The Postcranial Skeleton of *Kayentatherium wellesi* from the Lower Jurassic Kayenta Formation of Arizona and the Phylogenetic Significance of Postcranial Features in Tritylodontid Cynodonts

**Introduction**

The Tritylodontidae are a clade of derived, presumably herbivorous eucynodonts with a superficially somewhat rodent-like dentition, comprising enlarged, procumbent incisors and, separated from the latter by a prominent diastema, multi-cusped, multiple-rooted molariform teeth. They are currently known from the Lower and Middle Jurassic of Europe, the Lower Jurassic of western North America and southern Africa, the Lower or Middle Jurassic of Mexico, the Lower to Upper Jurassic of China and the Lower Cretaceous of Japan and Russia (Hopson & Kitching, 1972; Kemp, 1982; Kermack, 1982; Clark & Hopson, 1985; Sun & Li, 1985; Lewis, 1986; Sues, 1986a, b; Tatarinov & Matchenko, 1999; Matsuoka & Setoguchi, 2000). Initially considered basal mammals related to multituberculates (e.g., Simpson, 1928), the Tritylodontidae subsequently have been interpreted as derived gomphodont cynodonts by most authors (Watson, 1942; Young, 1947; Kühne, 1956; Crompton & Ellenberger, 1957; Crompton, 1972; Hopson & Kitching, 1972, 2001; Sues, 1985; Hopson & Barghusen, 1986; Hopson, 1991; Sidor & Hopson, 1998).

Kemp (1982, 1983) enumerated numerous derived characters in the postcranial skeleton shared by Tritylodontidae and Mammalia and proposed a sister-group relationship between these two groups. Sues (1985) argued that some of these features are also present in the traversodont eucynodont *Exaeretodon* from the Upper Triassic Ischigualasto Formation of northwestern Argentina. He followed Crompton (1972) in regarding Tritylodontidae and “Traversodontidae” as sister-taxis and suggested that tritylodontids are yet another example of the extensive parallelism among derived synapsids. Rowe (1988) attempted to reconcile these conflicting points of view by placing *Exaeretodon* as the sister-taxon of a clade containing Tritylodontidae and Mammaliaformes (= Mammalia *sensu* Luo et al., 2002), but he left the affinities of the other traversodonts unresolved. Hopson (1991, 697) cited *Exaeretodon* as providing “the best evidence for a relationship between tritylodontids and more primitive gom-
phodonts . . . [demonstrating] the likelihood that the mammal-like features of tritylodontids evolved independently of those of mammals within the gomphodont clade.” Wible (1991, 20), acknowledging that analyses of the craniodental evidence have provided no clear resolution to the controversy, observed that “overwhelming support for a Tritylodontidae/Mammaliaformes clade comes thus far from the postcranial skeleton.”

Mammalian features of the tritylodontid postcranial skeleton thus have been used as synapomorphies to support the hypothesis that Tritylodontidae are the sister-group of Mammalia, and alternatively have been interpreted as evidence for significant homoplasy in cynodont evolution.

Recent studies have not favored the view that tritylodontids and mammals are closely related. With the exception of similarities in the structure of the orbital wall, Luo (1994, 104) concluded that “support from other areas of the skull and dentition for the tritylodontid-mammal hypothesis is, at best, very weak and inconclusive.” A comprehensive cladistic analysis of Cynodontia by Hopson and Kitching (2001) hypothesized a dichotomy of eucynodonts into Probainognathia and Cynognathia, with Morganucodon nested in the former and Tritylodontidae in the latter. Interestingly, this analysis incorporated numerous postcranial features that, in studies by other authors, have been alleged to be mammal-like in tritylodontids. Hopson and Kitching (2001, 27) cited two Late Triassic cynodonts that are “very mammallike postcranially” as “critical evidence supporting the probainognathian-cynognathian dichotomy” (cf. Bonaparte & Barberena, 2001) “and the occurrence of a truly extraordinary amount of homoplasy in eucynodont evolution.”

