Transformation of the Quadrate (Incus) through the Transition from Non-Mammalian Cynodonts to Mammals
Author(s): Zhexi Luo and Alfred W. Crompton
Source: *Journal of Vertebrate Paleontology*, Vol. 14, No. 3 (Sep. 7, 1994), pp. 341-374
Published by: Taylor & Francis, Ltd. on behalf of The Society of Vertebrate Paleontology
Stable URL: http://www.jstor.org/stable/4523575
Accessed: 03-04-2017 21:44 UTC

Journal of Vertebrate Paleontology 14(3):341–374, September 1994

TRANSFORMATION OF THE QUADRATE (INCUS) THROUGH THE TRANSITION FROM NON-MAMMALIAN CYNODONTS TO MAMMALS

ZHEXI LUO[1] and ALFRED W. CROMPTON[2]
[1]Department of Biology, College of Charleston, Charleston, South Carolina 29424;
[2]Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

ABSTRACT—The quadrate (incus) bone underwent important evolutionary transformations through the cynodont–mammal transition. The following character transformations played crucial roles in modifying the cynodont quadrate into the mammalian incus: 1) progressively greater rotation of the dorsal plate relative to the trochlea; 2) the contact facet of the dorsal plate becomes concave; 3) development of a constricted neck between the dorsal plate and the trochlea; 4) simplification of the quadrate–cranium joint, resulting in better mobility of the joint; and 5) introduction of a stapedial process (crus longum). The dorsal plate rotation, the concave contact facet, the constricted neck, the mobile joint of the quadrate and the cranium are also present in some advanced non-mammalian cynodonts. Broad phylogenetic distributions of these features suggest that the major features of the incus of early mammals, as represented by *Morganucodon,* originated much earlier in phylogenetic history among non-mammalian cynodonts. Apomorphies of the quadrate (incus) among the advanced non-mammalian cynodonts favor a sister-group relationship of tritheledontids and mammals. The hypothesis on the postdentary origin of the mammalian tympanic membrane is favored by transformation of the quadrate through the cynodont–mammal transition. Three most important modifications of the quadrate (incus) through the cynodont–mammal transition are: formation of the concave contact facet, progressively greater rotation of the dorsal plate, and decrease in the number of cranial bones articulating with the quadrate. These modifications would simplify the quadrate–cranial joint and increase the mobility of the quadrate (incus) relative to the cranium while a functioning tympanic membrane was maintained on the mandible, improving the sensitivity of the postdentary tympanum. *Probainognathus* is among the earliest known non-mammalian cynodonts with a concave contact facet and a rotated dorsal plate in the quadrate. Thus we hypothesize that it represents a critical step in the phylogenetic transformation that led to the origin of the modern mammalian middle ear and tympanic membrane.

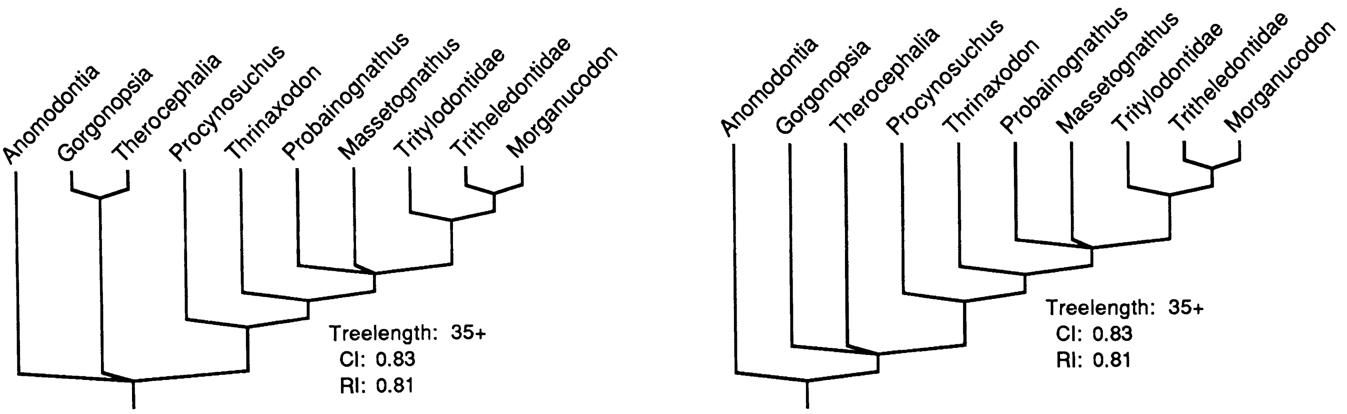
INTRODUCTION

The homology of the quadrate of diapsid reptiles and the incus of extant mammals has long been recognized (Reichert, 1837; Gaupp, 1913; Goodrich, 1916; Maier, 1990). The differentiation from the Meckelian cartilage of early embryos into the malleus and incus of adults has been described in exquisite detail for every major extant mammalian group (Gaupp, 1913; McClain, 1939; Kuhn, 1971; Zeller, 1989; Maier, 1990; Filan, 1991). Evolution of the mammalian middle ear is also documented by a reasonably good fossil record of non-mammalian cynodonts and early mammals (Allin, 1975; Crompton and Parker, 1978; Allin and Hopson, 1992). The articular and quadrate functioned as both the jaw joint and the sound conducting apparatus in non-mammalian cynodonts. The malleus and incus in mammals, the homologous bones of the articular and the quadrate, are specialized to transmit the vibration of sound. This evolutionary transition was accomplished by a series of structural transformations of the quadrate (incus) bone. The purpose of this paper is to document the phylogenetic distribution of the quadrate characters among some advanced non-mammalian cynodonts and *Morganucodon.* It is our hope that the new information on the distribution of the quadrate (incus) characters among these taxa will help to shed light on the phylogenetic and functional evolution of the quadrate (incus). Our first goal is to use characteristics of the quadrate (incus) to test the competing hypotheses of phylogenetic relationships of these taxa, and to evaluate how these competing phylogenetic hypotheses differ in their respective prediction of the quadrate transformation. Our second goal is to interpret the functional implications of the quadrate (incus) transformation. Third, we will make an effort to address the long-standing problem of the origins of the mammalian tympanic membrane, in light of the new information.

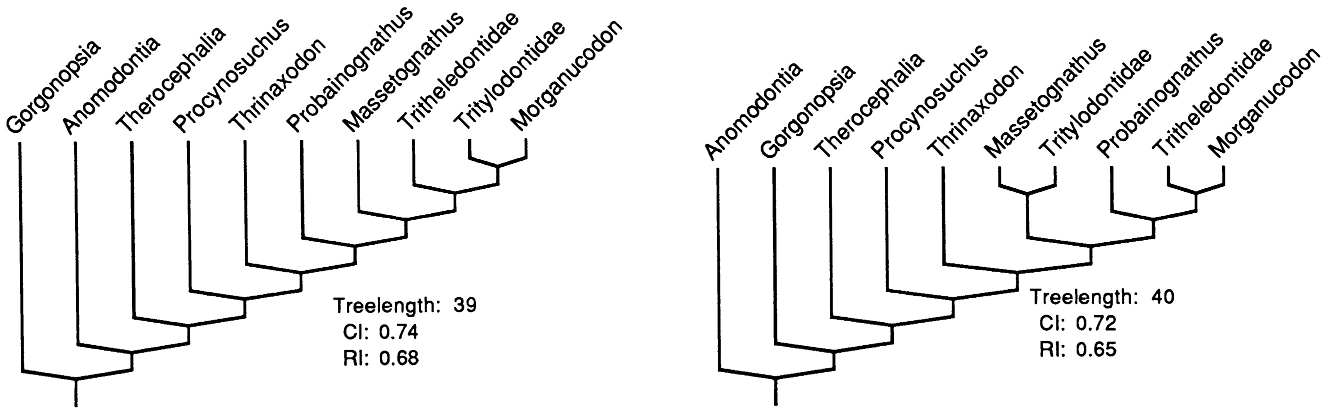
Institutional Abbreviations—CUP, former Catholic University of Peking (collection currently housed in Field Museum of Natural History, Chicago); IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing; MCZ, Museum of Comparative Zoology, Harvard University; SAM, South African Museum.

SYSTEMATIC FRAMEWORK AND METHODS

The following fossil taxa are included in this study: *Thrinaxodon, Probainognathus, Massetognathus, Exaeretodon, Tritylodon, Bienotheroides, Kayentather-*



A. Strict Consensus Tree B. Preferred Tree



C. After Rowe (1988, 1993) & Wible (1991) D. After Hopson and Barghusen (1986)

FIGURE 1. Tests of phylogenetic relationships of non-mammalian cynodonts and *Morganucodon* by quadrate characters (matrix in Table 1, character list in Appendix 1, tree measurements estimated by MacClade 3.0). **A**, strict consensus tree (based on three equally parsimonious trees from exhaustive search of PAUP 3.1.1 on the matrix in Table 1, with un-ordered multiple character states). **B**, preferred phylogenetic tree of this study (slightly different from the strict consensus tree in the position of gorgonopsians). **C**, test of phylogenetic relationships of cynodonts proposed by Rowe (1988, 1993) and Wible (1991). **D**, test of phylogenetic relationships of cynodonts proposed by Hopson and Barghusen (1986), Hopson (1991) and Rougier et al. (1992). The sister-group relationship of *Pachygenelus* and *Morganucodon* is supported by characters of the quadrate among advanced non-mammalian cynodonts and *Morganucodon*. Abbreviations: **CI**, consistency index; **RI**, retention index.

ium, Yunnanodon, Pachygenelus, Morganucodon, Dinnetherium, the Cloverly Formation triconodontid, and several other non-mammalian cynodonts. *Thrinaxodon, Probainognathus, Massetognathus,* Tritylodontidae, *Pachygenelus,* and *Morganucodon* are considered the in-group taxa of this analysis (Eldredge and Cracraft, 1980; Wiley, 1981). *Morganucodon* is treated as a representative of early mammals because it is best known from previous studies (Kermack et al., 1973, 1981; Kermack and Musset, 1983; Crompton and Sun, 1985; Crompton and Luo, 1993; Luo, in press), and from several well preserved specimens under our study. Although *Sinoconodon* has been hypothesized as the sister taxon to all known mammals (Crompton and Luo, 1993; Luo, in press), it is not included in this study because its quadrate is not preserved in any available specimen.

Character states are polarized by out-group comparison (Farris, 1982; Maddison et al., 1984; Gauthier et al., 1988). In order to assess the transformation of the quadrate (incus) from a broader phylogenetic perspective, we have based our out-group analysis on the systematic frameworks proposed in several previous studies (Kemp, 1982, 1988; Rowe, 1986, 1988, 1993; Hopson and Barghusen, 1986; Hopson, 1991), which covered a much wider range of taxa and more characters from diverse sources. Most of the recent phylogenetic studies of non-mammalian cynodonts suggest that, among known non-cynodont therapsids, therocephalians are more closely related to the common ancestry of all cynodonts than other non-cynodont therapsids (Kemp, 1982, 1988; Hopson and Barghusen, 1986; Hopson, 1991; Rowe, 1986, 1993). Within the Cynodontia, procynosuchids are hypothesized to be the sister-group of a monophyletic taxon consisting of *Thrinaxodon* and other cynodonts, as well as mammals (Kemp, 1979, 1988; Hopson and Barghusen, 1986; Rowe, 1988; Hopson, 1991). Based on this phylogenetic scheme (Fig. 1A), *Procynosuchus,* therocephalians, gorgonopsians and anomodonts are taken as the out-groups that are successively more distant from the common ancestry of *Thrinaxodon* and other cynodonts plus mammals.

The relationships of gorgonopsians and dicynodonts have been debated recently (for review see Kemp, 1988). Rowe (1986, 1988, 1993) argues that dicynodonts are the sister taxon to a group that includes therocephalians and the Cynodontia, to the exclusion of gorgonopsians. According to Hopson and Barghusen (1986; Hopson, 1991), gorgonopsians are the sister taxon to therocephalians and cynodonts, to the exclusion of anomodonts (including dicynodonts). Primitive dromasaurian anomodonts (Brinkman, 1981) lack many derived features of therocephalians plus cynodonts, and they are more primitive than gorgonopsians. In this study, we follow Hopson and Barghusen (1986) in regarding gorgonopsians to be more closely related to therocephalians and cynodonts than anomodonts (including dicynodonts).

Description and distribution of the quadrate characters are summarized in Table 1 and Appendix 1. In the character analysis of the quadrate, no individual character was weighed over any other characters. All multiple character states were treated as un-ordered data in the phylogenetic algorithms, to avoid any a priori conception of characters that could bias the phylogenetic and functional interpretation of results. Tests of alternative phylogenetic hypotheses by the quadrate characters were based on the criterion of least number of transformational steps (Fig. 1). The phylogenetic trees were generated from two phylogenetic programs for Macintosh computers: MacClade (version 3.0; Maddison and Maddison, 1992) and PAUP (version 3.1.1; Swofford, 1993).

QUADRATE MORPHOLOGY

Out-groups

Before we consider the quadrate of cynodonts and early mammals, it is necessary to review the published literature on the quadrate morphology of such out-groups as anomodonts, gorgonopsians, therocephalians, and procynosuchids (Olson, 1944; Crompton, 1955, 1964; Parrington, 1955; Camp, 1956; Brink, 1963a, b; Kemp, 1969, 1972a, b, 1979; Brinkman, 1981). The quadrate bone in therapsids consists of a ventral and horizontal trochlea that articulates with the articular, and a dorsal plate that contacts the surrounding bones in the cranium (Fig. 2). The posterior surface of the dorsal plate is termed the contact facet.

In gorgonopsians, both the lateral trochlear condyle (lt.tr.co) and medial trochlear condyle (m.tr.co) are set anteromedially and at a small angle to the axis of the trochlea so that the trochlea is "screw-shaped" (Parrington, 1955; Kemp, 1969). The lateral trochlear condyle is larger than the medial condyle. The contact facet on the posterior surface of the dorsal plate is convex both vertically and transversely; but near the junction with the trochlea it is slightly concave (Fig. 2A). The dorsal margin of the dorsal plate of the quadrate is rounded (Olson, 1944; Parrington, 1955; Kemp, 1969). The medial margin of the dorsal plate is expanded anteromedially to form the epipterygoid wing, which abuts against the quadrate ramus of the epipterygoid (Olson, 1944; Kemp, 1969). The posteromedial face of the epipterygoid wing is a broadly concave recess ("stapedial recess," Fig. 2). Associated with this recess is a groove on the medial trochlear condyle. Parrington (1955) termed this the "stapedial groove," which presumably received the distal end of the stapes. However, Olson (1944:fig. 13) and Kemp (1969) demonstrated that the whole recess on the posterior face of the epipterygoid wing received the large distal end of the stapes. Thus we identify the whole concave area plus the groove as the "stapedial recess" (Fig. 2A).

The quadrate attaches to the cranium via the squamosal, the epipterygoid, and the quadratojugal. The convex posterior face of the dorsal plate of the quadrate and the concave quadrate recess of the squamosal form a "ball in socket" joint that could be mobile during the movement of the jaw (Kemp, 1969). Kemp (1969) suggests that the contact between the epipterygoid wing of the quadrate and the quadrate ramus of the epipterygoid could serve as a fulcral point for the movement of the quadrate. The lateral margin of the quadrate is sutured with and wrapped by the quadratojugal (QJ. Fig. 2A) (Parrington, 1955).

Therocephalians (sensu Hopson and Barghusen, 1986) are a diverse group. The quadrate shows much broader morphological variations in this group than in gorgonopsians (Crompton, 1955; Brink, 1963a; Kemp, 1972b). In whaitsiid therocephalians (Kemp, 1972a, b), the anterior face of the dorsal plate of the quadrate is flat. Most of the posterior face is flat, although it is slightly concave ventrally near the trochlea. The dorsal margin of the quadrate is truncated in whaitsiids (Kemp, 1972a, b) and *Bauria* (Crompton, 1955). The dorsal margin in *Ictidosuchops* appears to have a pointed angle (Crompton, 1955). In *Regisaurus* (Mendrez, 1972), the shape of the quadrate recess of the squamosal suggests that the quadrate also has a pointed dorsal angle. The medial margin of the dorsal plate flares anteriorly, and is termed the "pterygoid wing" by Kemp (1972a, b). This wing is similar to the epipterygoid wing in the quadrate of gorgonopsians in that it flares anteriorly. However, the articulation of this wing differs from the epipterygoid wing of gorgonopsians. The epipterygoid wing of the quadrate in gorgonopsians only abuts the ramus of the epipterygoid but does not contact the pterygoid. The pterygoid wing of the quadrate in therocephalians overlaps on the lateral side of the rami of both the pterygoid and epipterygoid, similar to the condition in dicynodonts (Camp, 1956; Rowe, 1986). The posterior end of the quadrate ramus of the pterygoid fits into a recess on the posteromedial face of the wing of the quadrate. The paroccipital process of the opisthotic bone also contacts the pterygoid wing in this broad concave area in

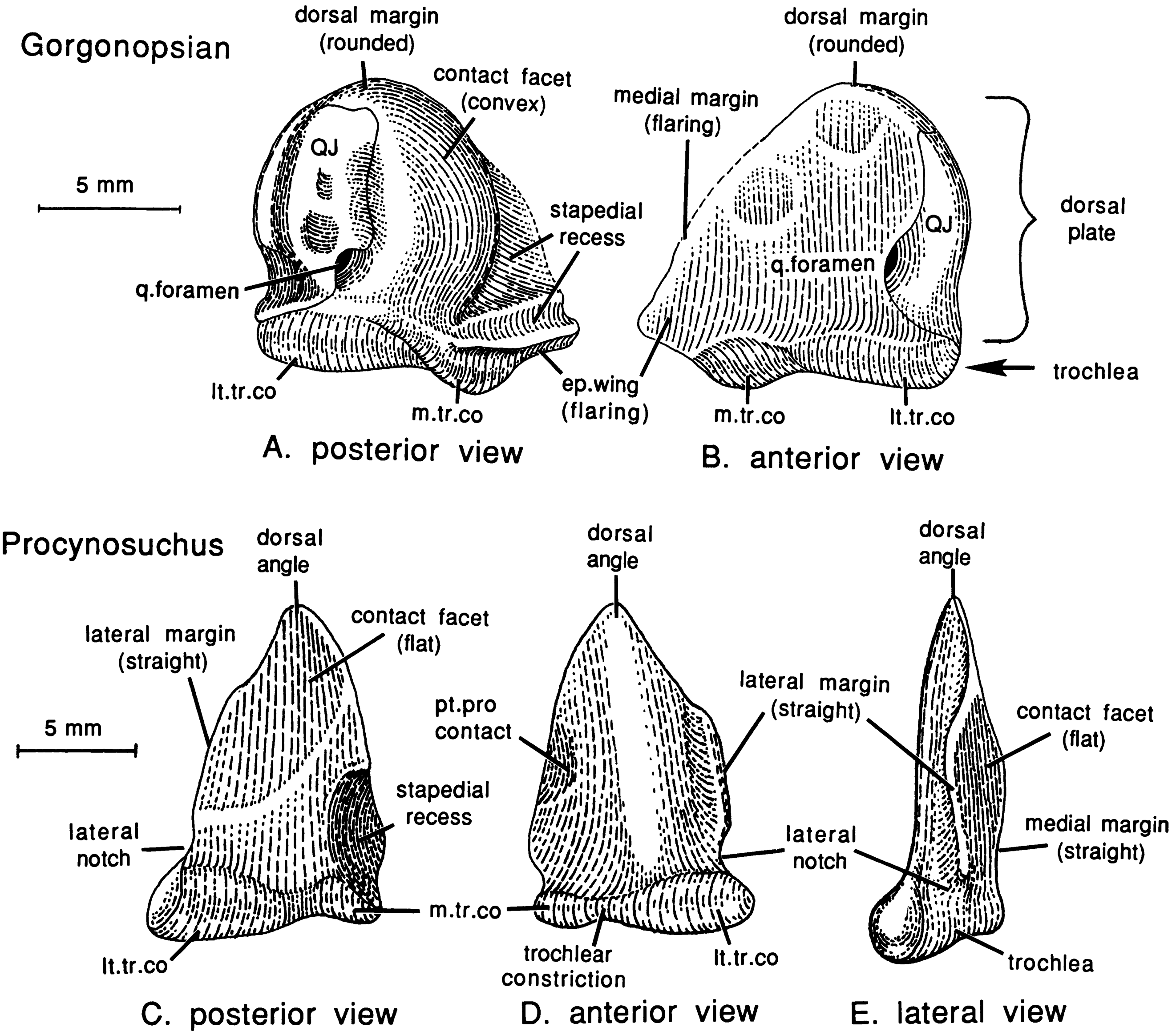


FIGURE 2. The left quadrate–quadratojugal complex of a gorgonopsian and the left quadrate of *Procynosuchus* (**A**, **B**, after Parrington (1955) and Kemp (1969); **C**, **D**, **E**, modified from Kemp (1979) on the basis of MCZ 8968). Abbreviations: **ep.wing**, epipterygoid wing of the quadrate; **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlear condyle; **pt.pro.contact**, contacting area (on the quadrate) for the quadrate ramus of the pterygoid and the lateral flange of the prootic; **q.foramen**, quadrate foramen; **QJ**, quadratojugal.

whaitsiids and *Bauria* (Crompton, 1955; Kemp, 1972b). The lateral margin of the dorsal plate of the quadrate is straight and thickened; it abuts the quadratojugal in whaitsiids (Kemp, 1972a, b). This is similar to dicynodonts (Camp, 1956; Rowe, 1986) but different from gorgonopsians, in which the lateral margin of the dorsal plate of the quadrate is wrapped by the quadratojugal.

The lateral trochlear condyle is much larger than the medial condyle. A "stapedial process" on the medial end of the trochlea was identified in some therocephalians (Broom, 1936; Olson, 1944; Crompton, 1955), but it varies widely in size and morphology. It is prominent in *Lycedops* (Broom, 1936) and in another unidentified therocephalian (Olson, 1944:fig. 13), but very small in some other therocephalians (Crompton, 1955: figs. 5, 6). In whaitsiids (Kemp, 1972a, b), the stapedial articulation of the quadrate is continuous with its pterygoid wing, and does not form an independent projection as in the case of the crus longum (stapedial process) in *Morganucodon* (Kermack et al., 1981). It is doubtful that the so-called stapedial process in therocephalians, as identified by Olson (1944), is homologous to the crus longum (stapedial process) of *Morganucodon,* or the stapedial process of tritylodontids (Kühne, 1956; Hopson, 1966; Sues, 1986a; Sun and Cui, 1989).

The quadrate of *Procynosuchus* (="*Leavachia,*" Hopson and Kitching, 1972; Kemp, 1979) has a triangular outline in both the anterior and posterior views (Fig. 2). The dorsal plate of the quadrate has a pointed dorsal angle, in contrast to the rounded dorsal margin of gorgonopsians and the truncated margin of the whaitsiid therocephalians. The lateral margin of the dorsal plate is straight and forms a slightly thickened ridge. This ridge is similar to, but not as well-developed as, the "posterior flange" on the lateral margin of the quadrate of *Thrinaxodon* (Crompton, 1972a; Fourie, 1974). The lateral margin is separated from the quadratojugal by a squamosal septum. A shallow lateral notch is present between the ventral end of the lateral margin ("posterior flange") and the lateral end of the trochlea, presumably for the ventral articulation of the quadratojugal. The anterior face of the dorsal plate is convex mediolaterally.

The medial margin of the quadrate in *Procynosuchus* lacks an anteriorly flaring pterygoid wing that is present in gorgonopsians and therocephalians. On the anterior side of the medial margin, a broad and shallow concavity receives the posterior ends of the quadrate ramus of the pterygoid (pt.pro. contact, Fig. 2D) and the lateral flange of the prootic (homologue to a part of the mammalian petrosal). By contrast, in dicynodonts and therocephalians, the posteromedial face of the medial margin ("pterygoid wing") of the quadrate contacts the quadrate ramus of the pterygoid. In gorgonopsians, it is the edge of the medial margin ("epipterygoid wing") that contacts the epipterygoid.

