tympanic cavity bounded by a specialized tympanic membrane, and furthermore such structures would not have significantly compensated for the constraint imposed on hearing performance imposed by the substantial mass of the elements involved. The inferred physical properties of the system therefore point to an ability to hear only relatively low frequencies of up to perhaps 1–2 kHz, a conclusion that is consistent with the small size of the cochlea recess of cynodonts (Luo et al., 1995).

Allin's (1975) theory is therefore supported to the extent that sound reception in cynodonts involved the homologues of the mammalian ectotympanic bone (angular) and ear ossicles (articular and quadrate) while they were still associated with the dentary, rather than there having been a modern reptile-like postquadrate tympanic membrane. However, it is also concluded that a significant modification to his theory is necessary, because of the inferred absence at this stage of a tympanic cavity and specialized tympanic membrane.

### Evolutionary Implications

When reviewed by Allin (1975) three decades ago, no satisfactory understanding of hearing in pre-cynodont therapsids had been reached, and this is still the case. In particular, arguments concerning the possible acoustic function of their large reflected lamina of the angular and associated angular recess bounded by it remain unresolved. One of the possibilities, supported by several authors including Allin himself, is that the recess contained an air-filled chamber bounded by the reflected lamina, and that both were implicated in sound reception even before the cynodont grade. However, it is implicit in the present study that no such air-filled recessus mandibularis was present in therapsids, and therefore that the main alternative view of the function of the reflected lamina and its recess as an area for insertion of ventral jaw musculature is more feasible and should be reconsidered.

The present analysis also has implications for the transition from acoustic reception in the eucynodont stage to that found in mammals. The critical step was removal of the stress transmission function of the jaw articulation, which could only happen with the evolution of the direct dentary-squamosal articulation. This made possible the reduction of the mass of the postdentary rod and quadrate, which increased their sensitivity to higher frequency sound. The reduction in size of these bones would also have compacted them within a small enough volume to render an air-filled tympanic cavity, bounded by a tympanic membrane, anatomically feasible. This would have further increased the efficiency of sound transmission by increasing the compliance of the system.

There is a functional paradox here: as long as the jaw hinge retained its stress transmission function, the postdentary rod and quadrate could not become smaller, yet for the acoustic abilities to have improved as they did in the transition to mammals, they must have become smaller. A possible resolution may be found in the miniaturisation that evidently occurred in the particular lineage leading from a eucynodont ancestral grade to the basal mammals (Kemp, 2005, page 135). While by no means all eucynodont lineages experienced phylogenetic size reduction (Sidor, 2001), the one culminating in mammals undoubtedly did. Not only are all the early Jurassic mammals relatively small in size,

with skull lengths of 2 to 6 cm, but also the tritheledontids, which are widely interpreted as constituting the sister group of Mammaliaformes, are too. The largest known tritheledontid is in fact *Elliotherium*, with an estimated skull length of 5.5 cm (Sidor and Hancox, 2006); the largest known of the early mammaliaforms is *Sinoconodon* with skull length ranging from 2.3 to about 6.2 cm (Crompton and Sun, 1985; Crompton and Luo, 1993; Luo et al., 2001). As both these forms are at the extreme end of the size range for their taxa, the ancestral mammalian condition may be inferred to have been substantially smaller. Predictable consequences of the evolution of greatly reduced body size in a eucynodont include: a proportionate reduction in the absolute mass of the postdentary rod and quadrate; a relative, allometric reduction in the mass of the hinge bones because of the allometric decrease in the magnitude of muscle forces with body size; a relative increase in brain volume to skull volume because of the allometric relationship between body and brain sizes, and therefore a reduction in the distance between quadrate and fenestra ovalis needing to be spanned by the stapes. This series of anatomic transitions alone would tend to bring the hind end of the dentary into close apposition to the squamosal, while simultaneously reducing the mass of the elements of the eucynodont acoustic transformer system. The moment a direct contact between dentary and squamosal occurred, the postdentary rod and quadrate were freed of the functional constraint of stress transmission and therefore their function of acoustic transformation could be optimized.

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