The contact facet on the posterior face of the dorsal plate is basically flat. Only a small dorsal area of the dorsal plate articulates with the squamosal recess; much of the posterior face of the quadrate is exposed posteriorly below the ventral edge of the squamosal (MCZ 8968; Crompton, 1972a; Kemp, 1979). A rather large recess for the articulation of the distal end of the stapes is present on the posteromedial face of the dorsal plate (Fig. 2C). This stapedial recess occupies a large area on the medial end of the trochlea and on the medial margin of the dorsal plate (Brink, 1963b; Crompton, 1972a; Kemp, 1979). The lateral condyle of the trochlea is considerably larger than the medial condyle. The lateral and medial condyles are separated by a constriction in the middle of the trochlea. The quadrate of *Procynosuchus* is quite similar to that of *Thrinaxodon* in its structure and in the attachment to the cranium (Crompton, 1972a; Kemp, 1979).

Thrinaxodon

The quadrate of *Thrinaxodon* articulates with the squamosal, the paroccipital process of the opisthotic, the lateral flange of the prootic, the quadrate ramus of the pterygoid, the stapes and the quadratojugal (Fig. 3; also see Fourie, 1974). An isolated quadrate of *Thrinaxodon* has a roughly triangular outline in anterior view (Figs. 3D, 4E). The dorsal plate has a pointed dorsal angle (Parrington, 1946). The anterior face of the dorsal plate is convex mediolaterally and slightly concave vertically (Fig. 4). The anterior surface of the medial margin is slightly corrugated. It contacts the quadrate ramus of the pterygoid and the lateral flange of the prootic (pt.pro. contact, Fig. 4E), a condition quite similar to that in *Procynosuchus* (Kemp, 1979). On the anterior face of the dorsal plate of the quadrate, a shallow vertical groove is present between the lateral margin ("posterior flange" of Crompton, 1972a) and the convex part of the anterior face (lateral groove, Fig. 4D).

The posterior face of the dorsal plate has a sigmoid surface (Fig. 4). It is slightly concave along its lateral margin, largely flat in the middle and convex along the medial and dorsal margins (Fig. 4A, B). The convex area of the posterior face fits into the shallow quadrate recess on the squamosal, while a small area in the ventromedial corner of the posterior face of the dorsal plate overlaps the lateral end of the paroccipital process of the opisthotic (homologous to part of the mammalian "petrosal") (Fig. 3A, B). The lateral margin of the dorsal process flares posteriorly (thus referred to as the "posterior flange" by Crompton, 1972a), and fits into the quadrate notch of the squamosal (Q-notch, Fig. 3A). The ventral end of the lateral margin ("posterior flange") is separated from the trochlea by a notch (lateral notch) which receives the hook-like medial process of the quadratojugal (Fig. 3A, C). The lateral groove on the anterior surface of the dorsal plate is connected to the lateral notch. The groove also receives the hook-like medial process of the quadratojugal. The quadratojugal is slender, and helps to brace the quadrate because it articulates with both the quadrate and the squamosal. As in other cynodonts, the quadratojugal fits in the quadratojugal notch of the squamosal (Fig. 3A).

The trochlea is slightly constricted in the middle (Fig. 4F). The lateral condyle is slightly larger than the medial one. When viewed ventrally, the dorsal plate appears to be slightly twisted relative to the long axis of the trochlea because of the posterior flaring of the lateral margin of the dorsal plate (posterior flange).

Probainognathus

Probainognathus (Romer, 1970) differs from *Thrinaxodon* both in the structure of the quadrate and in the attachment of the quadrate to other cranial bones (Figs. 5–7). In *Probainognathus,* the squamosal completely separates the dorsal plate of the quadrate from the paroccipital process of the opisthotic. The cranial moiety of the squamosal not only covers the lateral end of the paroccipital process, but also protrudes anteromedially to join the ramus of the epipterygoid (q.r.ep), flanking a part of the pterygo-paroccipital foramen (ppf) (see the large arrow in Fig. 7C). A lappet of the squamosal overlaps the anterior face of the dorsal plate of the quadrate (sq.la, Fig. 5C). This is different from anomodonts, gorgonopsians, therocephalians, *Procynosuchus,* and *Thrinaxodon,* in which the quad-

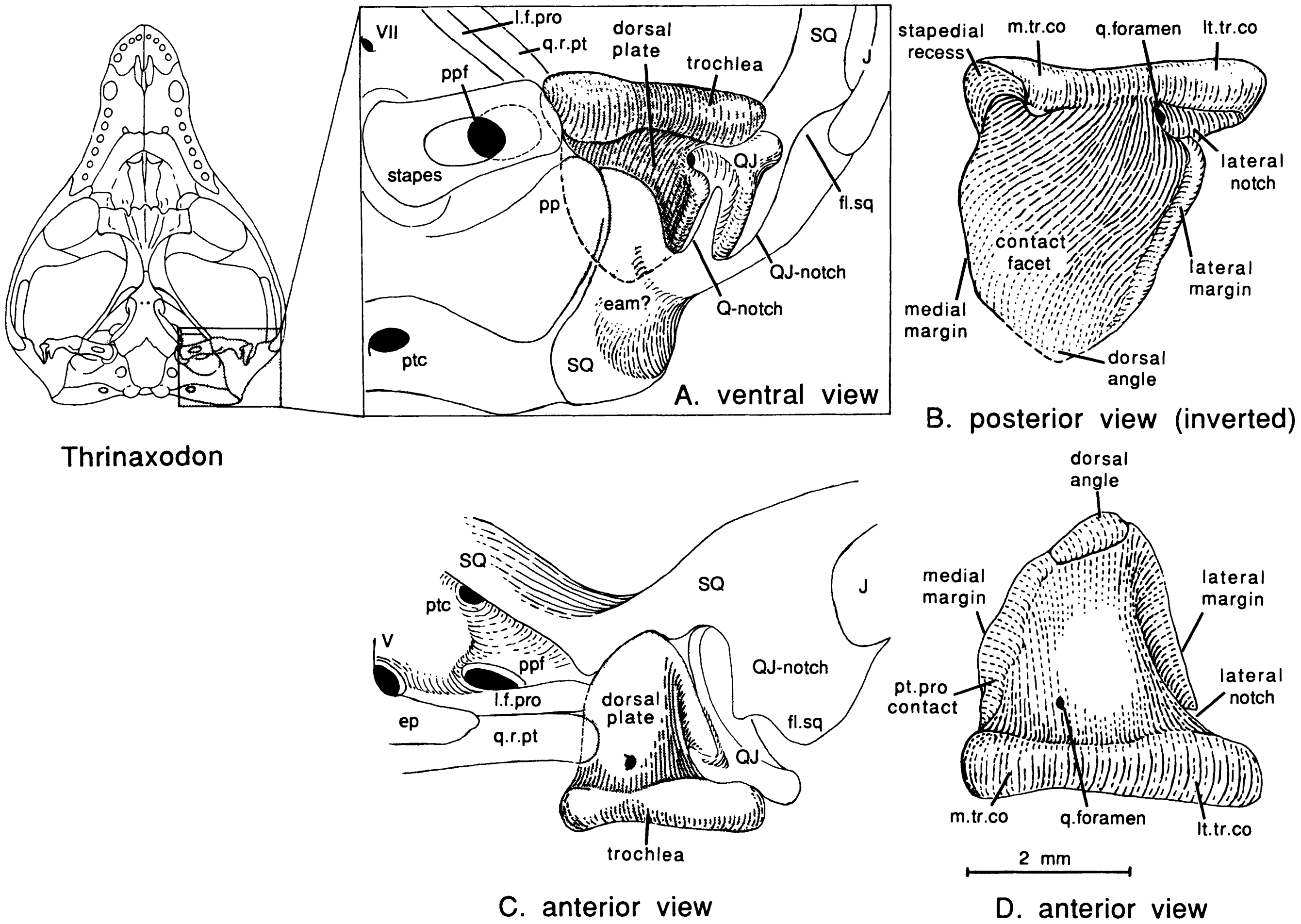


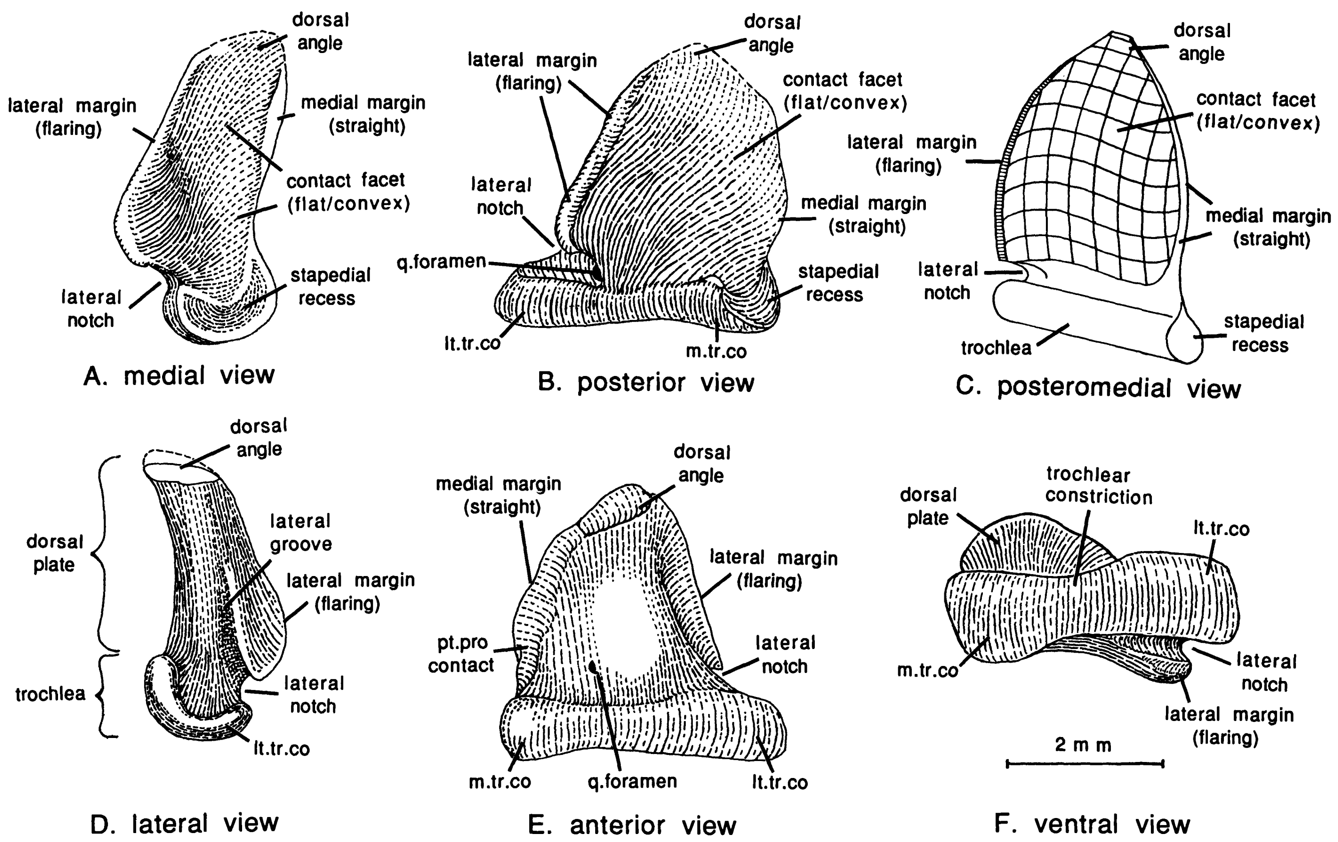
FIGURE 3. *Thrinaxodon.* **A**, articulation of the quadrate to the cranium (left ventral view, the quadrate highlighted). **B**, isolated quadrate (left, posterior view, inverted). **C**, articulation of the quadrate to the cranium (left, anterior view, the quadrate is highlighted). **D**, isolated quadrate (left, anterior view). Abbreviations: **eam?**, putative "external auditory meatus"; **ep**, epipterygoid; **fl.sq**, articulating flange of the squamosal; **J**, jugal; **l.f.pro**, lateral flange of the prootic; **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlear condyle; **pp**, paroccipital process (of opisthotic); **ppf**, pterygo–paroccipital foramen; **ptc**, post-temporal canal; **Q-notch**, notch for the quadrate in the squamosal; **q.foramen**, quadrate foramen; **QJ**, quadratojugal; **QJ-notch**, notch for the quadratojugal in the squamosal; **q.r.pt**, quadrate ramus of the pterygoid; **SQ**, squamosal; **V**, foramen for the trigeminal nerves.

rate contacts at least a small part of the paroccipital process, and the quadrate recess of the squamosal is an anteriorly open fossa. The quadrate ramus of the epipterygoid extends posteriorly in *Probainognathus* (q.r.ep in Fig. 5C). The ramus of the epipterygoid contacts the anterior face of the dorsal plate of the quadrate and the squamosal lappet. By contrast, in *Procynosuchus* and *Thrinaxodon,* the quadrate ramus of the pterygoid (rather than the epipterygoid) contacts the anterior face of the dorsal plate of the quadrate.

The quadratojugal of *Probainognathus* is a gracile bone. Its ventral end contacts the lateral notch of the quadrate (Romer, 1970; Crompton, 1972a), but the ventral suture of the quadratojugal is not clear on the available specimens (Fig. 5). It probably has the hook-like medial process of the quadratojugal in *Thrinaxodon.*

Probainognathus has developed an incipient glenoid on the squamosal for the articulation of the surangular on the mandible (gl, Fig. 5A) (Crompton, 1972a; Crompton and Jenkins, 1979). The glenoid faces medioventrally and is positioned immediately lateral to the quadratojugal notch in the squamosal. Because the quadratojugal notch is broadened as a result of the development of the squamosal glenoid for the surangular, the quadratojugal notch in the squamosal is much wider than in *Thrinaxodon.* The quadratojugal bone is slender and the contact of the quadratojugal with the squamosal is loose. The quadrate notch of the squamosal is also much wider in *Probainognathus* than in *Thrinaxodon.* With these modifications in the squamosal, the quadrate-quadratojugal complex was more mobile than that of *Thrinaxodon* (Fig. 7).

The dorsal angle in *Probainognathus* tapers more sharply than in *Thrinaxodon* (Figs. 5, 6, 7). The medial margin of the dorsal plate flares and protrudes ante-



A. medial view B. posterior view C. posteromedial view

D. lateral view E. anterior view F. ventral view

FIGURE 4. Left quadrate of *Thrinaxodon*. C represents a generalized model of the quadrate of *Thrinaxodon* in posteromedial view. Abbreviations: **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlear condyle; **q.foramen**, quadrate foramen.

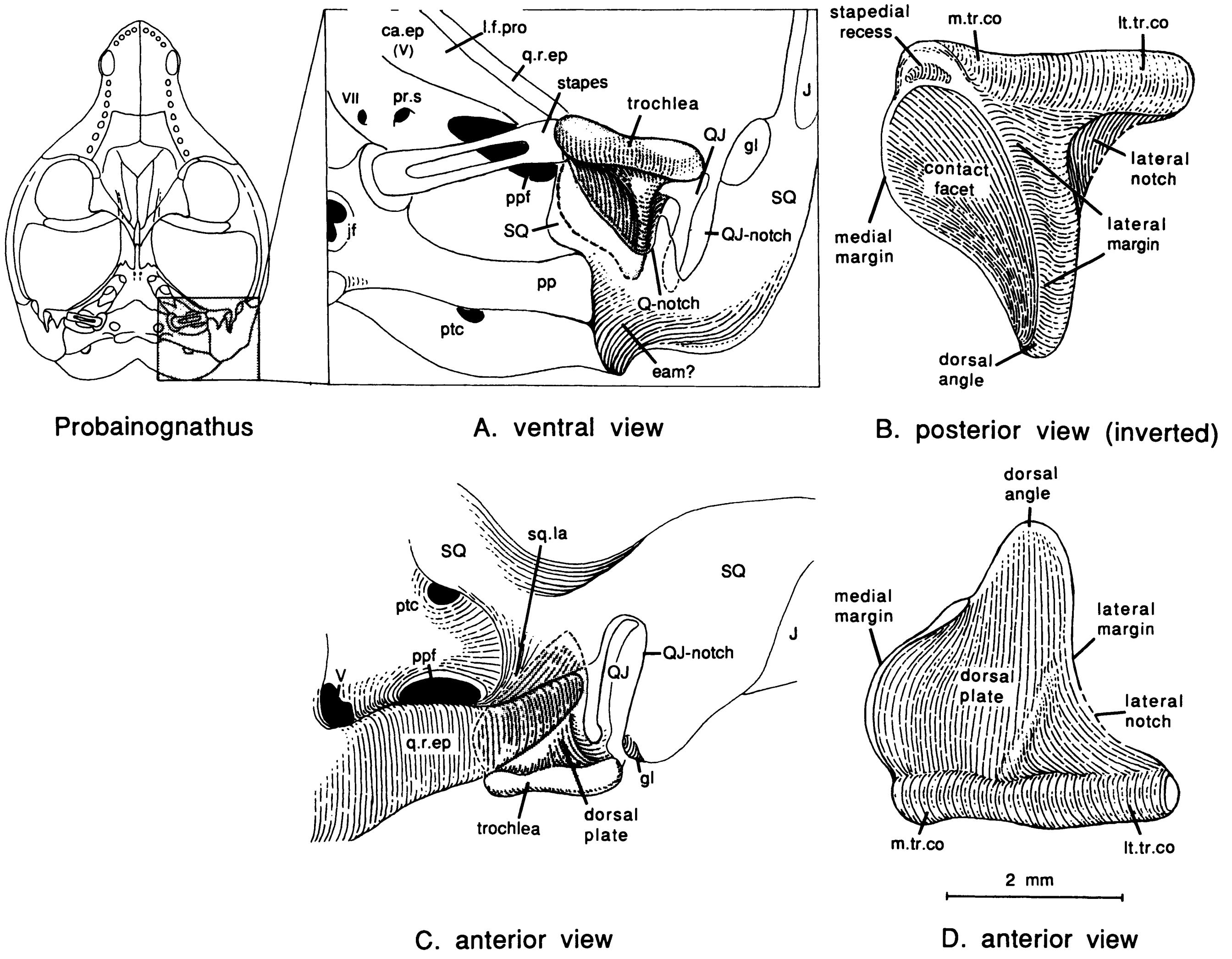
riorly. The anterior face of the dorsal plate is strongly convex anteriorly near the medial margin (Fig. 6D, E). The lateral margin of the posterior contact facet for the squamosal is positioned near the mid-line in the posterior view of the quadrate. It curves medially and reaches ventrally toward the stapedial recess of the trochlea (Fig. 6B, C). By contrast, the lateral margin of the dorsal plate in *Thrinaxodon* reaches toward the lateral end of the trochlea (Fig. 7).

The ventral part of the lateral margin is separated from the trochlea by a very broad lateral notch. In *Thrinaxodon,* the lateral notch between the lateral margin of the dorsal plate and the trochlea is narrow. As a result of the anterior flaring of the medial margin, and the posterior flaring plus the medial shift of the lateral margin, the dorsal plate of *Probainognathus* is twisted for about 45° relative to the axis of the trochlea (clockwise in ventral view of the inverted left quadrate: see Figs. 6C, D, 7D). The contact facet on the posterior surface of the dorsal plate is twisted to face posteromedially, rather than facing posteriorly as in *Procynosuchus, Thrinaxodon,* and other non-cynodont therapsids (Fig. 7). The contact facet on the quadrate for the squamosal is uniformly concave; whereas the same facet is convex in gorgonopsians, and flat to slightly convex in *Procynosuchus* and *Thrinaxodon.* The difference between a convex contact facet in *Thrinaxodon* and a concave contact facet of the dorsal plate in *Probainognathus* represents a major change in the geometry of the quadrate-cranial articulation. The change in the curvature of the posterior contact facet and the twisting of the dorsal plate are correlated to the anteromedial protrusion of the squamosal (large arrow in Fig. 7C).

The quadrate trochlea for the articular is cylindrical. The constriction of the trochlea is closer to the medial end so that the lateral trochlear condyle (lt.tr.co, Fig. 6) is larger than the medial trochlear condyle (m.tr.co, Fig. 6).

Massetognathus

The quadrate of *Massetognathus* (Romer, 1967) is suspended from the cranium entirely by the squamosal (Fig. 8). The cranial moiety of the squamosal extends anteriorly to flank a part of the pterygo-paroccipital foramen (Fig. 8). This anterior extension of the squamosal also forms a thick sheet of bone that covers the entire medial end of the quadrate trochlea (Fig. 8A). A notch in the squamosal is present posterior and medial to the trochlea of the quadrate but anterior and lateral to the paroccipital process. This notch is continuous with the so-called external auditory meatus (eam?, Fig. 8). Although no stapes is preserved in situ in any specimen available for this study, it is possible that this notch supported a tympanic membrane, which


Probainognathus

A. ventral view

B. posterior view (inverted)

C. anterior view

D. anterior view

FIGURE 5. *Probainognathus.* **A**, articulation of the quadrate to the basicranium. Left side, ventral view, quadrate highlighted; skull after Romer (1970) and Allin and Hopson (1992). **B**, left quadrate left posterior view, inverted; (based on MCZ 4015; MCZ 4019; MCZ 4021; MCZ 4276; MCZ 4287). **C**, articulation of the quadrate to the cranium (left side, anterior view; quadrate is highlighted). **D**, quadrate (left, anterior view). Abbreviations: **ca.ep (v)**, cavum epiptericum for the trigeminal nerve ganglion; **eam?**, putative "external auditory meatus;" **gl**, glenoid for the surangular; **J**, jugal; **l.f.pro**, lateral flange of the prootic; **pr.s**, tympanic opening of the prootic sinus; **Q-notch**, notch for the quadrate (in the squamosal); **QJ**, quadratojugal; **QJ-notch**, notch for the quadratojugal (in the squamosal); **q.r.ep**, the quadrate ramus of the epipterygoid; **SQ**, squamosal; **VII**, foramen for the facial nerve.

attached to the distal end of the stapes. Parrington (1949, 1979) and Watson (1953) suggested that a similar notch supported the tympanic membrane in *Diademodon,* a taxon related to *Massetognathus* (Crompton, 1972a; Kemp, 1982; Sues, 1985; Hopson and Barghusen, 1986; but see Rowe, 1988, 1993). The overlapping squamosal on the medial end of the trochlea makes it unlikely that the quadrate trochlea articulates directly with the stapes in the available specimens. However, in *Exaeretodon,* a genus closely related to *Massetognathus,* direct articulation of the quadrate trochlea and the stapes is present. It is conceivable that, in life, the quadrate might have had a cartilaginous extension to contact the stapes in *Massetognathus.*

The quadratojugal is an anteroposteriorly oriented plate, and it is tightly fused to the ventral part of the dorsal plate of the quadrate. The dorsal plate of the quadrate of *Massetognathus* is basically similar to that of *Probainognathus* except for some minor differences (Fig. 8). The anterior face of the dorsal plate is triangular in outline. It has a slightly concave surface and a pointed dorsal angle (MCZ 4218). The dorsal angle is partially covered by the cranial moiety of the squamosal, a condition comparable to, but less developed than, that of *Probainognathus.* The contact facet on the posterior side of the dorsal plate is strongly concave. This concave facet articulates with the squamosal. The lateral margin of the dorsal plate forms a prominent lateral flange ("posterior flange" of Crompton, 1972a), and it wedges into the quadrate notch of

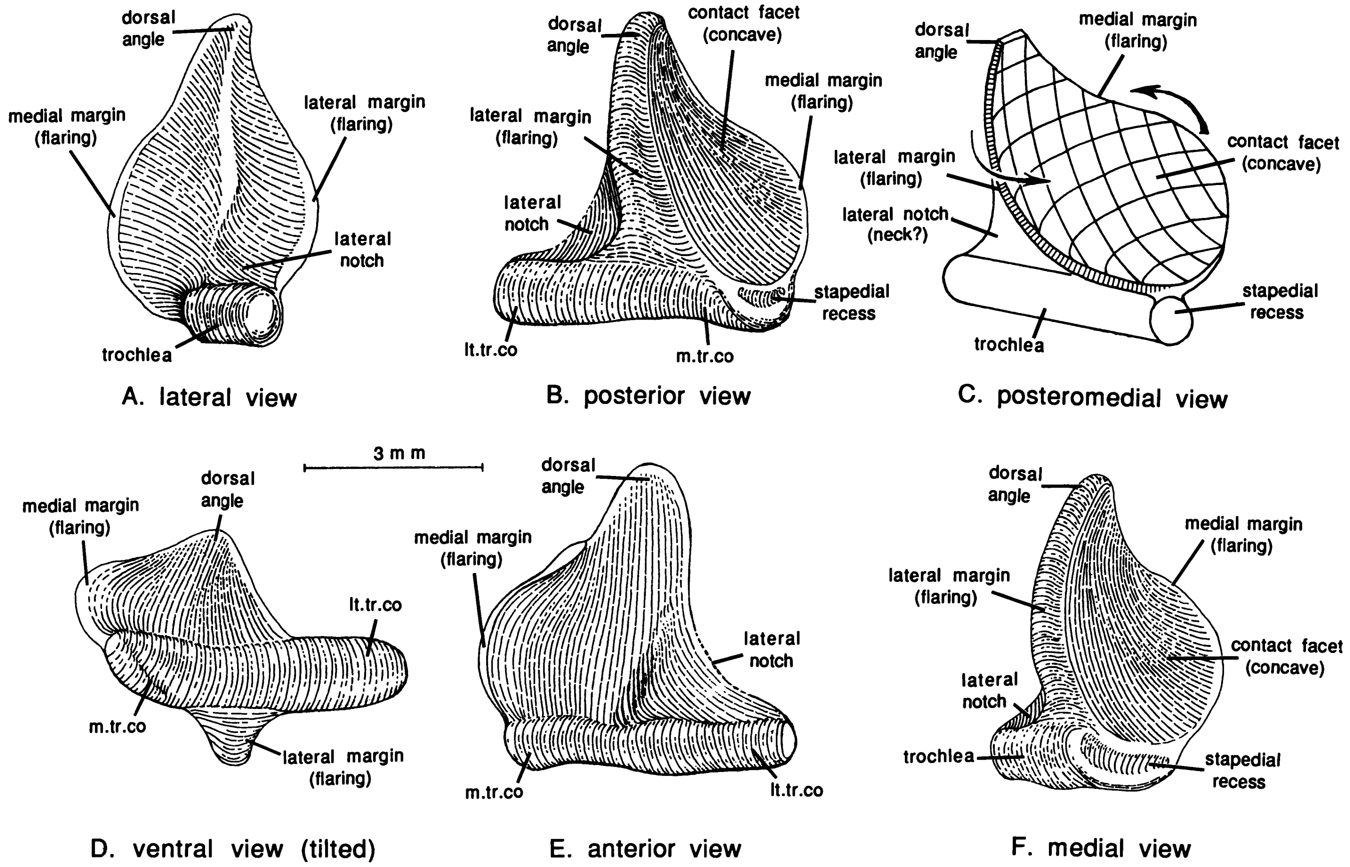


FIGURE 6. Restoration of the left quadrate of *Probainognathus* (based on MCZ 4276, 4287, 4019, 4021). C represents a generalized model of the quadrate of *Probainognathus* in the posteromedial view. Abbreviations: **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlear condyle.

the squamosal (Fig. 8A). The quadrate has a very pronounced lateral trochlear condyle and a trough in the middle of the trochlea. The medial end of the trochlea curves ventrally and flanks the medial side of the trough. The broad articulating trough and the extremely large lateral condyle of the quadrate trochlea are oriented more or less anteroposteriorly and oblique to the transverse axis of the trochlea. By contrast, the trochlea of the quadrate in most other non-mammalian cynodonts is cylindrical and oriented transversely. Among synapsids, parallel examples of this type of trochlea are present in sphenacodont pelycosaurs (Romer and Price, 1940; Romer, 1956) and in anomodonts (dromasaurs, Brinkman, 1981; dicynodonts, Camp, 1956; Crompton and Hotton, 1967).

It has been established that *Massetognathus,* with the multi-cuspate postcanines adapted to herbivory, moved the lower jaw posteriorly and dorsally during the power stroke of the occlusion (Crompton, 1972b; Sues, 1985). We suggest that the quadrate of *Massetognathus,* which is a part of the craniomandibular joint, is specialized in correlation with this mode of occlusion. During the occlusion of the lower jaw, the trough and the lateral condyle served to guide the posteriorly directed occlusal movement of the mandible.

Tritylodontidae

The quadrate of tritylodontids is best represented by *Oligokyphus* (Kühne, 1956; Crompton, 1964), *Kayentatherium* (Sues, 1986a), and *Bienotheroides* (Sun, 1984; Sun and Cui, 1989). The bone is also preserved in *Tritylodon, Bienotherium* (Hopson, 1965), and *Yunnanodon* (Cui, 1976, 1986). The quadrate is primarily supported by the bulbous anterior paroccipital process of the petrosal (Crompton, 1964; Hopson, 1966). The dorsal plate bears an elongated dorsal process ("posterodorsal process" of Hopson, 1966). In *Bienotherium* (Hopson, 1966) and *Yunnanodon* (IVPP 5071), in which the quadrate is preserved in situ, the dorsal process of the quadrate reaches posteriorly and dorsally toward the external auditory meatus. The tip of the dorsal process contacts the squamosal. The quadrate-squamosal contact is absent in *Bienotheroides* (Sun, 1984) and *Kayentatherium* (Sues, 1986a). The quadrate also articulates with the quadratojugal which, in turn, contacts the squamosal (IVPP 5071; Crompton, 1964; Hopson, 1966; Sues, 1985).

The quadrate of *Oligokyphus* (Kühne, 1956; Crompton, 1964) has a broad and slightly concave contact facet with a transversely elongated outline (Fig. 9). Its

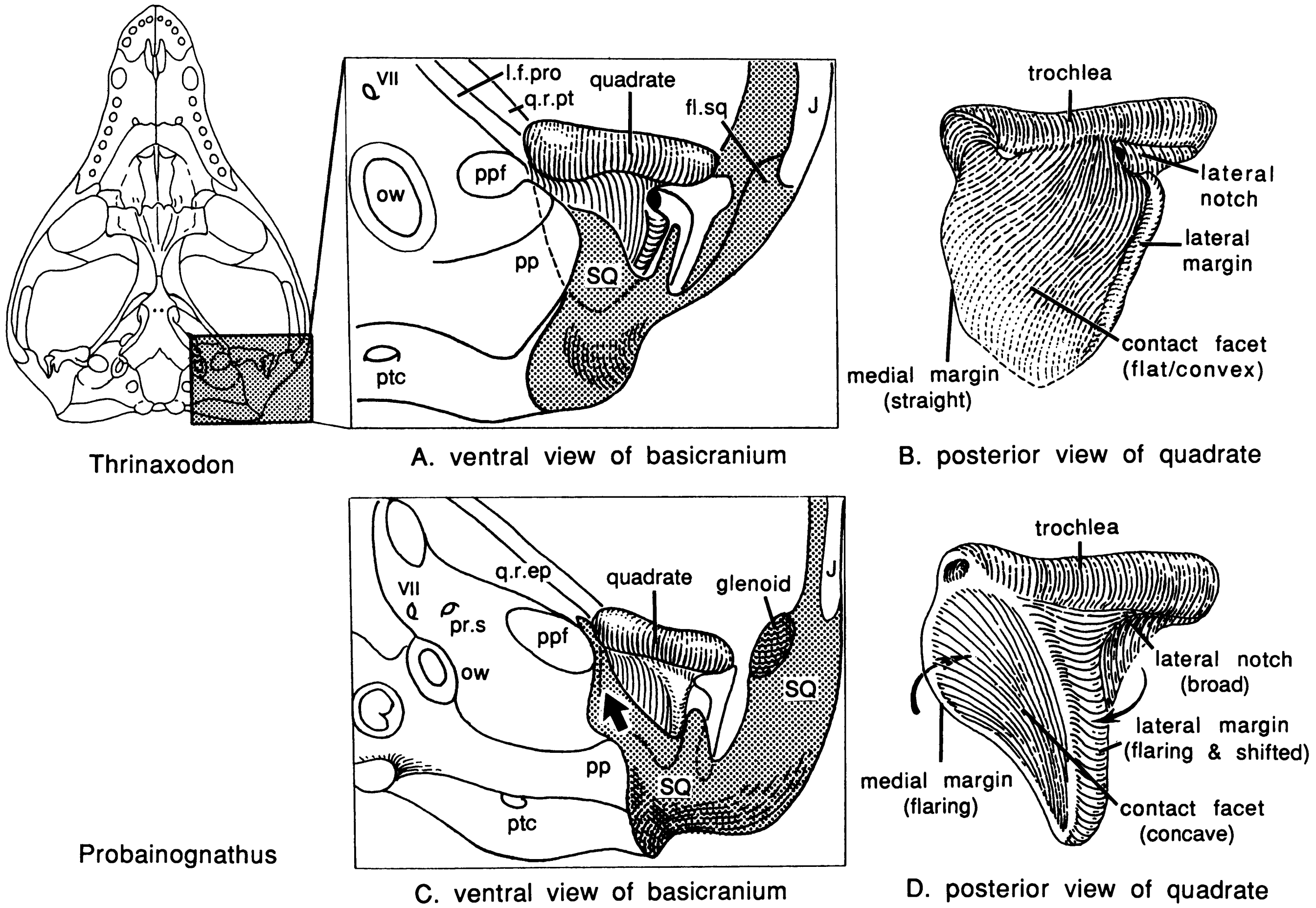
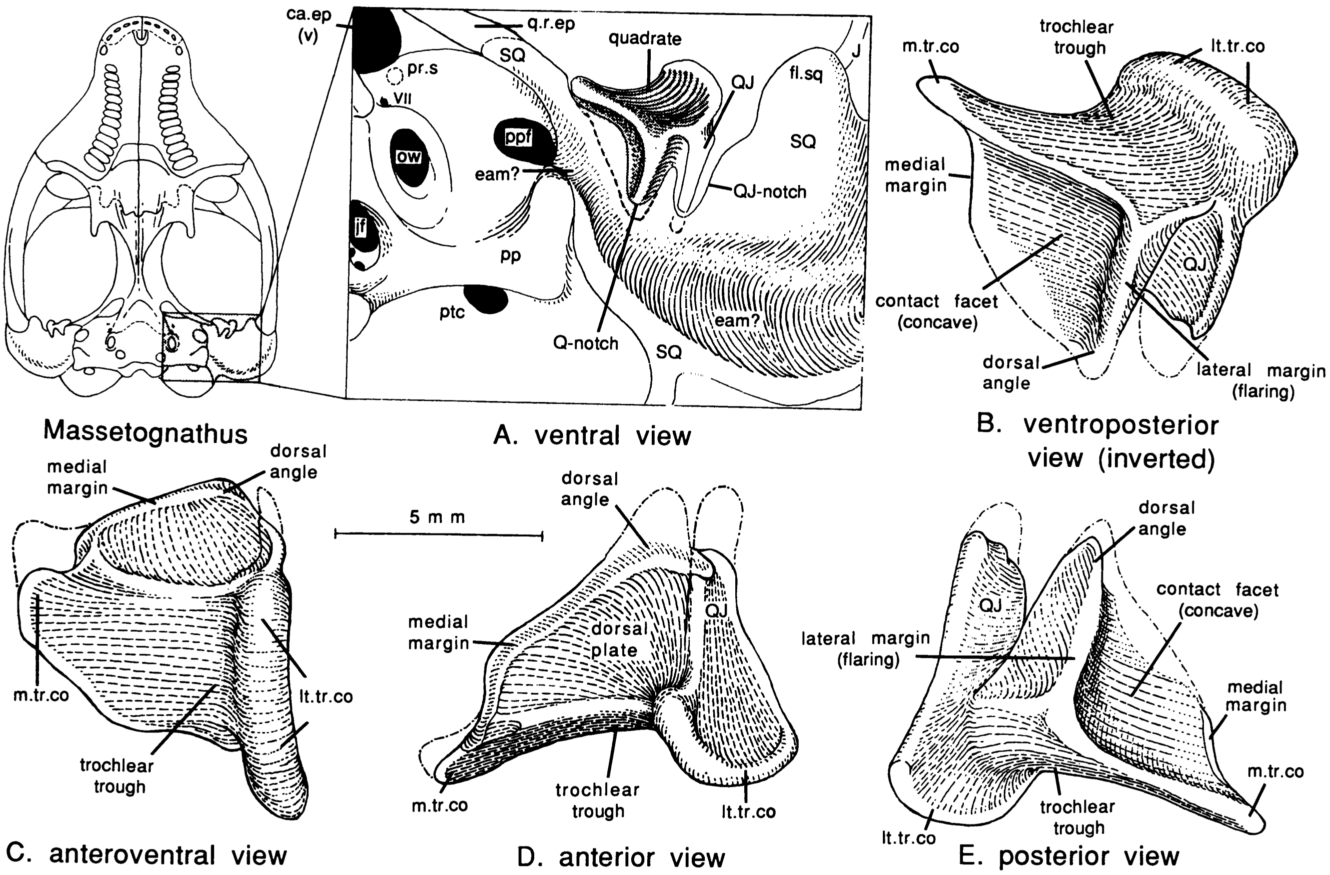


FIGURE 7. Correlation of morphological changes of the quadrate and the squamosal in advanced non-mammalian cynodonts. **A**, *Thrinaxodon:* ventral view of the left basicranium. **B**, *Thrinaxodon:* posterior view of the left quadrate. **C**, *Probainognathus:* ventral view of the left basicranium. **D**, *Probainognathus:* posterior view of the quadrate. In *Probainognathus,* the medial expansion of the squamosal (represented by the large arrow) is correlated with the anterior flaring of the medial margin and introduction of the posterior concavity of the dorsal plate. The shift of the lateral margin of the dorsal plate and broadening of the lateral notch are correlated to the establishment of the craniomandibular joint (glenoid) between the squamosal and the surangular. Abbreviations: see Figs. 3, 5 and 8.

concave contact facet articulates with the massive and bulbous anterior paroccipital process of the petrosal ("crista parotica" of Hopson, 1965, 1966). The ventral margin of the contact facet is raised from the trochlea by a constricted sheet of bone, which is referred to as the neck (Fig. 9). The contact facet is oriented in a horizontal plane nearly parallel to the axis of the trochlea. The quadrate possesses a peg-like posterodorsal process which is similar, thus homologous, to the dorsal angle of the quadrate of *Procynosuchus, Thrinaxodon,* and *Probainognathus.*

The quadrate of tritylodontids has some distinctive characters that are absent in *Thrinaxodon, Probainognathus,* and *Massetognathus.* These include the constricted neck, the broad contact facet oriented parallel to the trochlea (Sun and Cui, 1989), and the direct articulation of the quadrate with the anterior paroccipital process of the petrosal. However, three other quadrate features show considerable variation among known tritylodontids: the stapedial process, the dorsal angle ("posterodorsal process" of Hopson, 1966), and the trochlea.

The homology of the stapedial process of tritylodontids to the crus longum of *Morganucodon* is problematic. Sues (1986a) pointed out that the stapedial process of *Kayentatherium* was oriented differently from the crus longum of *Morganucodon.* The stapedial process is very large in *Kayentatherium* (Sues, 1986a) and *Bienotheroides* (Sun and Cui, 1989). The process, however, is fairly small in *Oligokyphus* (Kühne, 1956), and is not known in *Yunnanodon* (IVPP 5071). In *Bienotherium* (Hopson, 1966), *Oligokyphus,* and *Kayentatherium,* the stapedial process projects from the medial margin of the dorsal contact facet (Fig. 9); whereas in *Bienotheroides* the process projects from the neck and is separated from the medial margin of the contact facet by a notch (Fig. 10). The stapedial process is pointed toward the distal end of the stapes. The crus



A. ventral view

B. ventroposterior view (inverted)

C. anteroventral view

D. anterior view

E. posterior view

FIGURE 8. *Massetognathus.* **A**, attachment of the quadrate to the cranium (left side, ventral view; based on MCZ 3739, 3807, 4012, 4208). **B**, restoration of an isolated quadrate–quadratojugal complex (left, inverted, ventroposterior view). **C**, restoration of the same complex in anteroventral view. **D**, the same complex in anterior view; **E**, the same complex in posterior view (with slight tilt). Abbreviations: **ca.ep (v)**, cavum epiptericum for the trigeminal nerve; **eam?**, putative "external auditory meatus;" **fl.sq**, articulating flange of the squamosal; **J**, jugal; **jf**, jugular foramen; **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlear condyle; **Q-notch**, notch for the quadrate (in the squamosal); **QJ**, quadratojugal; **QJ-notch**, notch for the quadratojugal (in the squamosal); **ow**, oval window (fenestra vestibularis); **pp**, paroccipital process; **ppf**, pterygo–paroccipital foramen; **pr.s**, tympanic opening of the prootic sinus canal; **ptc**, post-temporal canal; **q.r.ep**, quadrate ramus of epipterygoid; **SQ**, squamosal; **VII**, foramen for the facial nerve.

longum of mammals is projected from the neck region and forms a right angle with the distal end of the stapes. Hopson (1966) suggests that the "stapedial process" of tritylodontids is a functional analogue of the crus longum of the mammalian incus. Rowe (1988) goes further to argue for the homology of the stapedial process in both tritylodontids and *Morganucodon.* It is unclear whether the "stapedial process" of tritylodontids is homologous to the crus longum of mammals (Sues, 1986a; Wible, 1991) (see "Character Analysis").

The most variable feature of the quadrate among tritylodontids is the dorsal angle (process). A pointed dorsal process is present in *Oligokyphus* (Kühne, 1956; Crompton, 1964), *Bienotherium* (Hopson, 1966), *Yunnanodon* (IVPP 5071), and a specimen of *Dianzhongia* (IVPP 8694). This process is homologous to the dorsal angle of the dorsal plate of other non-mammalian cynodonts. Yet, it is absent in *Kayentatherium* (Sues, 1986a) and *Bienotheroides* (Sun and Cui, 1989), in which the dorsal margin of the contact facet is rounded.

The trochlea of the quadrate also shows in-group variation among the tritylodontids. In *Oligokyphus,* the lateral trochlear condyle (close to the dorsal process of the dorsal plate) is larger than the medial condyle, a condition similar to that in most other non-mammalian cynodonts. However, in *Kayentatherium,* the medial condyle is larger than the lateral condyle in ventral view (Fig. 9D). The trochlea is very small relative to the size of the dorsal plate in *Oligokyphus* and *Bienotherium* (Kühne, 1956; Crompton, 1964; Hopson, 1966), but less so in *Tritylodon, Kayentatherium* (Sues, 1986a) and *Bienotheroides* (Sun and Cui, 1989).

Based on a number of dental and cranial characters, Clark and Hopson (1985; see also Sues, 1986b) suggest that *Oligokyphus* is the sister-group to all other tritylodontids; *Tritylodon* and *Bienotherium* are the next

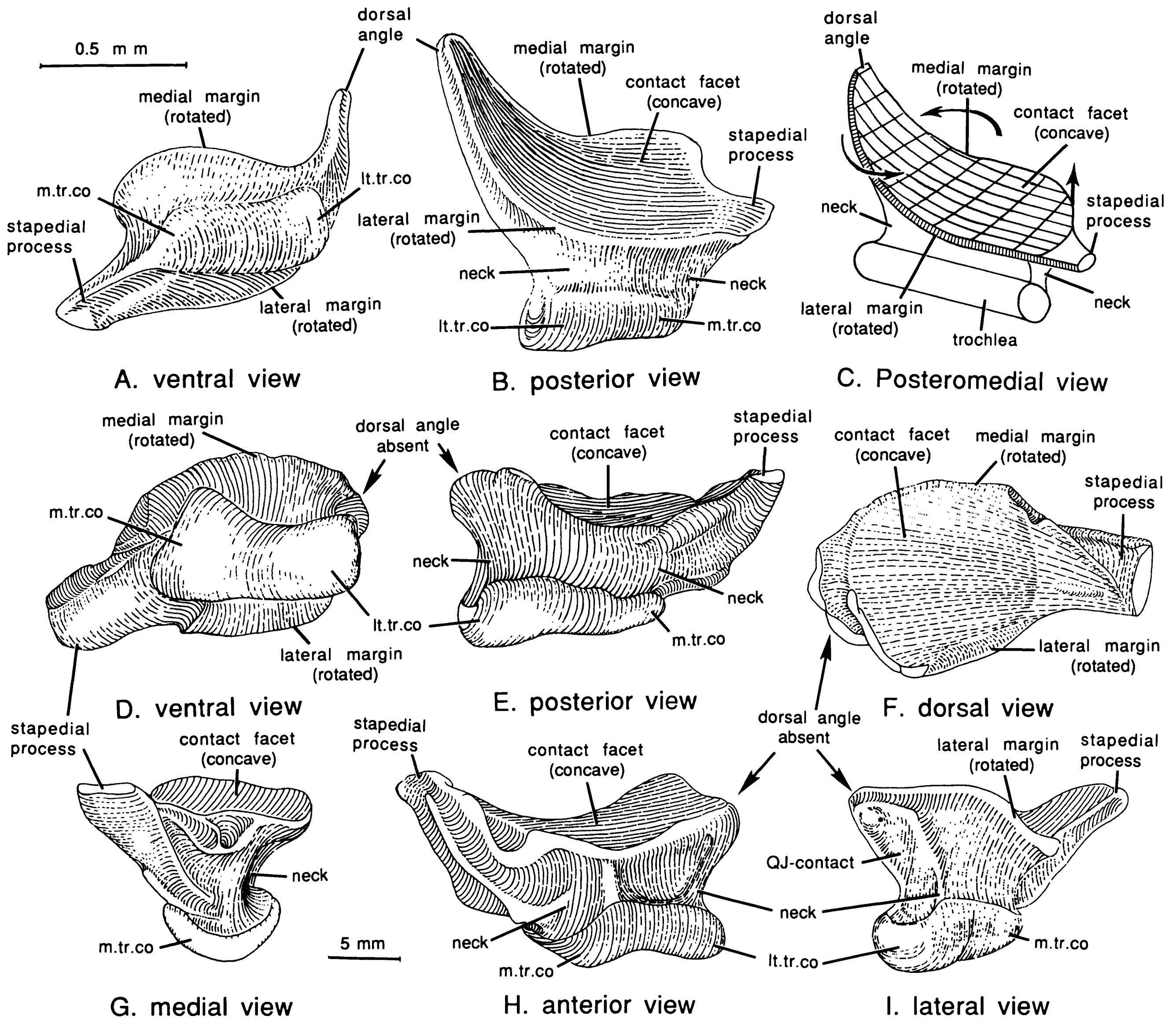


FIGURE 9. Left quadrates of *Oligokyphus* and *Kayentatherium*. **A**, **B**, *Oligokyphus* (after Kühne, 1956; Crompton, 1964). **C**, a generalized model of the quadrate of tritylodontids in posteromedial view (based on *Oligokyphus*). **D**, **E**, **F**, **G**, **H**, and **I**: *Kayentatherium* (MCZ 8812, modified from Sues, 1986a). Abbreviations: **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlear condyle; **QJ-contact**, contact for the quadratojugal (in the quadrate).

most primitive taxa. *Kayentatherium* and *Bienotheroides* are among the more derived groups. We follow this hypothesis of relationship in considering the in-group variation of the quadrate in tritylodontids. In cases where characters of the quadrate vary among tritylodontids, we regard the character states of *Oligokyphus* and *Bienotherium* (both of which are the more primitive genera) as ancestral states for the entire Tritylodontidae.

Thus, we follow Hopson (1966), Sues (1986a), and Rowe (1988) in regarding the presence of a small "stapedial process" extended from the edge of the contact facet as a plesiomorphic feature of tritylodontids, as represented in *Oligokyphus*. The large stapedial process in *Kayentatherium* and *Bienotheroides* is considered as a secondarily derived feature (Figs. 9, 10). We also recognize the presence of a large and pointed dorsal angle ("posterodorsal process") in *Oligokyphus* as a plesiomorphic condition of the Tritylodontidae. The lack of the dorsal process of the quadrate in *Kayentatherium* and *Bienotheroides* suggests that the process was secondarily lost in these more derived taxa. Likewise, we regard a larger lateral than medial trochlear condyle as a plesiomorphic condition for tritylodontids.

Pachygenelus

The quadrate in the Tritheledontidae is entirely suspended by the squamosal (Crompton, 1972a; Cromp-

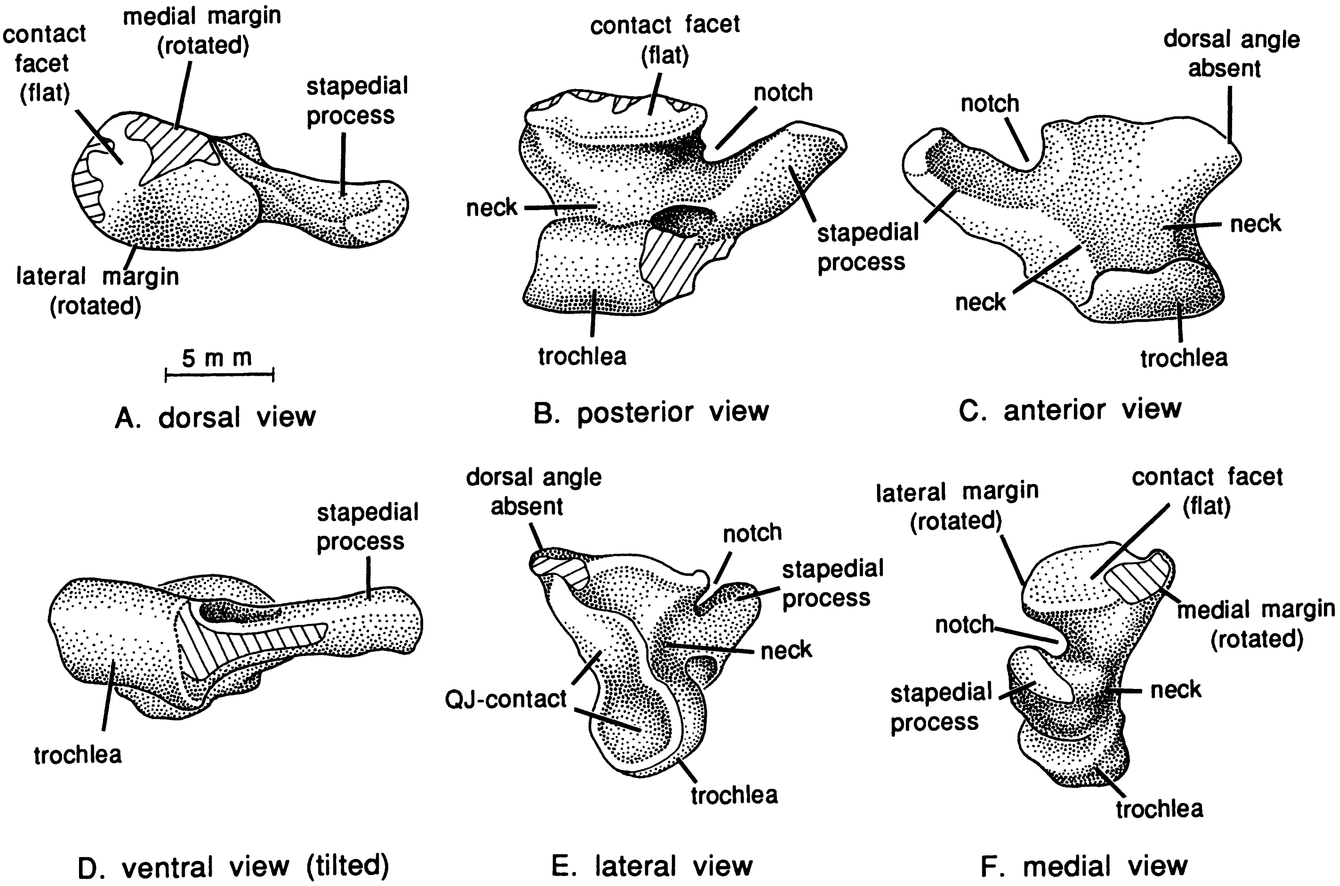


FIGURE 10. Left quadrate of *Bienotheroides* (based on IVPP 7913; courtesy of Professor Sun and Mr. Cui). Abbreviations: **QJ-contact**, contact for the quadratojugal (on the quadrate).

ton and Hylander, 1986; Allin and Hopson, 1992). The dorsal plate of the quadrate fits into a deep squamosal pocket (Fig. 11B, sq.pocket). The squamosal pocket is homologous to the shallow quadrate recess on the anterior side of the cranial moiety of the squamosal in *Procynosuchus, Thrinaxodon,* and *Massetognathus,* but it faces ventrally, rather than anteriorly as in these taxa. Medial to the squamosal pocket is a large triangular boss (Fig. 11B, sq.boss). The convex surface of the squamosal boss contacts the concave contact facet of the quadrate. The medial side of this squamosal boss covers the lateral end of the anterior paroccipital process of the petrosal, thus separating the anterior paroccipital process from the contact facet of the quadrate. Posterolateral to the squamosal pocket is a small spur that is homologous to the squamosal septum that separates the quadrate notch from the quadratojugal notch in other non-mammalian cynodonts. The spur helps to brace the dorsal plate of the quadrate (Fig. 11, sq.spur). The quadratojugal of *Pachygenelus* is not known. The rotated lateral margin of the dorsal plate fits into the quadrate notch between the squamosal spur and the squamosal boss.

The convex squamosal boss and the concave contact facet of the quadrate form a ball-in-socket joint. The squamosal pocket is much larger than the size of the dorsal plate of the quadrate, and the quadrate notch is also a broad gap. The quadrate could rotate around the fulcral point of the squamosal boss. It could also rock mediolaterally and glide anteroposteriorly (the range of this movement is indicated by the dash-lines in Fig. 11C, D).

The dorsal plate in the quadrate of *Pachygenelus* has a rounded dorsal margin and lacks any pointed dorsal angle (Fig. 12) (Hopson and Crompton, unpubl. data). The contact facet of the quadrate is strongly concave and has a quadrangular outline. It faces anteromedially. The dorsal plate is oriented in a plane oblique to the long axis of the articulating trochlea, forming an angle of about 120° (Fig. 12). The contact facet is raised by the neck which is a constriction between the trochlea and the contact facet. On the lateral side of the neck, a lateral vertical ridge (lt.v.ridge, Fig. 12) extends dorsally from the lateral end of the trochlea to the dorsal margin of the contact facet. On the posterior side of the bone, an oblique ridge extends from the medial margin ventrolaterally toward the lateral end of the trochlea (p.ob.ridge, Fig. 12A, B). On the medial side of the neck, a short medial vertical ridge runs from the medial margin of the contact facet. The ventral end of this vertical ridge flares out posteriorly and laterally. Its ventral end is separated from the stapedial end of

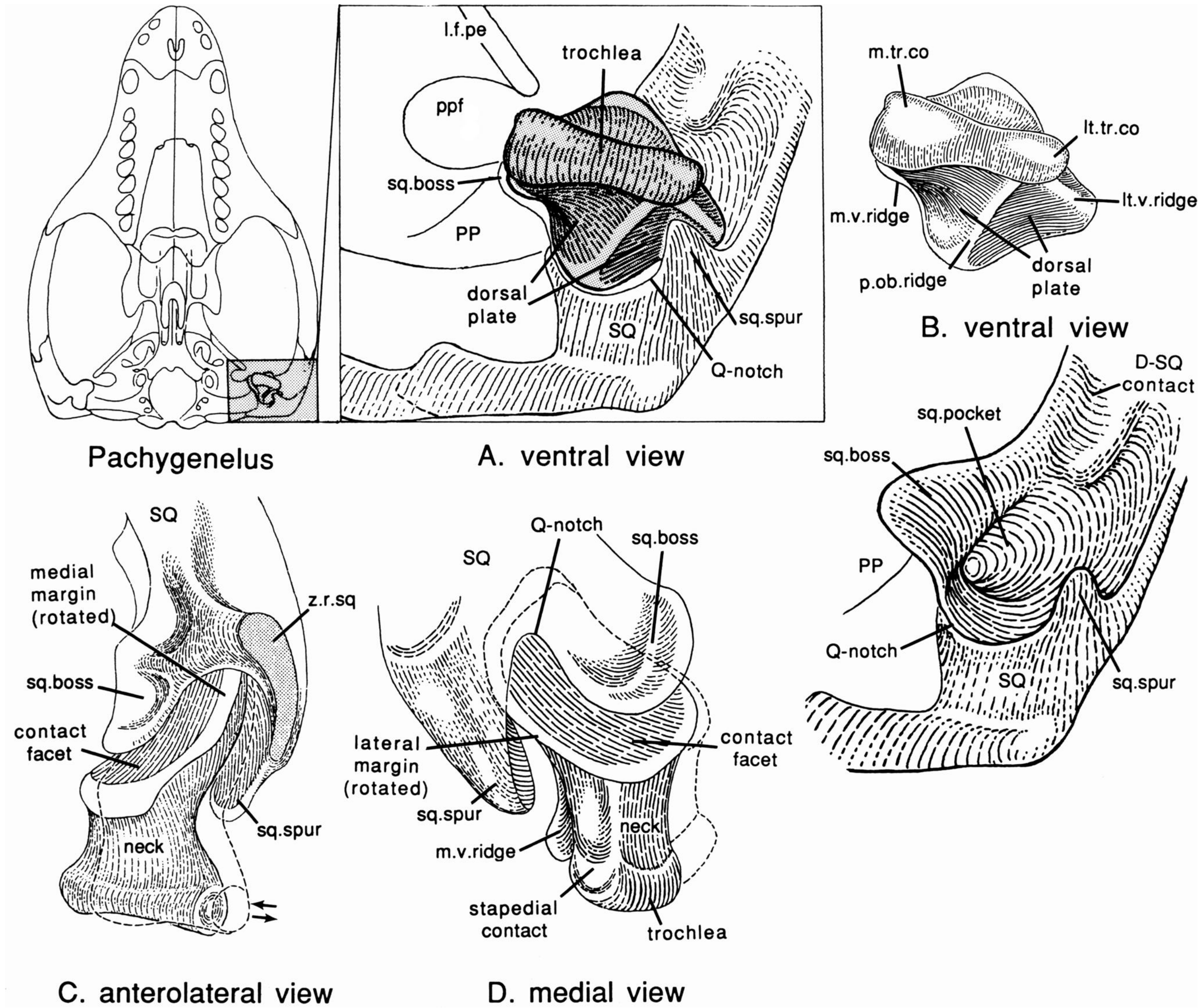
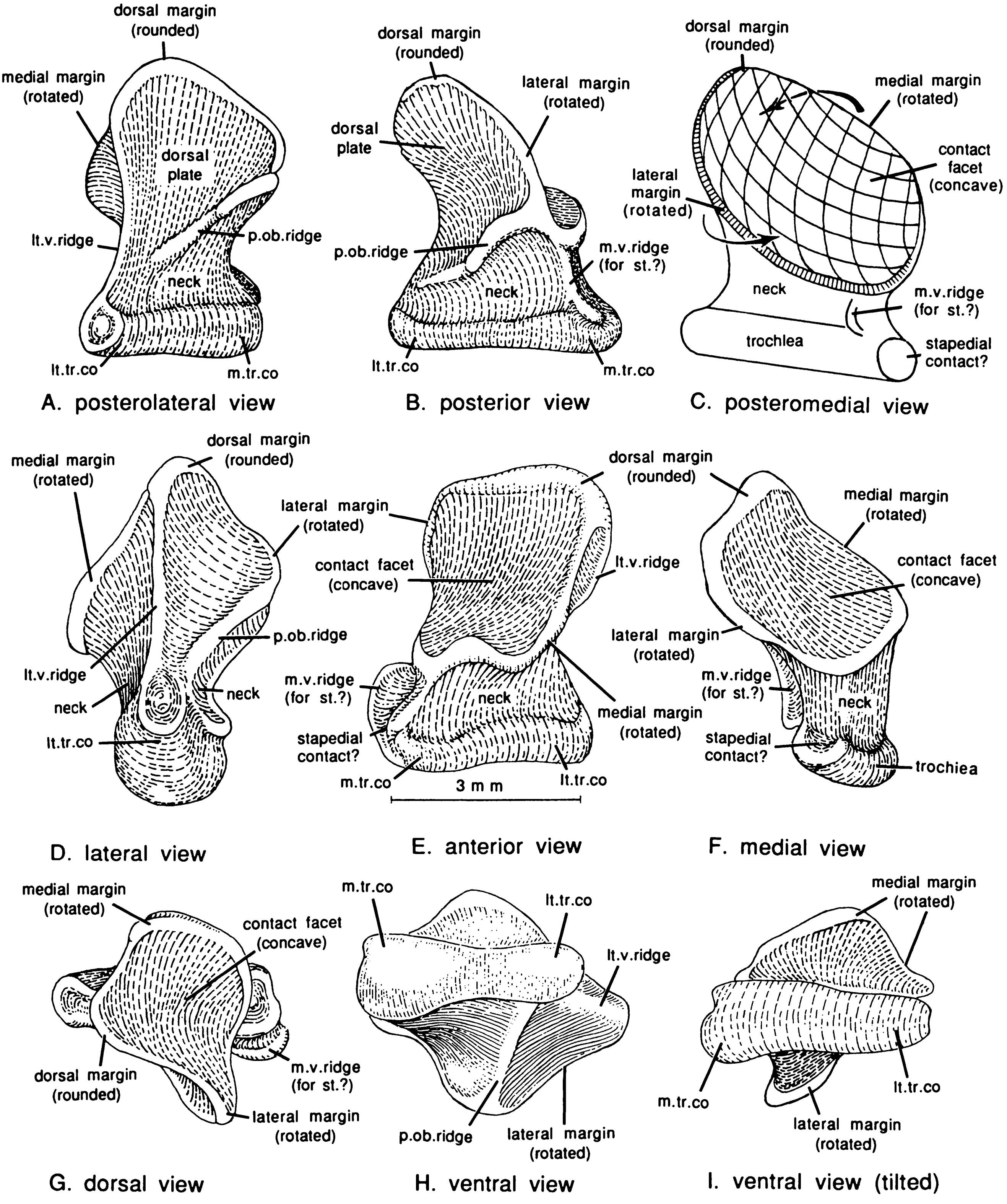


FIGURE 11. *Pachygenelus* (skull restoration after Allin and Hopson, 1992; Hopson and Crompton, unpubl. data). **A**, articulation of the quadrate to the basicranium (left side, ventral view; based on SAM K139). **B**, disarticulated quadrate and squamosal (left, ventral view). **C**, anterolateral view of the quadrate–squamosal articulation. **D**, medial view of the quadrate–squamosal articulation. Dash-lines in C and D indicate the possible range of movement of the quadrate in the squamosal pocket. Abbreviations: **D-SQ** contact, dentary and squamosal contact; **l.f.pe**, lateral flange of the petrosal; **lt.v.ridge**, lateral vertical ridge of the quadrate; **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlea condyle; **m.v.ridge**, medial vertical ridge of the quadrate; **p.ob.ridge**, posterior oblique ridge of the quadrate; **pp**, paroccipital process; **Q-notch**, notch for the quadrate (in the squamosal); **SQ**, squamosal; **sq.boss**, boss in the squamosal for articulating with the quadrate; **sq.pocket**, pocket in the squamosal for the dorsal plate of the quadrate; **sq.spur**, spur in the squamosal contact of the dorsal plate of the quadrate.

the trochlea by a small notch. The flaring medial ridge is so close to the stapedial recess that it may have contacted the distal end of the stapes. It bears some resemblance to the crus longum of the incus in *Morganucodon,* as the crus longum (stapedial process) in *Morganucodon* also projects posteriorly from the neck. The trochlea is slightly curved in the horizontal plane. The lateral end of the trochlea is smaller than the medial end. The stapedial end of the trochlea is slightly concave and has a semicircular outline in medial view (Fig. 12E, F).

Pachygenelus is similar to *Morganucodon,* but different from other non-mammalian cynodonts, in possessing several derived quadrate characters: a rounded dorsal margin of the dorsal plate, the medial trochlear condyle larger than the lateral condyle, and the angle of rotation of the dorsal plate (see below). Two additional but more equivocal features of *Pachygenelus*



A. posterolateral view

B. posterior view

C. posteromedial view

D. lateral view

E. anterior view

F. medial view

G. dorsal view

H. ventral view

I. ventral view (tilted)

FIGURE 12. Left quadrate of *Pachygenelus* (based on SAM K139). **C**, a generalized model of the quadrate of tritheledontids. Abbreviations: **lt.v.ridge**, lateral vertical ridge of the quadrate; **lt.tr.co**, lateral trochlear condyle; **m.v.ridge (for st?)**, medial vertical ridge of the quadrate (possibly for stapedial contact); **m.tr.co**, medial trochlea condyle; **p.ob.ridge**, posterior oblique ridge of the quadrate.

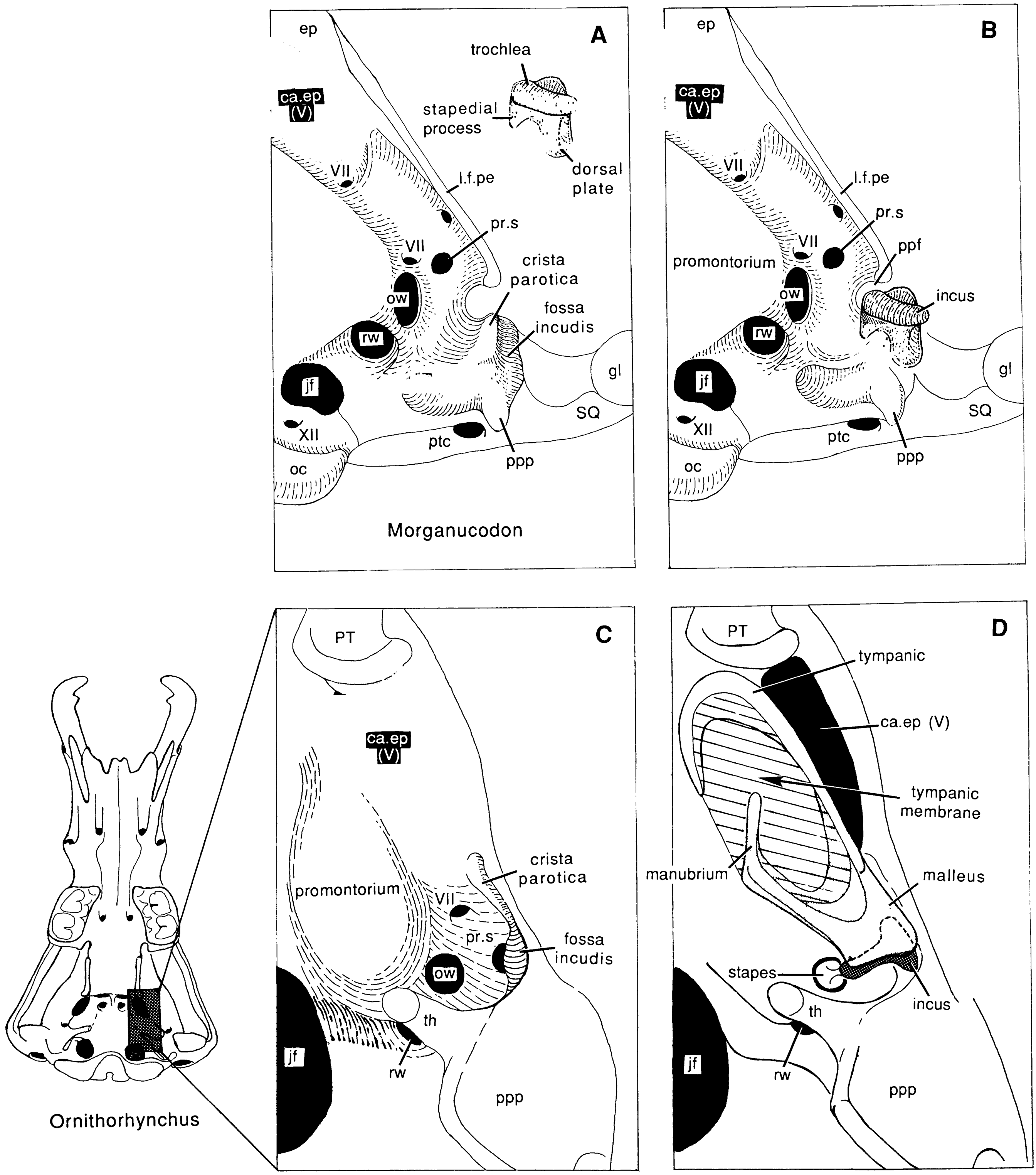


FIGURE 13. The quadrate (incus) articulation in *Morganucodon* and *Ornithorhynchus*. **A**, left basicranium of *Morganucodon*, with a disarticulated incus (modified from Kermack et al., 1981 on the basis of IVPP 8682, 8684). **B**, restoration of the articulation of the incus to the petrosal in *Morganucodon* (based on IVPP 8682; 8684). **C**, left basicranium of *Ornithorhynchus*, with the incus, stapes, malleus, and tympanic removed. **D**, articulation of the middle ear bones to the basicranium in *Ornithorhynchus* (hatched area represents the tympanic membrane). Abbreviations: **ca.ep (v)**, cavum epiptericum for the trigeminal ganglion; **ep**, epipterygoid; **gl**, glenoid for the dentary articulation; **jf**, jugular foramen; **l.f.pe**, lateral flange of the petrosal; **ow**, oval window (fenestra ovalis); **ppf**, pterygo–paroccipital foramen; **ppp**, posterior paroccipital process; **pr.s**, tympanic opening of the prootic sinus canal; **ptc**, post-temporal canal; **rw**, round window (fenestra cochlearis); **SQ**, squamosal; **th**, tympanohyal; **VII**, foramina for the facial nerves; **XII**, foramen for the hypoglossal nerve.

may be interpreted as resembling *Morganucodon*: the contact facet of the dorsal plate is more concave, and the the posterior flaring of the medial vertical ridge is reminiscent of the posteriorly projecting crus longum in *Morganucodon.*

Morganucodon

The quadrate is supported by the anterior paroccipital process of the petrosal (Fig. 13) (Crompton and Luo, 1993; Luo, in press). In *Morganucodon oehleri* (IVPP 8684) from Yunnan of China, and some specimens of *Morganucodon watsoni* from the Welsh fissure deposits, a low crest is present on the ventral side of the anterior paroccipital process ("ct.p.occ."—crest of paroccipital process; Kermack et al., 1981:figs. 75, 77, 80). Lateral to this crest is a shallow fossa or pocket. In *Morganucodon oehleri,* the crest on the anterior paroccipital process fits into the concave contact facet of the quadrate while the fossa lateral to the crest receives the dorsal and lateral margins of the contact facet of the quadrate. We interpret the paroccipital fossa receiving the dorsal and lateral margins of the quadrate as the homologue of the fossa incudis in the petrosals of triconodontids and *Ornithorhynchus* (Crompton and Sun, 1985; Luo, 1989; Crompton and Luo, 1993). The crest on the anterior paroccipital process is homologous to the crista parotica of monotremes (Kuhn, 1971; Zeller, 1989).

We also believe that the squamosal does not cover the fossa incudis in *Morganucodon* (IVPP 8682; IVPP 8684) and *Dinnetherium* (MCZ 20970; 20971), and thus provided no support for the dorsal plate (lamina) of the quadrate. In *M. oehleri* (IVPP 8684 and CUP 2320, Kermack et al. 1981:fig. 5) and *Dinnetherium* (Jenkins et al., 1983; Crompton and Luo, 1993), the quadrate is preserved in situ on the anterior paroccipital process while the squamosal is completely broken from the specimen. In other *M. oehleri* specimens (e.g., IVPP 8682), the quadrate is detached from the cranium while the squamosal is preserved in situ. This suggests that there was no substantial articulation between the squamosal and the quadrate. A similar pattern is also present in multituberculates (Miao and Lillegraven, 1986; Miao, 1988; Luo, 1989). The quadratojugal of *Morganucodon* is absent in all known specimens.

The quadrate (incus) of *Morganucodon* was described in great detail by Kermack et al. (1981) (Fig. 14). The bone is constricted by a neck between the trochlea and the dorsal plate ("dorsal lamina" of Kermack et al., 1981), a character shared by tritylodontids and tritheledontids. The posterior contact facet of the dorsal plate is concave, a feature shared by *Probainognathus, Massetognathus,* tritylodontids and tritheledontids. *Morganucodon* resembles *Pachygenelus* more closely than any other non-mammalian cynodonts in three characters of the quadrate: 1) the dorsal plate is oriented in a plane oblique to the axis of the trochlea, and forms an angle of over 90° to the trochlea; 2) the dorsal and lateral margins of the contact facet are rounded; 3) the lateral end of the trochlea tapers off distally and is smaller than the medial end. *Morganucodon* also differs from known non-mammalian cynodonts in possessing a stapedial process (the crus longum) that projects from the medial side of the quadrate neck perpendicular to the axis of the quadrate trochlea. Although this process bear some resemblance to the stapedial ("medial") process in tritylodontids and the posterior flaring of the medial vertical ridge in *Pachygenelus,* the morphological detail seems to vary widely among these forms.

CHARACTER ANALYSIS

In order to establish the pattern of character transformation of the quadrate, we coded the character states for the non-mammalian cynodonts and *Morganucodon* for the algorithms of MacClade (Maddison and Maddison, 1992) and PAUP (Swofford, 1993). The quadrate and the articulation of the quadrate to the cranium are important sources of phylogenetic information on non-mammalian cynodonts and early mammals. Coding of the characters makes it possible to use the quadrate characters to test the competing phylogenetic hypotheses. Moreover, coding of quadrate characters would allow transformation of the quadrate character to be considered within broader phylogenetic frameworks based on characters from other areas of the cranium, the dentition, and the postcranial skeleton (Kemp, 1982, 1983, 1988; Hopson and Barghusen, 1986; Hopson, 1991; Rowe, 1988, 1993). The justification for the coding of the characters is as follows.

Orientation of Dorsal Plate

Orientation of the dorsal plate varies relative to the axis of the trochlea in non-mammalian cynodonts and *Morganucodon* (Table 1 and Appendix 1: character 1; Fig. 15). *Thrinaxodon* and *Pachygenelus* represent, respectively, the most plesiomorphic state and the most apomorphic state. In *Thrinaxodon* (Fig. 15A), the main plane of the dorsal plate (bb') is set at about 10° from the vertical plane that contains the trochlea (aa'). The contact facet for the squamosal faces posteriorly. The contact facet facing posteriorly is regarded as the ancestral state "0" because it is also present in *Procynosuchus* (Brink, 1963b; Crompton, 1972a; Kemp, 1979), therocephalians (Broom, 1936; Kemp, 1972a, b), gorgonopsians (Parrington, 1955; Kemp, 1969), dicynodonts, and a number of other non-cynodont therapsids (Crompton, 1955; Camp, 1956). The character state of *Probainognathus* (Fig. 15B) is designated "1," in which the main plane of the dorsal plate (bb') is oblique (about 45°) to the vertical plane that contains the axis of the trochlea (aa'). The contact facet faces posteromedially. *Massetognathus* is nearly identical to *Probainognathus* in this feature, and thus should be assigned the same character state.

The dorsal plate of tritylodontids differs from all

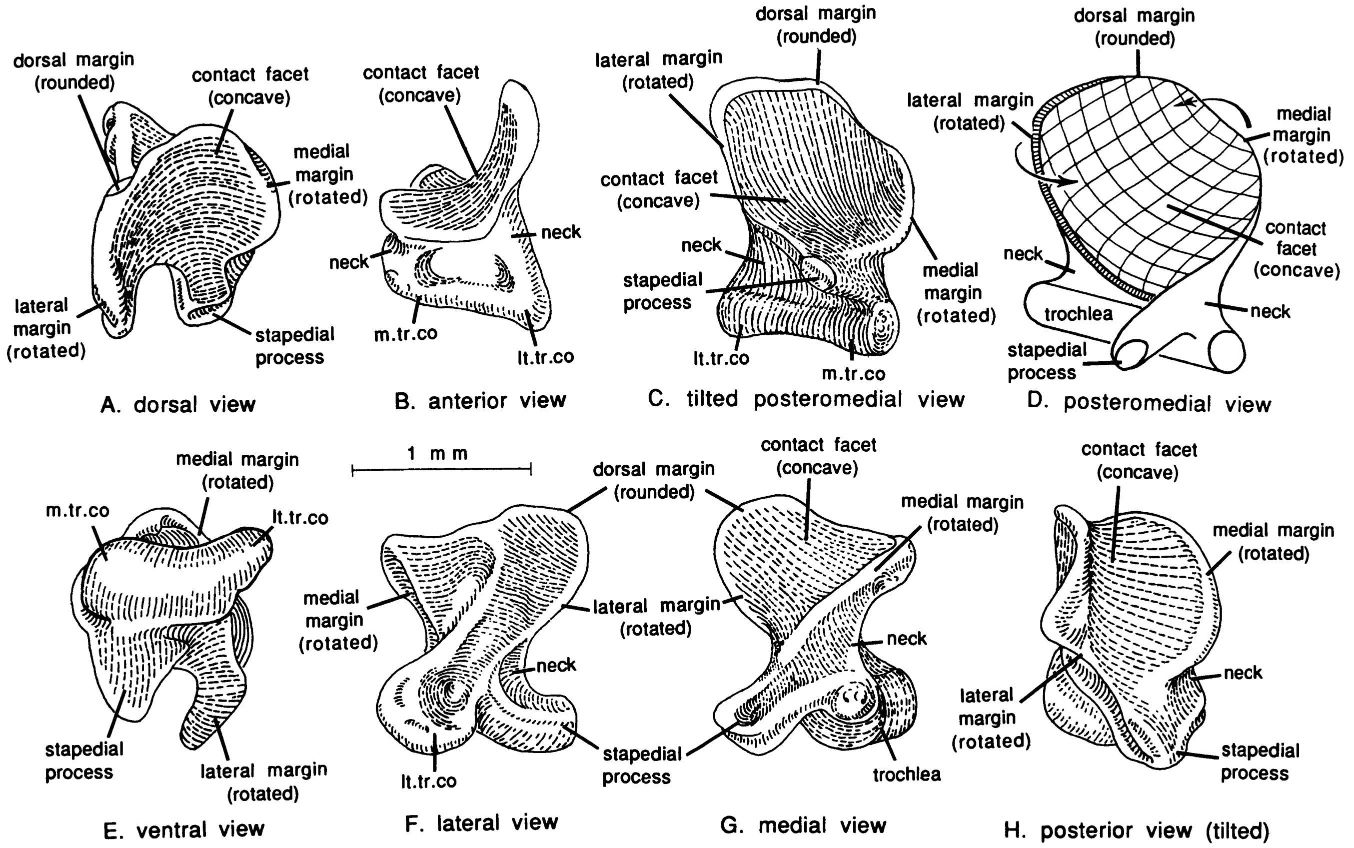


FIGURE 14. Quadrate of *Morganucodon* (**A**, **B**, **D**, **E**, **F**, **G** after Kermack et al., 1981; **C** is based on a specimen of Museum of Zoology, Cambridge University). **D** represents a generalized model of the quadrate in posteromedial view. Abbreviations: **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlear condyle.

other non-mammalian cynodonts and *Morganucodon.* The plane of the dorsal plate is oriented almost horizontally, and is nearly parallel to the axis of the trochlea (Kühne, 1956; Crompton, 1964; Hopson, 1965; Sun, 1984; Sues, 1986a; Sun and Cui, 1989). The contact facet faces dorsally (Fig. 15E, F). The orientation of the dorsal plate is so different in tritylodontids that the parallel relationships of the dorsal plate and the trochlea can only be seen in the anterior (Fig. 15E) or posterior view (Fig. 16F), instead of the ventral view as in other non-mammalian cynodonts. The character state of tritylodontids is designated "2." In *Morganucodon* (Fig. 15D), the main plane of the dorsal plate is set at 90° to the axis of the trochlea, and the contact facet faces dorsally and medially. In *Pachygenelus* (Fig. 15C), the plane of the dorsal plate is about 120° to the vertical plane that contains the trochlea; the contact facet faces dorsally and anteromedially; the degree of the dorsal plate rotation is greater than in *Morganucodon.* The conditions in *Pachygenelus* and *Morganucodon* are assigned character state "3," in which the dorsal plate has rotated over 90° while maintaining an oblique angle to the trochlea.

Curvature of Contact Facet

Curvature of the posterior contact facet of the quadrate shows considerable variations among the non-mammalian cynodonts and *Morganucodon* (Table 1 and Appendix 1: character 2; Figs. 16, 17). In *Procynosuchus* (Fig. 16B; Kemp, 1979) and whaitsiid therocephalians (Kemp, 1972a, b) the contact facet is flat or nearly flat. This is recognized as ancestral character state "0." In *Thrinaxodon* the contact facet is slightly convex in the dorsal and medial parts but flat in the middle (Fig. 16C). This is coded "1." A convex contact facet is also present in the quadrate of gorgonopsians (Fig. 16A). The convex contact facet forms a "ball-in-socket" joint with the squamosal (Kemp, 1969). The contact facet is concave in *Probainognathus, Massetognathus,* tritylodontids, *Pachygenelus,* and *Morganucodon.* The concave contact facet is designated character state "2" (Fig. 16D–H). Concavity of the contact facet is slightly more developed in *Pachygenelus* and *Morganucodon* than in *Probainognathus, Massetognathus,* and most tritylodontids (Figs. 16G, H and 17G, H).

Relative Size of Trochlear Condyles

The size of the medial trochlear condyle relative to the size of the lateral trochlear condyle is recognized as a character (Table 1 and Appendix 1: character 3; Figs. 16, 17). The trochlea is constricted in the middle; the medial and lateral ends of the trochlea are relatively enlarged, and termed medial and lateral condyles re-

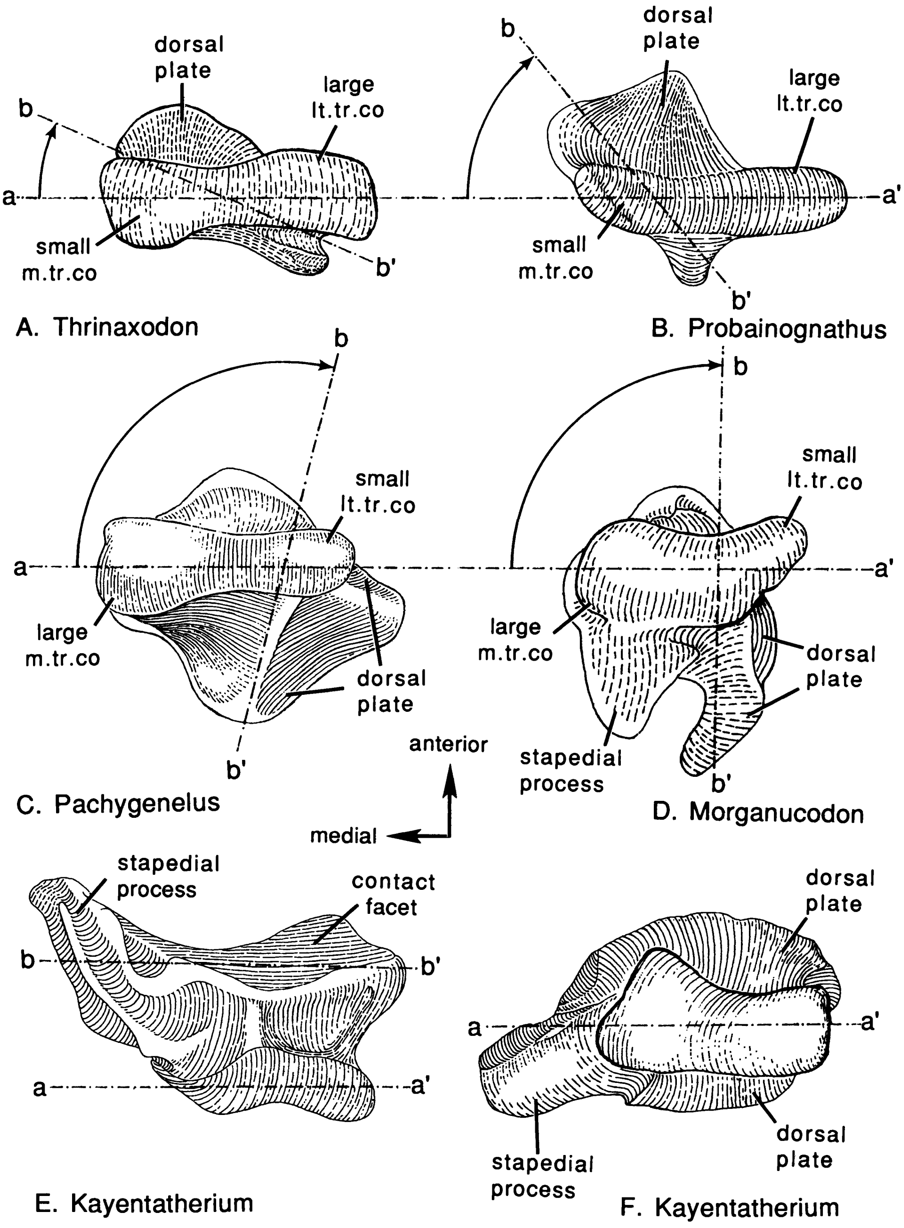


FIGURE 15. Morphological character states of the quadrate (incus) of some advanced non-mammalian cynodonts and *Morganucodon* (ventral or anteroventral views of the left quadrate). (**C**, after Hopson and Crompton, unpublished data; **D**, after Kermack et al., 1981; **E**, **F**, modified from Sues, 1986a based on MCZ 8812). Line aa′ represents the axis of the trochlea; line bb′ represents the main plane of the dorsal plate. Because the dorsal plate is nearly horizontal and parallel to the axis of the trochlea in tritylodontids, an anterior view of *Kayentatherium* (E) is added to show the parallel relationships of the dorsal plate (and the contact facet) to the trochlea. Abbreviations: **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlear condyle.

spectively. In gorgonopsians (Parrington, 1955; Kemp, 1969), therocephalians (Kemp, 1972a, b), *Procynosuchus* (Brink, 1963b; Crompton, 1964; Kemp, 1979), and *Thrinaxodon,* the constriction of the trochlea is closer to the medial (proximal) end of the trochlea than to its lateral (distal) end. Consequently the lateral condyle is considerably longer and larger than the medial condyle. This condition is present in *Probainognathus* (MCZ 4287, MCZ 4021, MCZ 4019). In *Oligokyphus* (Kühne, 1956), the lateral end of the trochlea is larger than the medial end. But this size difference is absent in *Kayentatherium* (Fig. 9) and less developed in *Bienotheroides* (Fig. 10). We take the condition in *Oligokyphus* as the plesiomorphic character state of the Tritylodontidae. The pattern in which the medial end (or condyle) of the trochlea is smaller than the lateral end (or condyle) is regarded as the ancestral character state “0.” In *Pachygenelus* (Figs. 15, 16), the medial end is larger than the lateral end of the trochlea, and is thus defined as character state “1.” In *Morganucodon,* the

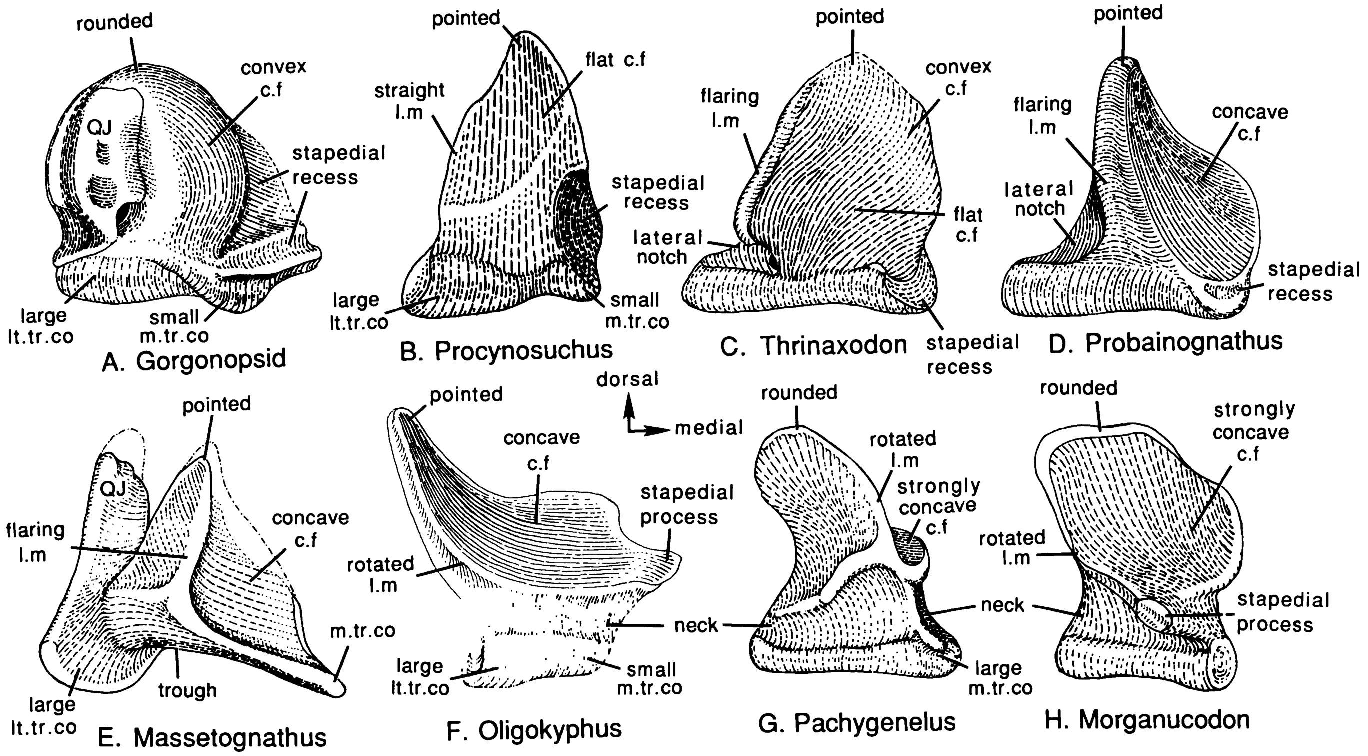


FIGURE 16. Morphological character states of the quadrate (incus) of some advanced non-mammalian cynodonts and *Morganucodon* (left quadrate, posterior view). (**A**, after Parrington (1955) and Kemp (1969); **B**, modified from Kemp, (1979) on the basis of MCZ 8986; **F**, after Kühne (1956); **G**, based on SAM K139; **H**, modified from Kermack et al. (1981) based on a specimen in the Cambridge University collection) Abbreviations: **c.f**, contact facet; **l.m**, lateral margin; **lt.tr.co**, lateral trochlear condyle; **m.tr.co**, medial trochlear condyle; **QJ**, quadratojugal.

lateral trochlear condyle is smaller and tapers distally, and it too is considered character state "1" (Fig. 15D).

Shape of Trochlea

Shape of the quadrate trochlea has two character states (Table 1 and Appendix 1: character 4; Figs. 16, 17). "0" represents the more uniform and cylindrical trochlea in most non-mammalian cynodonts and *Morganucodon.* In *Massetognathus,* the lateral condyle is enlarged to form a crest and the middle part of the trochlea becomes a trough. This trough and crest configuration of the trochlea is assigned character state "1." This configuration of the trochlea is also present in the anomodont *Galeops* (Brinkman, 1981) and dicynodonts (Camp, 1956; Crompton and Hotton, 1967). Among the more primitive synapsids, this trough and crest configuration is also present in pelycosaurs (Romer and Price, 1940).

TABLE 1. Character/taxon matrix of quadrate characters in non-mammalian cynodonts and *Morganucodon* (see Appendix 1 for definition and description of characters).

	Character													
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Anomodontia	0	0	0	1	0	0	0	0	0	1	0	0	0	0
Gorgonopsia	0	1	0	0	0	1	1	0	0	2	1	0	0	0
Therocephalia	0	0	0	0	0	1	0	0	0	1	1	0	0	0
Procynosuchus	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Thrinaxodon	0	1	0	0	1	0	0	1	1	0	0	0	0	1
Probainognathus	1	2	0	0	1	1	0	2	1	2	2	1	1	1
Massetognathus	1	2	0	1	1	1	0	2	1	2	0	0	1	1
Tritylodontidae	2	2	0	0	2	2	0	3	1	2	0	2	2	2
Tritheledontidae	3	2	1	0	2	2	1	3	?	2	0	1	1	3
Morganucodon	3	2	1	0	2	2	1	3	?	2	0	2	3	4

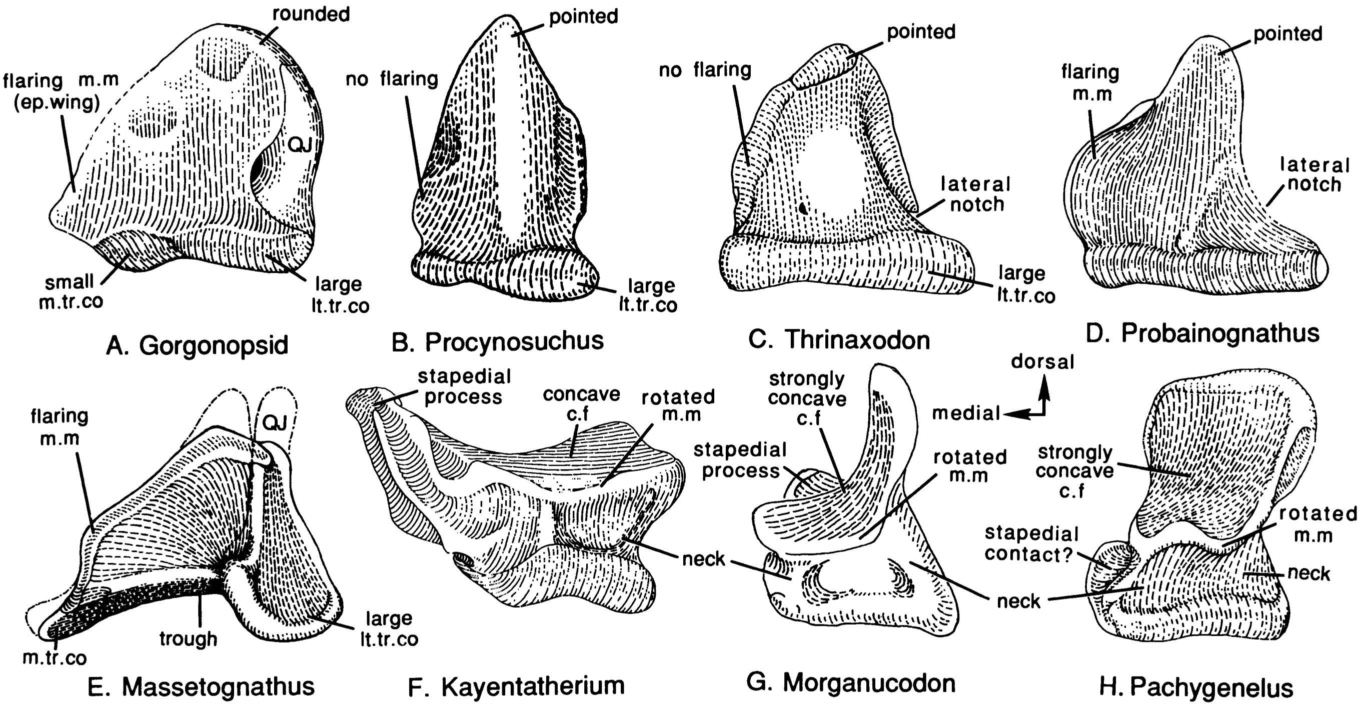


FIGURE 17. Morphological character states of the quadrate (incus) of some advanced non-mammalian cynodonts and *Morganucodon* (anterior view of the left quadrate). (**A**, after Parrington (1955) and Kemp (1969); **B**, modified from Kemp (1979) on the basis of MCZ 8986; **F**, after Kühne (1956); **G**, after Kermack et al. (1981); **H**, SAM K139, Hopson and Crompton, unpubl. data). Abbreviations: **c.f**, contact facet; **lt.tr.co**, lateral trochlear condyle; **m.m**, medial margin of the dorsal plate; **m.tr.co**, medial trochlear condyle.

Lateral Margin of Dorsal Plate

The character states of the lateral margin have been discussed in many previous studies (Table 1 and Appendix 1: character 5; Fig. 16) (see Crompton, 1972a; Kemp, 1982; Hopson and Barghusen, 1986; Rowe, 1988). The straight lateral margin of the dorsal plate (i.e., lacking the posterior flaring) is designated character state "0." This character state is present in anomodonts (Brinkman, 1981; Camp, 1956), gorgonopsians (Parrington, 1955), therocephalians (Olson, 1944; Crompton, 1955; Kemp, 1972a, b), and *Procynosuchus* (Crompton, 1972a; Kemp, 1979). In *Thrinaxodon, Probainognathus,* and *Massetognathus,* the lateral margin of the dorsal plate flares posteriorly ("posterior flange" sensu Crompton, 1972a). The posteriorly flaring margin ("flange") wedges into the quadrate notch in the squamosal (Crompton, 1972a; Kemp, 1982; Hopson and Barghusen, 1986; Rowe, 1988). This character state is coded as "1." In tritylodontids, *Pachygenelus,* and *Morganucodon,* the lateral margin not only flares but it is also rotated further posteromedially, which is designated character state "2."

Medial Margin of Dorsal Plate

The medial margin in the quadrate of *Procynosuchus* and *Thrinaxodon* is nearly straight and does not flare anteriorly; this is coded as character state "0" (Table 1 and Appendix 1: character 6; Figs. 7, 17). Among the out-groups of this analysis, this character state is present in anomodonts (Olson, 1944; Camp, 1956) but absent in Therocephalia and Gorgonopsia. Thus it is unclear whether this can be regarded as the ancestral character state. The medial margin of the dorsal plate flares anteriorly in the gorgonopsian *Arctognathus* (Kemp, 1969). It is termed "epipterygoid wing" by Kemp because it flares forward to articulate with the quadrate ramus of the epipterygoid. The anterior flaring of the medial margin of the dorsal plate is also present in therocephalians (Eutherocephalia sensu Hopson and Barghusen, 1986). It is described as the "pterygoid wing" in *Whaitsia* (Kemp, 1972a, b), and it is also present in *Ictidosuchops* (Crompton, 1955) and *Bauria* (Crompton, 1955; Brink, 1963a). Similar to the condition in therocephalians, the medial margin of the quadrate flares anteriorly in *Probainognathus* and *Massetognathus.* This condition is designated as character state "1."

The medial margin is not only strongly flaring anteriorly but also rotated anterolaterally in tritylodontids, *Pachygenelus,* and *Morganucodon.* The medial margin is rotated in such a way that the contact facet can be seen in anterior view in these three taxa (Fig. 17F–H); this is designated character state "2." By contrast, this facet can only be seen in the posterior view in other cynodonts and non-cynodont therapsids.

Dorsal Margin of Dorsal Plate

The dorsal margin of the quadrate in *Thrinaxodon* forms a pointed angle (process) (Table 1 and Appendix 1: character 7; Fig. 16). *Probainognathus* and *Massetognathus* also possess a pointed dorsal angle. This is assigned ancestral character state "0" because it is present in anomodonts (Olson, 1944; Camp, 1956; Brinkman, 1981), procynosuchids (MCZ 8968; Brink, 1963b; Kemp, 1979), and some therocephalians (Crompton, 1955; Kemp, 1972b). Among the primitive tritylodontids, *Oligokyphus* has a similar dorsal process (Kühne, 1956; Crompton, 1964). Hopson (1966) termed this process the "posterodorsal process." *Bienotherium* (Hopson, 1966) and *Yunnanodon* (IVPP 5071) appear to have a pointed dorsal process. Advanced tritylodontids, such as *Kayentatherium* (Sues, 1986a) and *Bienotheroides* (Sun, 1984; Sun and Cui, 1989), lack this pointed process (angle) (Figs. 9, 10). Our interpretation of the tritylodontid quadrate is that the pointed dorsal process was secondarily lost in both *Kayentatherium* and *Bienotheroides*. Tritylodontidae as a whole should be assigned "0" for this character. The dorsal margin of the quadrate in *Pachygenelus* and *Morganucodon* is broadly rounded and has no pointed angle or process as in *Thrinaxodon, Probainognathus,* and primitive tritylodontids. This is coded as character state "1." The rounded dorsal margin is also found in gorgonopsians (Parrington, 1955; Kemp, 1969).

Lateral Notch and Neck

In *Thrinaxodon* (Fig. 16C), a lateral notch separates the lateral end of the trochlea from the lateral margin of the contact facet. This deep notch receives the hook-like ventral end of the quadratojugal. The condition of *Thrinaxodon* is coded as "1" (Table 1 and Appendix 1: character 8; Figs. 16, 17). The lateral notch is poorly developed in therocephalians (Broom, 1936; Olson, 1944; Crompton, 1955; Brink, 1963a; Kemp, 1972a, b) and *Procynosuchus* (Kemp, 1979), and it is altogether absent in out-group gorgonopsians (Parrington, 1955; Kemp, 1969) and anomodonts (Brinkman, 1981; Camp, 1956). The absence of a deep lateral notch in the out-groups is regarded as the ancestral character state "0." The lateral notch is much broader in *Probainognathus* and *Massetognathus* than in *Thrinaxodon.* The lateral margin of the contact facet has shifted posteromedially, and the contact facet only borders on the trochlea near the medial end of the trochlea in the former two taxa (e.g., Fig. 7D). The much broader lateral notch in *Probainognathus* and *Massetognathus* is coded as "2."

Differing from *Thrinaxodon, Probainognathus,* and *Massetognathus,* the margins of the contact facet in tritylodontids, *Pachygenelus,* and *Morganucodon* are raised from the trochlea by a constricted neck (Figs. 16, 17). Consequently the concave contact facet no longer borders on the trochlea. The complete separation of the contact facet from the trochlea by a constricted neck is designated character state "3." It is conceivable that the constricted neck, a more derived condition, could be developed from a further incision of an increasingly wide and deep lateral notch toward the medial end of the trochlea.

Articulation with the Quadratojugal

The way in which the quadratojugal articulates with the quadrate is recognized as a character (Table 1 and Appendix 1: character 9). In gorgonopsians (Fig. 16E), the lateral edge of the dorsal plate of the quadrate is sutured with (and covered by) the quadratojugal, as in pelycosaurs. The quadratojugal abuts the lateral edge of the dorsal plate of the quadrate in the primitive anomodont *Galeops* (Brinkman, 1981) and is sutured with the dorsal part of the quadrate in dicynodonts (Olson, 1944; Camp, 1956:fig. 13). In therocephalians, the quadratojugal is in juxtaposition with (abutting) the lateral edge of the dorsal plate. The condition in which the quadratojugal is abutting (or sutured with) the lateral edge of dorsal plate of the quadrate is coded as ancestral character state "0." In most non-mammalian cynodonts considered in this study, the quadratojugal is separated from the lateral margin of the dorsal plate (Figs. 3, 5, 7, 8). This is designated as character state "1." The quadratojugal has never been found in any known specimens of *Pachygenelus* and *Morganucodon* and is coded "?."

Articulation with the Pterygoid

The quadrate ramus of the pterygoid of *Thrinaxodon* overlaps the anterior face of the medial margin of the dorsal plate of the quadrate (Crompton, 1972a; Fourie, 1974), a condition also present in *Procynosuchus* (Kemp, 1979). The contact of the pterygoid on the anterior face of the quadrate is designated "0" because a similar articulation occurs in many primitive synapsids (Table 1 and Appendix 1: character 10; Fig. 3). The articulation of the quadrate ramus of the pterygoid differs in therocephalians. The posterior end of the quadrate ramus of the pterygoid is received by a broad recess on the posteromedial face of the "pterygoid wing" (formed by the flaring part of the medial margin of the dorsal plate) (Crompton, 1955; Kemp, 1972a, b). Thus in therocephalians the quadrate ramus contacts the medial side of the quadrate rather than the anterior side of the quadrate as in *Thrinaxodon.* In anomodonts, the medial side of the quadrate also overlaps the quadrate ramus of the pterygoid (Brinkman, 1981; Camp, 1956). The therocephalians and anomodonts are coded character state "1." The quadrate does not articulate with the pterygoid in the gorgonopsian *Arctognathus* (Kemp, 1969), *Probainognathus, Massetognathus,* tritylodontids, *Pachygenelus* and *Morganu-*

codon. The absence of the articulation of the quadrate and the pterygoid is recognized as "2."

Articulation with the Epipterygoid

An articulation of the quadrate with the quadrate ramus of the epipterygoid is present in gorgonopsians (Kemp, 1969) and *Probainognathus* (Fig. 5), but absent in all other non-mammalian cynodonts and early mammals surveyed in this study (Table 1 and Appendix 1: character 11). Absence of the articulation between the epipterygoid and the quadrate is designated "0." The quadrate ramus of the epipterygoid (Olson, 1944; Kemp, 1969) abuts against the edge of the prominent epipterygoid wing in gorgonopsians (Kemp, 1969; "pterygoid wing" sensu Parrington, 1955); this is designated "1." By contrast, in *Probainognathus* (Fig. 5), the posterior end of the quadrate ramus of the epipterygoid contacts broadly the anterior face of the dorsal plate of the quadrate, which is designated "2."

Articulation with the Squamosal

The dorsal plate of the quadrate articulates with the squamosal in three different ways among non-mammalian cynodonts and *Morganucodon* (Table 1 and Appendix 1: character 12). The dorsal plate fits into an anteriorly open recess in the squamosal in anomodonts, gorgonopsians, therocephalians, *Procynosuchus,* and *Thrinaxodon* (Kemp, 1969, 1979; Crompton, 1972a; Mendrez, 1972; Fourie, 1974). We regard an anteriorly open recess in the squamosal to be the most plesiomorphic character state, which is coded "0." In *Massetognathus,* the cranial moiety of the squamosal is broadly expanded to flank the pterygo-paroccipital foramen (Fig. 8). This anterior expansion of the squamosal also covers the medial end of the trochlea of the quadrate (Fig. 8A). The dorsal plate of the quadrate attaches to the cranium by fitting into an anteriorly open recess in the squamosal, although the dorsal angle of the quadrate is partially covered by the squamosal. Character state "0" should also be assigned to *Massetognathus.*

In *Probainognathus,* a squamosal lappet covers the anterior face of the dorsal plate (sq.la, Fig. 5C). The squamosal is expanded anteromedially to contribute to the enclosure of the pterygo–paroccipital foramen (Fig. 7). The medial expansion of the squamosal is similar to that in *Massetognathus.* The quadrate of *Pachygenelus* is completely supported by the squamosal in a deep pocket that opens ventrally (Fig. 11). Both *Pachygenelus* and *Probainognathus* are designated character state "1" for lacking the anteriorly open squamosal recess.

In the Tritylodontidae, the quadrate has very little contact with the squamosal (*Yunnanodon,* IVPP 5071; also see Crompton, 1964; Hopson, 1965; Sues, 1986a). The contact between the squamosal and the dorsal plate of the quadrate is absent in *Morganucodon.* These are both designated character state "2."

Articulation with the Paroccipital Process of the Petrosal

The contact between the quadrate and the paroccipital process of the opisthotic (petrosal) is recognized as a phylogenetic character (Table 1 and Appendix 1: character 13; Fig. 13, also see Rowe, 1988; Wible, 1991). Partial contact of the quadrate to the paroccipital process is present in anomodonts (Olson, 1944; Camp, 1956), the gorgonopsian *Arctognathus* (Kemp, 1969), therocephalians (Crompton, 1955; Kemp, 1972a, b), and *Procynosuchus* (Brink, 1963b; Crompton, 1964; Kemp, 1979). The quadrate of *Thrinaxodon* also partially contacts the paroccipital process (Crompton, 1964; Fourie, 1974). This is recognized as ancestral character state "0." The quadrate–opisthotic contact is absent in *Probainognathus* (Fig. 5), *Massetognathus* (Fig. 8), and *Pachygenelus* (Fig. 11) because of the expansion of the squamosal medial to the quadrate; thus these three taxa are coded "1."

In tritylodontids, the bulbous and massive anterior paroccipital process provides a broad contacting surface for the quadrate. *Morganucodon* and *Dinnetherium* are similar to tritylodontids in that the anterior paroccipital process is the major structure supporting the quadrate (Luo, 1989; Crompton and Luo, 1993). However, the detailed structure of the articulation differs between the two groups (Luo, in press). The anterior paroccipital process of *Morganucodon* has a crest ("crista parotica") that fits the concave contact facet, and an associated fossa incudis that receives the margin of the dorsal plate (IVPP 8684) ("dorsal lamina" of Kermack et al., 1981). The joint is formed by a tongue (the crista parotica) in groove (concave contact facet of the quadrate) articulation. This is an important difference between morganucodontids and tritylodontids. Thus we coded character state "2" for the articulation of the quadrate to the bulbous and massive anterior paroccipital process in tritylodontids and a separate character state "3" for the tongue-in-groove articulation between the quadrate and the crista parotica in *Morganucodon.*

Articulation with the Stapes

The contact area between the quadrate and the stapes is considerably smaller in cynodonts than in non-cynodont therapsids (Table 1 and Appendix 1: character 14; Fig. 16). In most non-cynodont therapsids, the stapes articulates with the quadrate in a large stapedial recess on the posteromedial side of the dorsal plate (Figs. 2, 16A, B; also see Olson, 1944; Crompton, 1955; Parrington, 1955; Kemp, 1969, 1979). The recess that receives the stapes in dicynodonts, gorgonopsians and procynosuchids occupies a broad area on the posterior face of the pterygoid (or epipterygoid) wing of the quadrate and part of the medial end of the trochlea (Fig. 16A, B). This is designated the ancestral state "0."

Therocephalians (sensu Hopson and Barghusen, 1986) show a wide range of variation in the quadrate-stapedial articulation. Broom (1936) and Olson (1944) illustrated a large "stapedial process" in *Lycedops* (Broom, 1936) and an unidentified therocephalian (Olson 1944:fig. 13). Yet the same process is very small in scaloposaurids (Crompton, 1955). In whaitsiids (Kemp, 1972a, b), the "process" is continuous with the pterygoid wing of the quadrate, and does not form an independent projection as in the case of the "stapedial process" in tritylodontids and the crus longum (stapedial process) in *Morganucodon.* Given this in-group variation, we consider the absence of an independent stapedial process represents the primitive condition of therocephalians, and the condition for this group should be coded "0."

In *Thrinaxodon* and *Probainognathus,* the ancestral condition has been modified. The articulation of the stapes is confined to a much smaller concave facet on the proximal end of the quadrate trochlea, and this is designated character state "1." In *Massetognathus,* a thick sheet of the squamosal completely covers the proximal end of the quadrate trochlea. The proximal end of the quadrate trochlea does not protrude below the edge of the squamosal sheet (Fig. 8). This makes it almost impossible for the quadrate to have articulated with the lateral end of the stapes, although it is possible that the quadrate could have articulated with the stapes via some cartilaginous extension that was lost post mortum. In *Exaeretodon,* a traversodontid closely related to *Massetognathus,* the stapes articulates directly with the medial end of the quadrate trochlea. Inferring from *Exaeretodon,* we tentatively coded the character state in *Massetognathus* as "1," pending further study.

Tritylodontids have a distinct stapedial process (Kühne, 1956; Hopson, 1966; Sues, 1986a; Rowe, 1988; Sun and Cui, 1989). This is assigned character state "2" for the Tritylodontidae. As noted above, morphology of the stapedial process in tritylodontids not only shows some variations (compare *Kayentatherium* [Fig. 9] with *Bienotheroides* [Fig. 10]), but also differs from the stapedial process (crus longum) of mammals in some features (Sues, 1985). The quadrate of *Pachygenelus* possesses a medial vertical ridge that somewhat resembles the stapedial process of *Morganucodon.* This presence of this ridge is coded "3." The stapedial process of *Morganucodon* is treated separately as character state "4" because it differs from the stapedial process of tritylodontids and from the medial vertical ridge of *Pachygenelus.*

PHYLOGENETIC IMPLICATIONS

The phylogenetic position of the Tritylodontidae is a focal point in the current debate of the phylogenetic relationships of advanced non-mammalian cynodonts and mammals (Kemp, 1983; Sues, 1985; Hopson and Barghusen, 1986; Rowe, 1986, 1988, 1993; Wible, 1991; Hopson, 1991; Crompton and Luo, 1993; Luo, in press). Two hypotheses have been advanced to interpret the phylogenetic interrelationships of tritylodontids, tritheledontids, and mammals. One hypothesis suggests that gomphodonts (including traversodontids) and tritylodontids are sister taxa, emphasizing the similarities between the two taxa in skull and dental features (Crompton, 1972b; Sues, 1985; Hopson and Barghusen, 1986; Hopson, 1991). The other hypothesis suggests that tritylodontids are closely related to tritheledontids and mammals, based on shared derived cranial and postcranial characters (Kemp, 1983, 1988; Rowe, 1988). More recently, Wible (1991) and Rowe (1993) explicitly argue that tritylodontids are the sister-group to mammaliaforms (sensu Rowe, 1988 and Wible, 1991; the Mammalia of most other authors) to the exclusion of tritheledontids.

Characters of the quadrate and the articulation of the quadrate to the cranium were used to support the sister-group relationships of the Tritylodontidae to mammaliaforms by some (Rowe, 1988; Wible, 1991; Rowe, 1993), and the sister-group relationship of tritheledontids and mammals by others (Hopson and Barghusen, 1986; Hopson, 1991; Crompton and Luo, 1993; Luo, in press). To help clarify the interrelationships of tritylodontids, tritheledontids, and mammals, more quadrate characters should be examined to test the existing alternative phylogenetic hypotheses. The character-taxon matrix presented in Table 1 summarizes the phylogenetic distributions of 14 quadrate characters in *Morganucodon* and nine non-mammalian therapsid clades. Appendix 1 provides descriptions for all characters. The exhaustive search by PAUP (Phylogenetic Analysis Using Parsimony, version 3.1.1) on this matrix generated a strict consensus tree (Fig. 1A) from three equally parsimonious trees.

Given our interpretation of the quadrate morphology and distribution of the quadrate characters (Table 1, Appendix 1), the sister-group relationship of tritheledontids and *Morganucodon* is most compatible with the distribution of the quadrate characters (Fig. 1A, B). Tritylodontids are the sister-group to a monophyletic taxon formed by tritheledontids and mammals. The hypothesis of the sister-group relationships of tritylodontids and mammals to the exclusion of tritheledontids is less compatible with the distribution of the quadrate characters (Fig. 1C).

The phylogenetic schemes of non-mammalian therapsids and the topology of their phylogenetic trees differ according to Kemp (1983, 1988), Hopson and Barghusen (1986), and Rowe (1988, 1993). To see if the tritheledontid–*Morganucodon* sister-group relationship would be weakened by altering the arrangement of successive out-groups, we plotted the distribution of the quadrate characters of tritylodontids, tritheledontids, and mammals with different arrangements of other out-group non-mammalian therapsids using MacClade (version 3.0). We found that varying the arrangement of out-group therapsids does not alter the position of tritylodontids relative to the monophyletic group of tritheledontids and *Morganucodon.* Regardless of the difference in arrangement of anomodonts, gorgonopsians, therocephalians and *Procyno-*

suchus, the tritheledontid-*Morganucodon* sister-taxon hypothesis has consistently fewer steps in tree length than the tritylodont-*Morganucodon* hypothesis (also see Luo, in press). Although the difference in tree measurements between the tritheledontid sister-group hypothesis and the tritylodontid sister-group hypothesis is small, overall, the quadrate characters favor a sister-group relationship between tritheledontids and mammals (Fig. 1A, B).

The quadrate characters cannot resolve the position of *Massetognathus.* On the strict consensus tree generated by PAUP (Fig. 1A), *Massetognathus* is placed between *Thrinaxodon* and tritylodontids; but within this constraint, the position of *Massetognathus* (relative to the position of *Probainognathus*) cannot be fully resolved. Placing *Massetognathus* between *Probainognathus* and tritheledontids would increase the tree length (Fig. 1C). Likewise, grouping of *Massetognathus* and tritylodontids also increases the number of transformational steps (Fig. 1D).

The quadrate complex is very important in hearing and masticatory functions. However, the quadrate complex provides only one of many possible tests of competing hypotheses of cynodont relationships. Single character systems, such as the quadrate complex, do not always provide unambiguous tests, as is shown above by the unresolved relationships of *Massetognathus.* When single character systems do provide unambiguous support for a hypothesis as illustrated by the quadrate complex for the tritheledontid-*Morganucodon* sister group relationship, they should not be used alone as the final arbiter in a phylogenetic controversy. Ideally, acceptance or rejection of any phylogenetic hypothesis should be based on as many characters as possible.

ORIGIN OF THE MAMMALIAN MIDDLE EAR

The middle ear of modern mammals shows the following apomorphies that are absent in the middle ear of non-mammalian cynodonts. 1) The quadrate (incus) is much more mobile relative to the cranium. 2) The quadrate (incus) no longer bears the occlusal force from masticatory movement of the mandible (Bramble, 1978; Crompton and Hylander, 1986, Crompton, 1989). 3) A new stapedial process has become a part of the ossicle lever system, resulting in improvement of the volume–velocity of the inner ear (Durrant and Lovrinic, 1984). 4) The quadrate–articular joint is immobilized to transmit vibrations of the tympanic membrane to the stapes (Hopson, 1966; Fleischer, 1978). 5) The postdentary bones are detached from the mandible in adults so that the tympanic membrane, suspended by the retroarticular process of the articular and reflected lamina of the angular, is less constrained (Allin, 1975, 1986; Kermack et al., 1981; Maier, 1990).

The phylogenetic transformation of the quadrate through the cynodont–mammal transition has a direct bearing on the first four of these features. Based on the phylogenetic framework in Fig. 1A, B, we argue that the following phylogenetic transformations of the quadrate (incus) played crucial roles in the evolutionary origin of the mammalian middle ear structure and the tympanic membrane (Fig. 18, Appendix 2): a progressive rotation of the dorsal plate (and the contact facet) relative to the axis of the trochlea; the contact facet of the dorsal plate becoming concave; the development of a neck between the contact facet and the trochlea; the evolution of the stapedial process; and the simplification of the quadrate-cranial articulation through a reduction in the number of bones involved in the articulation. The fewer bones involved in the quadrate–cranium junction, coupled with a reduction in size of the quadrate, decreases the total contacting surface area of the quadrate–cranium junction. All these transformations have resulted in a greater mobility of the quadrate–cranium articulation.

It has long been recognized that the quadrate–cranium articulation had some limited mobility in a wide range of therapsids (Hopson, 1966; Kemp, 1969, 1972a, b, 1979; Allin, 1975, 1986). Kemp (1969, 1972b, 1979) suggested that the primary function of the mobile quadrate–cranium joint in gorgonopsians, therocephalians, and *Procynosuchus* was to maintain the craniomandibular articulation during the opening of the lower jaw. In the meantime, a mobile joint would also be capable of transmitting vibrations from the postdentary tympanic membrane to the stapes (Allin, 1975, 1986; Kemp, 1979). Kemp (1972a, b) suggested that, in therocephalians, the quadrate rotated around the ball in socket joint formed by the concave recess on the medial margin of the quadrate dorsal plate and the distal end of the paroccipital process of the opisthotic (petrosal). In *Procynosuchus,* a fulcrum was formed by the articulation between the medial margin of the dorsal plate, and the quadrate ramus of the pterygoid plus the lateral flange of the prootic (petrosal). The quadrate could move relative to the cranium, albeit very limitedly, around this point (Kemp, 1979).

Similar movement of the quadrate could also occur in *Thrinaxodon* (Fig. 19A). However, given the complexity of the quadrate–cranium articulation in *Thrinaxodon,* such a movement was, at best, very limited and complicated. Five cranial bones (excluding the stapes) participated in the articulation of the quadrate: the quadrate ramus of the pterygoid and the lateral flange of the prootic contacted the medial margin of the quadrate, the paroccipital process of the opisthotic and the squamosal articulated with the posterior contact facet of the quadrate, and the quadratojugal articulated with the lateral notch of the quadrate (Fig. 19A). If the quadrate could move because its articulation to other cranial bones was loose enough, such a movement was very much constrained. The contact facet of the quadrate is essentially flat to slightly convex, corresponding to the flat to slightly concave quadrate recess on the squamosal. Some translational movement by the quadrate could occur along the plane of contact. The articulation of the medial margin of the quadrate to the quadrate ramus of the pterygoid and the lateral

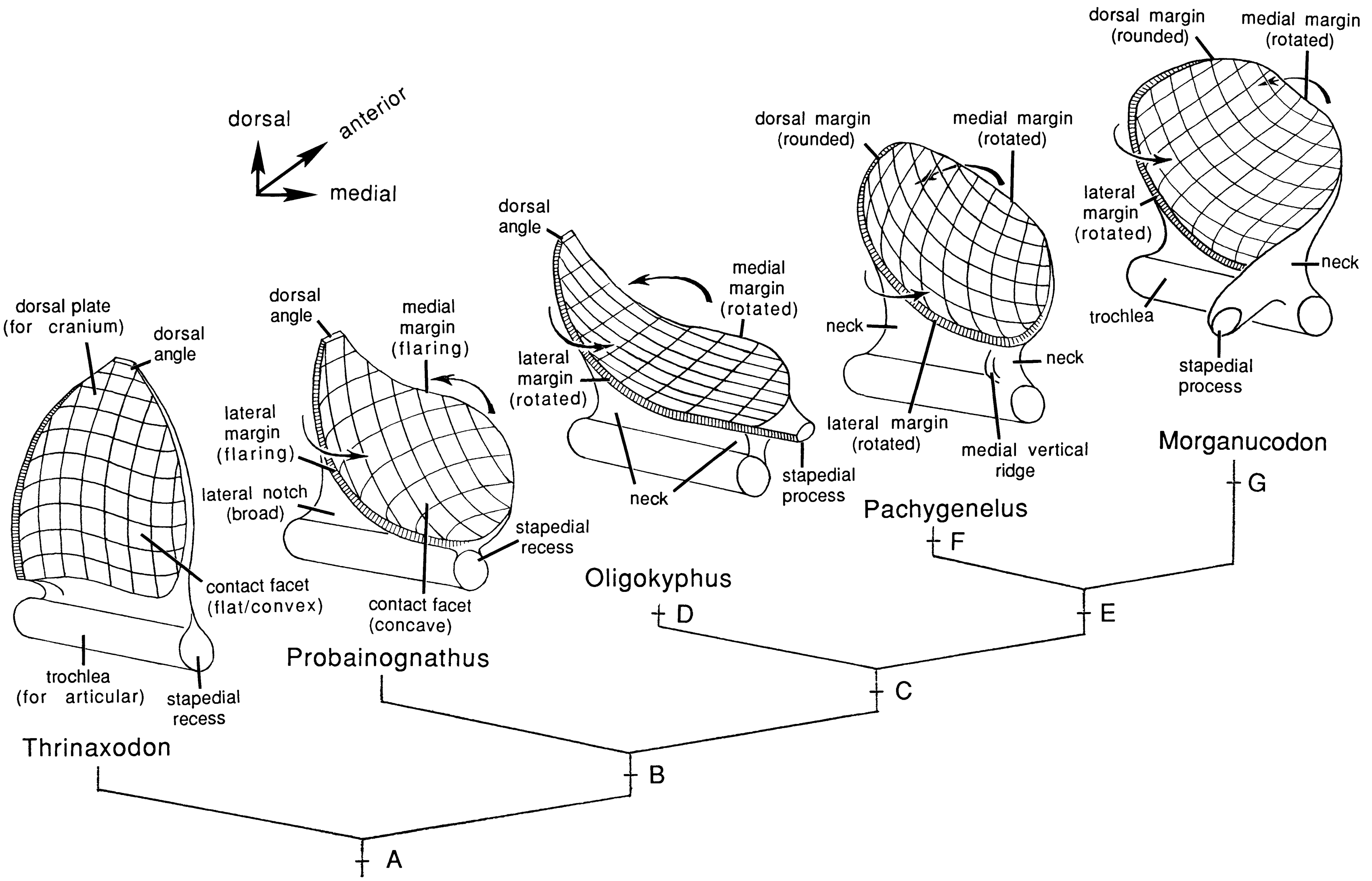


FIGURE 18. Transformation of the quadrate (incus) through the cynodont–mammal transition. See Appendix 2 for the list of the apomorphies at nodes A, B, C, D, E, F, and G. The cladogram is based on the strict consensus tree in Fig. 1A generated from Table 1.

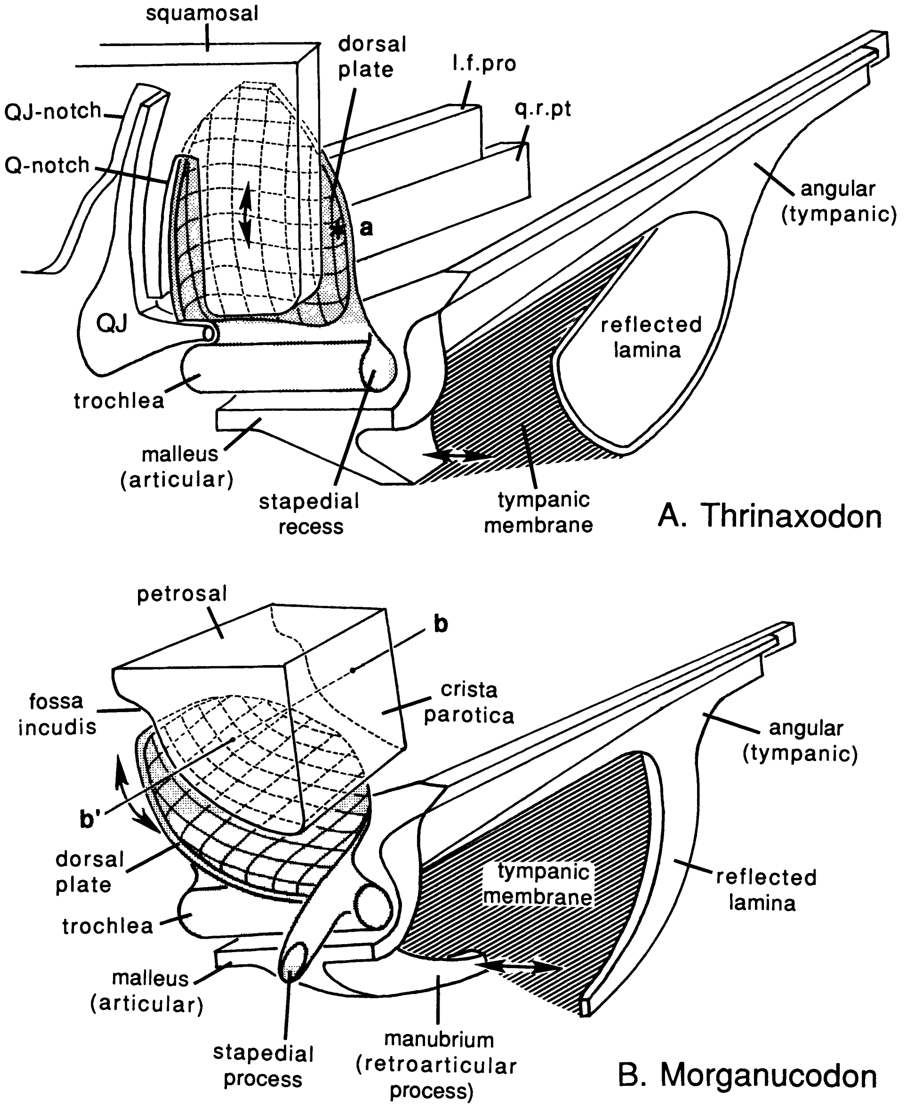


FIGURE 19. Transformation of the quadrate–cranium articulation through the cynodont–mammal transition. **A**, *Thrinaxodon* (as a representative of non-mammalian cynodonts). **B**, *Morganucodon* (as a representative of primitive mammals). In *Thrinaxodon,* to transmit the vibration of the postdentary tympanum, the quadrate would both translate along the surface of the posterior contact facet and rotate round the fulcrum formed by the lateral flange (of the petrosal), the paroccipital process (of the petrosal) and the quadrate ramus (of the pterygoid). The paroccipital process is not illustrated but its articulation is indicated by * a. The complex articulation of the quadrate to the cranium would limit the range of possible movement of the quadrate. In *Morganucodon,* the quadrate is only supported by the anterior paroccipital process (the crista parotica plus the fossa incudis); no other cranial bones articulate with the quadrate. The quadrate–petrosal joint would be a simple hinge joint in which the quadrate would rotate around axis bb′. The putative tympanic membrane is in hatched lines. Abbreviations: **l.f.pro**, lateral flange of the prootic; **Q-notch**, quadrate notch in the squamosal; **QJ-notch**, quadratojugal notch in the squamosal; **q.r.pt**, quadrate ramus of the pterygoid. Arrows indicate movement of the quadrate and the tympanic membrane.

flange of the prootic (q.r.pt and l.f.pro, Figs. 3, 19A) could function as a fulcrum (*a, Fig. 19A). The quadrate would rotate around the fulcral joint on its medial margin while translating along the posterior contact facet of the dorsal plate.

By contrast, the quadrate–cranium articulation of *Morganucodon* is greatly simplified and there is a much smaller contact between the quadrate and the cranium (Fig. 19B). First of all, fewer cranial bones articulate with the incus (quadrate). The anterior paroccipital process of the petrosal is the only cranial structure that articulates with the quadrate other than the stapes. In the skull specimens of *Morganucodon* which have preserved the incus (quadrate) in situ, the incus has no articulation with the squamosal, the lateral flange of the petrosal, the pterygoid, or the epipterygoid. There is no evidence for the presence of a quadratojugal: it is altogether absent in specimens with a well preserved craniomandibular joint, and it has not been found in association with any isolated squamosal or quadrate. Secondly, the geometry of the quadrate–cranium joint is drastically simplified. The joint is essentially a longitudinal "tongue-in-groove" hinge between the trough-like contact facet of the quadrate and the crest of the anterior paroccipital process (crista parotica). The contact facet of the dorsal plate faces posteriorly in primitive non-mammalian cynodonts (Fig. 19A); but the progressive rotation of the dorsal plate relative to the trochlea has caused the contact facet to be re-oriented and to face medially in *Morganucodon* (Fig. 19B). By reducing the number of bones participating in the quadrate–cranium articulation and simplifying the geometry of articulation, a simple hinge joint was formed in *Morganucodon.* In this simplified joint, the primary movement of the quadrate (incus) was to rotate around a roughly longitudinal axis formed by the crista parotica of the anterior paroccipital process. By comparison to the complicated quadrate–cranium articulation in *Thrinaxodon,* these changes in *Morganucodon* have greatly simplified the mechanical function of the quadrate–cranium joint.

A decrease in the contact surface area between the quadrate and other cranial bones will result in a decrease in the friction and an increase in the mobility of the quadrate–cranium articulation. The size of the quadrate in *Morganucodon* is much smaller than the quadrate in any known non-mammalian cynodont in both absolute and relative terms. *Morganucodon* is a much smaller animal than any non-mammalian cynodont. The size of its quadrate relative to the size of the skull is also smaller: the ratio of the transverse length of the trochlea to the length of the mandible in *Morganucodon* is only about half that of *Probainognathus,* and less than half that of *Thrinaxodon* (Crompton and Hylander, 1986). The great decrease in the size of the quadrate, coupled with morphological simplification of the quadrate–cranium articulation, would permit greater mobility of the quadrate (incus) than otherwise possible, thus improving the transmission of vibrations from the postdentary tympanic membrane to the stapes.

Because the quadrate is a part of the craniomandibular joint, the increased mobility of the quadrate–cranium joint would sacrifice the function of the quadrate to bear the occlusal force from the mandible during mastication and reduce the strength of the craniomandibular joint. The weakness of a simpler, smaller, and more mobile quadrate–cranium articulation would be compensated for in two ways: 1) Reducing the loading on the craniomandibular joint through reorganization of the mandibular adductor musculature, in correlation with progressive enlargement of the dentary and changing skull proportions in advanced cynodonts (Crompton, 1963, 1989; Crompton and Parker, 1978; Crompton and Hylander, 1986; Bramble, 1978). 2) Establishment of an additional surangular–squamosal articulation to divert the loading on the quadrate; this articulation is later replaced by an even stronger dentary–squamosal articulation (Crompton, 1972a). The reduction of the loading on the quadrate by both the reorganization of the adductor musculature and the additional squamosal articulation with the surangular and dentary would allow for further loosening of the quadrate from the cranium.

In the carnivorous *Probainognathus* (Crompton and Hylander, 1986), to compensate for loading on the craniomandibular joint from the powerful bite in the incisor–canine region, the anterior temporalis muscle and the deep masseter muscle were oriented obliquely and backwards, and the posterior temporalis oriented posteroventrally; thus the actual loading on the craniomandibular joint was minimized. In herbivorous tritylodontids, the loading on the articular–quadrate and quadrate–cranium joints resulting from postcanine mastication was considerably reduced by the resultant forces from a strong and anteriorly directed superficial masseter muscle, and from the more vertically oriented posterior temporalis and deep masseter muscles (Crompton and Hylander, 1986).

In *Probainognathus,* the surangular on the mandible articulates with an incipient glenoid fossa on the flange of the squamosal (Crompton, 1972a). This helps to divert the occlusal force which would be otherwise transmitted from the articular to the quadrate, and in turn, from the quadrate to the cranium. The articulation of the surangular with the flange of the squamosal is also present (although less developed) in diademodontids, traversodontids, *Probelesodon* and *Cynognathus.*

The Middle Triassic *Probainognathus* and *Massetognathus* are the earliest non-mammalian cynodonts in the fossil record that show the initial steps of several phylogenetic transformations of the quadrate. Establishment of the surangular–squamosal contact and the medial expansion of the squamosal are correlated with the concavity of the contact facet, and the initial rotation of the dorsal plate, both of which are crucial in transforming the quadrate and its articulation to the cranium (Fig. 7). The concave posterior face of the dorsal plate in *Probainognathus* and *Massetognathus* sets up the geometry of the quadrate (incus)–cranium joint in *Morganucodon.* The oblique orientation of the dorsal plate to the trochlea in *Probainognathus* represents an initial step toward greater rotation of the dorsal plate as seen among the non-mammalian cynodonts more closely related to *Morganucodon.* This led to a much more mobile longitudinal ("tongue-in-groove") hinge in *Morganucodon.*

In tritheledontids, the contact between the lateral ridge of the dentary and the squamosal was established (Crompton 1958, 1972a) in a manner comparable to that in *Sinoconodon* (Crompton and Luo, 1993; Luo, in press). In conjunction with the establishment of a dentary–squamosal articulation, the dorsal plate of the quadrate fitted loosely in the squamosal pocket. The dorsal plate is rotated over 90° relative to the trochlea and a well defined neck of the quadrate is present (Figs. 12, 15).

The fully developed dentary condyle and the squamosal glenoid in early mammals, such as *Morganucodon,* created a strong craniomandibular joint for load-bearing (Crompton, 1989; Crompton and Hylander, 1986). This condyle-glenoid joint completely relieves the articular–quadrate–petrosal articulation from disturbance caused by the occlusal force of the mandible. In the meantime, the size of the quadrate is greatly reduced, the articulation of the quadrate with the cranium is simplified, and the contact area between the quadrate and the cranium becomes much smaller. All these changes help to increase the mobility of this articulation and decrease the mass and rigidity of the middle ear ossicles.

The quadrate–petrosal joint of *Morganucodon* is most similar to that of *Ornithorhynchus* among extant mammals, in that the quadrate (incus) articulates directly to the petrosal (Fig. 13) (also see Luo, 1989; Crompton and Luo, 1993). In monotremes, the incus–petrosal joint fixes the rotational axis about which the malleus–incus complex rotates during sound transmission (Hopson, 1966; Aitkin and Johnstone, 1972; Gates et al., 1974). In extant therian mammals, the malleus–incus complex is suspended by several ligaments in the tympanic cavity. The incus not only rotates around an axis through the incudo–malleal joint and the ligaments (Kobrak, 1948; von Békésy, 1960), but also has translational movement (Guinan and Peake, 1967). Because the quadrate–cranium joint in *Morganucodon* fixes the rotation axis of the quadrate, it would be reasonable to assume that the quadrate rotated in much the same fashion as does the incus in *Ornithorhynchus.* The quadrate in *Morganucodon* probably lacked the translational movement that is present in the incus of extant therians during sound transmission.

The quadrate of *Morganucodon* has also developed the crus longum (stapedial process). Given rotational movement of the quadrate, the stapedial process would be necessary to increase the volume velocity of the stapes in addition to amplification of the pressure, thereby increasing the acoustic intensity of the middle ear (Durrant and Lovrinic, 1984).

We propose that the quadrate features crucial for transmitting the vibration of the tympanic membrane were introduced stepwise in the phylogenetic history of advanced synapsids. We also postulate that these mammalian quadrate (incus) structures of functional significance arose at several hierarchical levels in cynodont phylogeny prior to the origin of the Mammalia (Fig. 18; Appendix 2). The primitive morphotype of the cynodont quadrate is represented by *Procynosuchus* and *Thrinaxodon* (Node A of Fig. 18). It consists of the trochlea and a dorsal plate set at a small angle to the axis of the trochlea. Its nearly flat contact facet is continuous with the trochlea in both these taxa. In the most recent common ancestor of *Probainognathus, Massetognathus,* tritylodontids, tritheledontids, and mammals (Node B, Fig. 18 and Appendix 2), the contact facet becomes concave and the dorsal plate has begun to rotate relative to the axis of the trochlea by up to 45°; the lateral margin of the contact facet is partially lifted and separated from the trochlea by a deeper and broader lateral notch. In the common ancestor of tritylodontids, tritheledontids, and mammals (Node C, Fig. 18 and Appendix 2), the dorsal plate is further rotated. The margins of the contact facet are completely lifted from the trochlea by the constricted neck between the contact facet and the trochlea. In the common ancestor of tritheledontids and early mammals (Node E, Fig. 18 and Appendix 2), the dorsal plate has achieved the shape and orientation of the dorsal plate of the mammalian incus, as well as increased mobility of its joint with the cranium. *Morganucodon,* which represents the condition of the earliest known mammals, has developed a stapedial process from the neck region of the quadrate to articulate with the stapes. Otherwise it has done nothing more than reduce the size of the basic design inherited from the ancestor it shares with tritheledontids.

ORIGIN OF THE MAMMALIAN TYMPANIC MEMBRANE

Two alternative hypotheses on the origin of the mammalian tympanic membrane have been advanced. The postquadrate hypothesis postulates that the mammalian tympanic membrane was derived from a postquadrate tympanum in non-mammalian cynodonts, not unlike that of a modern lizard (Westoll, 1943, 1945; Parrington, 1949; Watson, 1953; Hopson, 1966). In cynodonts, the hypothetical precursor to the mammalian tympanic membrane was suspended posterior to the quadrate and at the end of a deep groove of the squamosal (eam?, Figs. 3, 5 and 8). In extant mammals, this membrane shifted to attach to the manubrium (retroarticular process) and ectotympanic (angular) (Hopson, 1966; Parrington, 1979). The postdentary hypothesis suggests that the mammalian tympanic membrane was derived from a precursor membrane in the mandible supported by the reflected lamina of the angular and the retroarticular process of the articular in cynodonts (Tomarkin, 1955; Allin, 1975). This tympanic membrane moved into the basicranium in extant mammals as the postdentary bones suspending the membrane became detached from the dentary.

We believe that the new information on the evolution of the quadrate among advanced non-mammalian cynodonts and *Morganucodon* favors the postdentary hypothesis. We postulate that the evolution of the postdentary tympanic membrane went through an intermediate stage in which a mobile quadrate–cranium joint was developed while the tympanic membrane continued to function on the mandible. While the mobility of the quadrate–petrosal articulation was improved, the postdentary bones from which the membrane was suspended became more gracile, and eventually were detached from the dentary. This scenario on the functional evolution of the tympanic membrane is plausible because it involves no shift in the attachment of the tympanic membrane.

If a postdentary tympanic membrane was present in advanced non-mammalian cynodonts and *Morganucodon,* it would have been suspended by the articular and the angular in a vertical plane through the cynodont-mammal transition (Allin, 1975; Maier, 1990). However, the basicranial bones underwent drastic changes and several cranial bones lost their articulation with the quadrate through this transition. The transversely oriented squamosal–quadrate joint of *Thrinaxodon* (Fig. 19A) was transformed into a nearly longitudinal hinge joint formed by the quadrate and the petrosal in *Morganucodon* (Fig. 19B). In response to the broad structural changes in the basicranium, especially the squamosal and petrosal, the dorsal plate of the quadrate rotated relative to the trochlea while the trochlea maintained articulation with the mandible. The rotation of the dorsal plate made it possible for major structural changes to occur at the quadrate–cranium joint while a functioning postdentary tympanic membrane was maintained in the mandible.

The rotation of the dorsal plate relative to the trochlea made it possible to achieve better mobility in the quadrate–cranium joint without disrupting the function of the tympanic membrane to receive air-borne sound while the membrane was still suspended vertically by the postdentary bones. The greater mobility of the quadrate–cranium joint would improve transmission of the air-borne sound by the postdentary tympanic membrane before the postdentary bones were detached from the mandible. Thus no shift of attachment of the tympanic membrane is required to improve the efficiency of sound transmission. Once the mobility of the quadrate–petrosal articulation was achieved, only minimal changes would be necessary to develop the basicranial tympanic membrane of extant monotremes and therians. The postdentary bones suspending the "precursor" tympanic membrane became more gracile. Eventually they detached from the mandible to migrate to the basicranium together with the tympanic membrane.

The phylogenetic transformations of the quadrate established here do not favor the postquadrate hypothesis. The rotation of the dorsal plate of the quadrate and the shift of the articulation of the quadrate from the squamosal to the petrosal would require that the hypothetical postquadrate tympanic membrane be first detached from the squamosal and the quadrate, and then re-attached to the angular and the articular. This would be far more disruptive than the incremental change postulated by the postdentary hypothesis. Presley (1984) shows that there is no embryological evidence for the homology of the postquadrate tympanic membrane of lizards to the tympanic membrane of mammals. Furthermore, the hypothesis is weakened because a postquadrate tympanic membrane would be too small for effective transmission of air-borne sound (Allin, 1975, 1986; Kermack et al., 1981; Kermack and Mussett, 1983; Rosowski and Graybeal, 1991; Rosowki, 1992).

SUMMARY AND CONCLUSIONS

1) The phylogenetic transformation of the quadrate (incus) in *Thrinaxodon, Probainognathus, Massetognathus,* tritylodontids, *Pachygenelus,* and *Morganucodon* is characterized by changes in several features: a progressively greater rotation of the dorsal plate relative to the trochlea in the clades more closely related to mammals; the contact facet of the quadrate becoming concave in *Probainognathus* and the clades closer to mammals; the development of a constricted neck among tritylodontids, tritheledontids and *Morganucodon;* the development of the stapedial process in *Morganucodon.*

2) The phylogenetic transformation of the quadrate–cranium articulation is characterized by a decrease in the number of cranial bones articulating with the quadrate, a decrease in the area of contact between the quadrate and the cranium because of the progressively smaller size of the quadrate, and changes in the geometry of the articulating facets of the quadrate–cranium joint. These changes have greatly simplified the quadrate–cranium articulation and increased its mobility. The transformation of the quadrate–cranium articulation in non-mammalian cynodonts led to a simple tongue-in-groove hinge joint in *Morganucodon* formed by the concave contact facet of the quadrate and the crest of the crista parotica of the petrosal.

3) All features of the quadrate (incus) of *Morganucodon* have broad phylogenetic distributions among non-mammalian cynodonts. Distribution of the quadrate (incus) characters among the non-mammalian cynodont clades closely related to mammals favors the sister-group relationship of tritheledontids and mammals over the sister-group relationship of tritylodontids and mammals.

4) The rotation of the dorsal plate of the quadrate played a crucial role in the evolution of the mammalian middle ear structure because it allowed drastic modification of the quadrate–cranium joint without disrupting the tympanic membrane suspended by the postdentary bones in the mandible. Thus this putative tympanic membrane could continue functioning as an air-borne sound receiver during the transformation of the quadrate–cranium joint. This suggests that evolution of the mammalian tympanic membrane passed through an intermediate stage in which a mobile incus–petrosal joint was achieved before the postdentary bones suspending the precursor tympanic membrane were detached from the mandible. This establishes a plausible scenario of functional evolution for the postdentary origin of the mammalian tympanic membrane.

ACKNOWLEDGMENTS

We are very grateful that Professor Sun Ailin and Mr. Cui Guihai of the Institute of Vertebrate Paleontology, Academia Sinica, Beijing have graciously allow us to study the specimens of *Sinoconodon, Morganucodon,* and tritylodontids. We are deeply indebted to Professor Farish A. Jenkins, Jr. for access to the materials of *Kayentatherium, Dinnetherium* and the Cloverly Formation triconodontid. In the course of this study we benefitted from discussion with Drs. E. F. Allin, J. A. Hopson, H.-D. Sues, T. Rowe, J. Rosowski, and W. T. Peake. Drs. Allin, Hopson, Rowe, and Sues shared with us their unpublished information. We thank Drs. Allin, Rowe, and Sues for their critical comments and suggestions for improvement on an earlier version of this paper. We also acknowledge the help of W. W. Amaral, who prepared many specimens used in the study; and C. Schaff, who provided assistance with the comparative collection. Mr. L. L. Meszoly and Dr. E. F. Allin helped with two illustrations. The research is supported by NSF grants BSR 8818098 and BSR 9020034 to A. W. Crompton, and the faculty research funds from the College of Charleston to Z. Luo.

LITERATURE CITED

Aitkin, L. M., and B. M. Johnstone. 1972. Middle ear function in a monotreme: the echidna (*Tachyglossus aculeatus*). Journal of Experimental Zoology 180:245–250.

Allin, E. F. 1975. Evolution of the mammalian middle ear. Journal of Morphology 147:303–437.

——— 1986. The auditory apparatus of advanced mammal-like reptiles and early mammals; pp. 283–294 *in* N. Hotton, III, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), The Ecology and Biology of Mammal-like Reptiles. Smithsonian Institution Press, Washington, D. C.

——— and J. A. Hopson. 1992. Evolution of the auditory system in Synapsida ("mammal-like reptiles" and primitive mammals) as seen in the fossil record; pp. 587–614 *in* D. B. Webster, R. R. Fay, and A. N. Popper (eds.), The Evolutionary Biology of Hearing. Springer-Verlag, New York.

Bramble, D. M. 1978. Origin of the mammalian feeding complex: models and mechanisms. Paleobiology 4:271–301.

Brink, A. S. 1963a. On *Bauria cynops* Broom. Palaeontologia Africana 8:39–56.

——— 1963b. A new skull of the procynosuchid *Leavachia duvenhagei* Broom. Palaeontologia Africana 8:57–75.

Brinkman, D. 1981. The structure and relationships of the dromasaurs (Reptilia, Therapsida). Breviora 465:1–34.

Broom, R. 1936. On the structure of the skull in the mammal-like reptiles of the suborder Therocephalia. Philosophical Transactions of the Royal Society of London B, 226:1–41.

Camp, C. L. 1956. Triassic dicynodont reptiles. Part II. Triassic dicynodonts compared. Memoirs of the University of California 13:305–341.

Clark, J. M., and J. A. Hopson. 1985. Distinctive mammal-like reptile from Mexico and its bearings on the phylogeny of Tritylodontidae. Nature 315:398–400.

Crompton, A. W. 1955. A revision of the Scaloposauridae with special reference to kinetism in this family. Researches of Nasionale Museum (South Africa: Bloemfontein) 1:149–181.

——— 1958. The cranial morphology of a new genus and species of ictidosaurian. Proceedings of the Zoological Society of London 130:183–216.

——— 1963. On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. Proceedings of the Zoological Society of London 140:697–750.

——— 1964. On the skull of *Oligokyphus*. Bulletin of the British Museum of Natural History (Geology) 9:69–82.

——— 1972a. The evolution of the jaw articulation of cynodonts; pp. 231–253 *in* K. A. Joysey and T. S. Kemp (eds.), Studies in Vertebrate Evolution. Oliver and Boyd, Edinburgh.

——— 1972b. Postcanine occlusion in cynodonts and tritylodontids. Bulletin of the British Museum of Natural History (Geology) 21:29–71.

——— 1989. The evolution of mammalian mastication; pp. 23–40 *in* D. B. Wake and G. Roth (eds.), Complex Organismal Function: Integration and Evolution in Vertebrates. John Wiley & Sons Ltd, New York and London.

——— and N. Hotton, III. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). Postilla 109:1–51.

——— and W. L. Hylander. 1986. Changes in mandibular function following the acquisition of a dentary-squamosal jaw articulation; pp. 263–282 *in* N. Hotton III, P. D. MacLean, J. J. Roth and E. C. Roth (eds.), The Ecology and Biology of Mammal-like Reptiles. Smithsonian Institution Press, Washington, D. C.

——— and F. A. Jenkins, Jr. 1979. Origin of mammals; pp. 59–72 *in* J. A. Lillegraven, Z. Kielan-Jaworowska and W. A. Clemens (eds.), Mesozoic Mammals: The First Two-thirds of Mammalian History. University of California Press, Berkeley.

——— and Z. Luo. 1993. The relationships of Liassic mammals *Sinoconodon, Morganucodon oehleri* and *Dinnetherium;* pp. 30–44 *in* F. S. Szalay, M. J. Novacek, and M. C. McKenna, (eds.), Mammal Phylogeny. Springer-Verlag, New York.

——— and P. Parker. 1978. Evolution of the mammalian masticatory apparatus. American Scientist 66:192–201.

——— and A. L. Sun. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon.* Zoological Journal of the Linnean Society (London) 85:99–119.

Cui, G. 1976. *Yunnania* a new tritylodontid from Lufeng, Yunnan. Vertebrata PalAsiatica 25:1–7.

——— 1986. *Yunnanodon,* a replacement name for *Yunnania* Cui, 1976. Vertebrata PalAsiatica 24:9.

Durrant, J. D., and J. H. Lovrinic. 1984. Bases of Hearing Science, 2nd ed. Williams and Wilkins, Baltimore and London, 276 pp.

Eldredge, N., and J. Cracraft. 1980. Phylogenetic Patterns and the Evolutionary Process: Method and Theory in Comparative Biology. Columbia University Press, New York, 349 pp.

Farris, J. S. 1982. Outgroups and parsimony. Systematic Zoology 31:328–334.

Filan, S. L. 1991. Development of the middle ear region in *Monodelphis domestica* (Marsupialia, Didelphidae): marsupial solution to an early birth. Journal of Zoology (London) 225:577–588.

Fleischer, G. 1978. Evolutionary principles of the mammalian middle ear. Advancement in Anatomy, Embryology and Cell Biology 55:3–70.

Fourie, S. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. Annals of the South African Museum 56:337–400.

Gates, G. R., J. C. Saunders, G. R. Bock, L. M. Aitkin, and M. A. Elliott. 1974. Peripheral auditory function in the platypus, *Ornithorhynchus anatinus.* Journal of the Acoustical Society of America 56:152–156.

Gaupp, E. 1913. Die Reichertsche Theorie (Hammer-, Amboss- und Kieferfrage). Archiv für Anatomie und Entwicklungsgeschichte. 1912:1–416.

Gauthier, J. A., A. G. Kluge, and T. Rowe. 1988. Amniote phylogeny and the importance of fossils. Cladistics 4:105–209.

Goodrich, E. S. 1916. The Chorda tympani and middle ear of reptiles, birds and mammals. Quarterly Journal of Microscopic Science 61:137–160.

Guinan, J. J., and W. T. Peake. 1967. Middle-ear characteristics of anesthetized cats. Journal of the Acoustical Society of America 41:1237–1261.

Hopson, J. A. 1965. Tritylodontid therapsids from Yunnan and the cranial morphology of *Bienotherium.* Unpublished Ph.D. dissertation, University of Chicago.

——— 1966. The origin of the mammalian middle ear. American Zoologist 6:437–450.

——— 1991. Systematics of nonmammalian Synapsida and implications for patterns of evolution in synapsids; pp. 635–693 *in* H.-P. Schultze and L. Trueb (eds.), Origins of the Higher Groups of Tetrapods—Controversy and Consensus. Cornell University Press, Ithaca.

——— and H. R. Barghusen. 1986. An analysis of therapsid relationships; pp. 83–106 *in* N. Hotton III, P. D. MacLean, J. J. Roth, and E. C. Roth (eds.), The Ecology and Biology of Mammal-like Reptiles. Smithsonian Institution Press, Washington, D. C.

——— and J. W. Kitching. 1972. A revised classification of cynodonts (Reptilia, Therapsida). Palaeontologia Africana 14:71–85.

Jenkins, F. A., Jr., A. W. Crompton, and W. R. Downs. 1983. Mesozoic mammals from Arizona: new evidence on mammalian evolution. Science 222:1233–1235.

Kemp, T. S. 1969. On the functional morphology of the gorgonopsid skull. Philosophical Transactions of the Royal Society of London B, 256:1–83.

——— 1972a. Whaitsiid Therocephalia and the origin of cynodonts. Philosophical Transactions of the Royal Society of London B, 264:1–54.

——— 1972b. The jaw articulation and whaitsiid Therocephalia; pp. 213–230 *in* K. A. Joysey and T. S. Kemp (eds.), Studies in Vertebrate Evolution. Oliver and Boyd, Edinburgh.

——— 1979. The primitive cynodont *Procynosuchus:* functional anatomy of the skull and relationships. Philosophical Transactions of the Royal Society of London B, 285:73–122.

——— 1982. Mammal-like Reptiles and the Origin of Mammals. Academic Press, London, 363 pp.

——— 1983. The interrelationships of mammals. Zoological Journal of the Linnean Society 77:353–384.

——— 1988. Interrelationships of the Synapsida; pp. 1–23 *in* M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals. Systematics Association Special Volume 35B. Oxford University Press, New York.

Kermack, K. A., and F. Mussett. 1983. The ear in mammal-like reptiles and early mammals. Acta Palaeontologia Polonica 28:148–158.

———, ——— and H. W. Rigney. 1973. The lower jaw of *Morganucodon.* Zoological Journal of the Linnean Society (London) 53:87–158.

———, ——— and ——— 1981. The skull of *Morganucodon.* Zoological Journal of the Linnean Society (London) 71:1–158.

Kobrak, H. G. 1948. Construction material of the sound conduction system of the human ear. Journal of the Acoustical Society of America 20:125–130.

Kuhn, H.-J. 1971. Die Entwichlung und Morphologie des Schädel von *Tachyglossus aculeatus.* Abhandlungen der Senchbergischen Naturforschenden Gesellschaft, Frankfurt am Main 528:1–224.

Kühne, W. G. 1956. The Liassic Therapsid *Oligokyphus.* British Museum (Natural History), London, 149 pp.

Luo, Z. 1989. The petrosal structures of Multituberculata (Mammalia) and the molar morphology of early Arctocyonidae (Condylarthra, Mammalia). Unpublished Ph.D. dissertation, University of California, Berkeley, 426 pp.

——— In press. Sister taxon relationships of mammals and transformations of diagnostic mammalian characters; *in* N. C. Fraser and H.-D. Sues (eds.), In the Shadow of Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge and New York.

Maddison, W. P., M. J. Donaghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. Systematic Zoology 33:83–103.

——— and D. R. Maddison. 1992. MacClade Program (Version 3.0). Sinaurs and Associates, Sutherland, Massachussetts.

Maier, W. 1990. Phylogeny and ontogeny of mammalian middle ear structures. Netherland Journal of Zoology 40:55–75.

McClain, J. A. 1939. The development of the auditory ossicles of the opossum (*Didelphys virginiana*). Journal of Morphology 64:211–265.

Mendrez, C. H. 1972. On the skull of *Regisaurus jacobi,* a new genus and species of Bauriamorpha Watson and Romer 1956 (=*Scaloposauria* Boonstra 1953), from the *Lystrosaurus*-zone of South Africa; pp. 191–212 *in* K. A. Joysey and T. S. Kemp (eds.), Studies in Vertebrate Evolution. Oliver and Boyd, Edinburgh.

Miao, D. 1988. Skull morphology of *Lambdopsalis bulla* (Mammalia, Multituberculata) and its implications to mammalian evolution. Contributions to Geology, University of Wyoming, Special Papers 4:1–104.

——— and J. A. Lillegraven. 1986. Discovery of three ear ossicles in a multituberculate mammal. National Geographic Research 2:500–507.

Olson, E. C. 1944. Origin of mammals based upon cranial morphology of the therapsid suborders. Special Papers, Geological Society of America 55:1–136.

Parrington, F. R. 1946. On the cranial anatomy of cynodonts. Proceedings of the Zoological Society of London 116:181–197.

——— 1949. Remarks on a theory of evolution of the tetrapod middle ear. Journal of Laryngology and Otology 63:580–595.

——— 1955. On the cranial anatomy of some gorgonopsids and the synapsid middle ear. Proceedings of the Zoological Society of London 125:1–40.

——— 1979. The evolution of the mammalian middle and outer ears: a personal review. Biological Reviews 54: 369–387.

Presley, R. 1984. Lizards, mammals and the primitive tetrapod tympanic membrane. Zoological Symposium (Zoological Society of London) 52:127–152.

Reichert, C. 1837. Über die Visceralbogen der Wirbeltiere in Allgemeinen und deren Metamorphosen bei den Vögeln und Säugetiereen. Archiv für Anatomie, Physiologie und Wissentschaftlische Medicin 1837:120–220.

Romer, A. S. 1956. The Osteology of Reptiles. The University of Chicago Press, Chicago, 772 pp.

——— 1967. The Chañares (Argentina) Triassic reptile faunas. III. Two new gomphodonts, *Massetognathus pascuali* and *M. teruggii.* Breviora 264:1–25.

——— 1970. The Chañares (Argentina) Triassic reptile fauna. VI. A chiniquodontid cynodont with incipient squamosal jaw articulation. Breviora 407:1–18.

——— and L. W. Price. 1940. Review of the Pelycosauria. Geological Society of America, Special Papers 28:1–538.

Rosowski, J. J. 1992. Hearing in transitional mammals: predictions from the middle-ear anatomy and hearing capabilities of extant mammals; pp. 615–631 *in* D. B. Webster, R. R. Fay, and A. N. Popper (eds.), The Evolutionary Biology of Hearing. Springer-Verlag, New York.

——— and A. Graybeal. 1991. What did *Morganucodon* hear? Zoological Journal of the Linnean Society (London) 101:131–168.

Rougier, G. W., J. R. Wible, and J. A. Hopson. 1992. Reconstruction of the cranial vessels in the Early Cretaceous mammal *Vincelestes neuquenianus:* implications for the evolution of the mammalian cranial vascular system. Journal of Vertebrate Paleontology 12:188–216.

Rowe, T. 1986. Osteological diagnosis of Mammalia (Linné 1758) and its relationship to extinct Synapsida. Unpublished Ph.D. dissertation, University of California, Berkeley.

——— 1988. Definition, diagnosis and origin of Mammalia. Journal of Vertebrate Paleontology 8:241–264.

——— 1993. Phylogenetic systematics and the early history of mammals; pp. 129–145 *in* F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), Mammal Phylogeny. Springer-Verlag, New York.

Sues, H.-D. 1985. The relationships of the Tritylodontidae (Synapsida). Zoological Journal of the Linnean Society (London) 85:205–217.

——— 1986a. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of Western North America. Bulletin of the Museum of Comparative Zoology 151:217–268.

——— 1986b. Relationships and biostratigraphic significance of the Tritylodontidae (Synapsida) from the Kayenta Formation of northeastern Arizona; pp. 279–284 *in* K. Padian (ed.), The Beginning of the Age of Dinosaurs. Cambridge University Press, London.

Sun, A. L. 1984. *Bienotheriodes.* Scientia Sinica (Series B) 27:970–984.

——— and G. H. Cui. 1989. Tritylodont reptile from Xinjiang. Vertebrata PalAsiatica 27:1–8.

Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony (Version 3.1.1). Privately distributed by Illinois Natural History Survey, Champaign, Illinois.

Tomarkin, A. 1955. On the evolution of the auditory conducting apparatus: a new theory based on functional considerations. Evolution 9:221–242.

von Békésy, G. 1960. Experiments in Hearing. McGraw-Hill, New York, pp. 745.

Watson, D. M. S. 1953. The evolution of the mammalian ear. Evolution 7:159–177.

Westoll, T. S. 1943. The hyomandibular of *Eusthenopteron* and the tetrapod middle ear. Proceedings of the Royal Society of London B, 131:393–414.

——— 1945. The mammalian middle ear. Nature 155: 114–115.

Wible, J. R. 1991. Origin of Mammalia: the craniodental evidence reexamined. Journal of Vertebrate Paleontology 11:1–28.

Wiley, E. O. 1981. Phylogenetics, the Theory and Practice of Phylogenetic Systematics. John Wiley and Sons, New York, 439 pp.

Zeller, U. 1989. Die Entwicklung und Morphologie des Schädels von *Ornithorhynchus anatinus* (Mammalia: Prototheria: Monotremata), Abhandlungen der Senchenbergischen Naturforschenden Gesellschaft, Frankfurt am Main. 545:1–188.

Received 7 July 1992; accepted 22, June 1993.

APPENDIX 1. List of the Characters of the Quadrate and the Quadrate Articulation in Table 1

Structure of the Quadrate (Incus)

1) Orientation of the dorsal plate relative to the trochlea: less than 10° rotation (0); oblique, with about 45° rotation (1); parallel (2); oblique, over 90° rotation (3).
2) Curvature of the contact facet on the posterior side of the dorsal plate: flat or nearly flat (0); convex (1); concave (2).
3) Size of the lateral trochlear condyle relative to the medial trochlear condyle: the lateral condyle larger than the medial condyle (0); the medial condyle larger than the lateral condyle (1).
4) Shape of the trochlea: cylindrical (0); trough-shaped (1).
5) Lateral margin of the dorsal plate: straight (0); flaring posteriorly (1); flaring and rotated posteromedially (2).
6) Medial margin of the dorsal plate: straight (0); flaring anteriorly (1); flaring and rotated anterolaterally (2).
7) Dorsal margin of the dorsal plate: with a pointed dorsal process ("dorsal angle") (0); rounded (1).
8) Lateral notch and neck (separation of the lateral margin of the contact facet from the trochlea): the lateral notch is absent or poorly developed (0); lateral notch developed, separating the lateral margin of the contact facet from the lateral end of the trochlea (1); lateral notch is broader and separation of the lateral margin of contact facet from the trochlea is wider, the lateral margin is shifted medially (2); development of the neck which raises the contact facet away from the trochlea (3).

Articulation of the Quadrate with Other Cranial Bones

9) Articulation of the quadratojugal with the lateral edge of the dorsal plate of the quadrate: the quadratojugal is abutting or sutured with the lateral edge of the dorsal plate (0); or separate from the lateral margin of the dorsal plate (1).
10) Articulation of the pterygoid to the medial margin of the quadrate: the quadrate ramus of the pterygoid

contacting the anterior face of the medial margin of the quadrate (0); the posterior end of the quadrate ramus of the pterygoid is laterally overlapped by the medial side of the quadrate (1); no articulation (2).

11) Articulation of the quadrate with quadrate ramus of the epipterygoid: absent (0); present, the ramus abutting the edge of the medial margin of the quadrate (1); present, the ramus contacting the anterior surface of the dorsal plate of the quadrate (2).
12) Articulation of the quadrate with the squamosal: via an anteriorly open and concave recess in the squamosal (0); the anteriorly open squamosal recess is absent (1); quadrate having little or no contact with the squamosal (2).
13) Articulation of the quadrate with the paroccipital process of the petrosal (opisthotic): small (0); totally absent (1); extensive, with a massive and rounded anterior paroccipital process of the petrosal (2); entirely by the petrosal, with well developed crista parotica and fossa incudis (3).
14) Articulation of the quadrate with the stapes: via a broad recess on the medial margin and the medial end of the trochlea (0); the stapedial contact restricted to the medial end of the trochlea (1); via a projection from the medial margin of the dorsal plate (2); via a medial vertical ridge in the neck (3); via a projection from the neck of the quadrate (4).

APPENDIX 2. List of the quadrate apomorphies of advanced non-mammalian cynodonts and *Morganucodon*

Node A. (*Thrinaxodon* (*Probainognathus* (*Oligokyphus* (*Pachygenelus, Morganucodon*)))): 1) Posterior flaring of the lateral margin (="posterior flange"); 2) Presence of a well defined lateral notch; 3) Stapedial recess confined to the medial end of the trochlea.

Node B. (*Probainognathus* (*Oligokyphus* (*Pachygenelus, Morganucodon*))): 1) Dorsal plate oriented obliquely, about 45° to the vertical plane that contains the trochlea; 2) Contact facet becoming concave; 3) Anterior flaring of the medial margin (also in gorgonopsians and therocephalians); 4) Lateral margin shifted medially so that the contact facet only borders on the trochlea near the medial end of the trochlea; 5) Lateral notch becomes wider and more pronounced; 6) Quadrate ramus of the pterygoid lost contact with the quadrate.

Node C. (*Oligokyphus* (*Pachygenelus, Morganucodon*)): 1) Rotation of the dorsal plate to the trochlea is greater than 45°; 2) Contact facet is completely separated from the trochlea by a constricted neck; 3) Quadrate ramus of the epipterygoid lost contact with the quadrate (also in *Massetognathus*); 4) Pterygo–paroccipital foramen open.

Node D. *Oligokyphus*: 1) Contact facet is parallel to the axis of the trochlea; 2) Presence of the stapedial process (the process projecting from the medial margin of the contact facet; also in *Morganucodon*); 3) Quadrate is primarily supported by the bulbous anterior paroccipital process of the petrosal (also in *Morganucodon*).

Node E. (*Pachygenelus, Morganucodon*): 1) Rotation of the dorsal plate to the trochlea is greater than 90°; 2) Rounded dorsal margin of the dorsal plate (=loss of the dorsal angle); 3) Medial trochlear condyle larger than the lateral trochlear condyle.

Node F. *Pachygenelus*: 1) Rotation of the dorsal plate to the trochlea is greater than 120°; 2) Vertical medial ridge on the neck.

Node G. *Morganucodon*: 1) Presence of the crus longum ("stapedial process" projecting from the neck, also in tritylodontids); 2) Tongue-in-groove articulation of the quadrate to the anterior paroccipital process of the petrosal.