Although the tritylodontid postcranial skeleton has been important to analyses of cynodont phylogeny, the available fossil evidence in fact has been rather limited. Aside from Kühne’s (1956) monographic study of Oligokyphus, little has been published to date on the postcranial skeleton of the Tritylodontidae. Kühne’s work was based on hundreds of dissociated skeletal remains from Early Jurassic fissure-fillings in southwestern England. A bimodal size distribution led Kühne to distinguish two species, Oligokyphus major and Oligokyphus minor, but the lack of skeletal association limits the utility of this material to comparisons of individual bones. Young (1947) described several limb bones referable to Bienotherium from the Lower Jurassic Lower Lufeng Formation of Yunnan (China). Fourie (1962) provided a brief account on the postcranial skeleton of Tritylodontoideus maximus (probably a subjective junior synonym of Tritylodon longaeus; Hopson & Kitching, 1972) from the Lower Jurassic Clarens Formation of South Africa; unfortunately, this
specimen is preserved only as a natural mold on two slabs of sandstone. Sun and Li (1985) reported on some postcranial remains of Bienotheroides wanhsienensis from the Middle or Upper Jurassic Shaximiao Formation of Sichuan (China). Winkler et al. (1991) commented on a partial postcranial skeleton of an indeterminate tritylodontid from the Lower Jurassic Navajo Sandstone of Arizona.

We present here a description of tritylodontid postcranial remains from the Lower Jurassic Kayenta Formation of northeastern Arizona, most notably a well-preserved partial skeleton of Kayentatherium wellesi Kermack, 1982 (including Nearctylodon broomi Lewis, 1986 as a subjective junior synonym; Sues, 1986a,b). Our intent is not only to place the structure of the postcranial axial and appendicular skeleton on record but also to explore the functional and phylogenetic inferences that may be drawn from the available material. We specifically review the issue of mammal-like features in the tritylodontid postcranial skeleton, an assessment that different authors have used to reach very different phylogenetic conclusions.

Sues et al. (1994) discussed the diversity, stratigraphic context, and distribution of the fossil vertebrates from the Kayenta Formation of northeastern Arizona, central and southern Utah. The first tritylodontid remains to be recovered from the Kayenta Formation were collected in the early 1950s from outcrops 2.5 to 3 m below the top of the formation (“typical facies”), just below the presumed contact with the overlying Navajo Sandstone, on Comb Ridge, 11.4 km airline, bearing 069° true, from Kayenta, Arizona (Lewis, 1986). The tritylodontid material described by Sues (1986a) and in this study was collected from exposures of the “silty facies” of the Kayenta Formation along the Adeii Eechii Cliffs on Ward Terrace, from the region of Dinnebito Wash to Tuba City, on lands of the Navajo Nation in northeastern Arizona.

The following institutional abbreviations are used: BMNH, The Natural History Museum [formerly British Museum (Natural History)], London; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA; MNA, Museum of Northern Arizona, Flagstaff; USNM, National Museum of Natural History (formerly United States National Museum), Washington, DC.

**Material**

The tritylodontid specimens that form the basis for this study were collected by joint field-parties from the Museum of Comparative Zoology and the Museum of Northern Arizona, led by F.A.J., Jr. between 1977 and
1982. Sues (1986a) provided a detailed anatomical account on the skull and dentition of two tritylodontid taxa, *Kayentatherium wellesi* and *Dine- nebitodon amarali*, and Sues (1986b) briefly reviewed the phylogenetic relationships and biostratigraphic significance of the tritylodontids from the Kayenta Formation.

The principal specimen used for the osteological description is MCZ 8812, a well-preserved partial skeleton of a large individual of *K. wellesi*, which includes the pectoral girdle and sternum, both forelimbs, and vertebral column (with most of the ribs in association) from the atlas-axis to the posterior dorsal region. The specimen was preserved lying on its left side, and the articular context of the bones was largely undisturbed. The posterior portion of the skeleton had already weathered out at the time of discovery, but screening of the talus below the site yielded pieces of the left ilium, several caudal centra, and unidentifiable fragments of bone. Additional postcranial material used in this study and referable to *K. wellesi* on the basis of associated dentitions comprises MCZ 8811 and MNA V3141, V3224, and V3235. MNA V3141 includes the glenoid regions of both scapulae, the right humerus, left ulna and radius, partial right manus, incomplete left femur, and the proximal ends of both tibiae. This material, which was collected as surface float, includes the distal end of a second right humerus and thus represents the intermingled remains of two individuals of similar body size. MNA V3224 and V3235 include fragmentary axial and appendicular elements. We tentatively refer several specimens to *K. wellesi* mainly on the basis of large size: MCZ 8832, 8835, and 8838. The ischium is based on a right element associated with a partial maxilla and dentary of *D. amarali* (MNA V3232). Most of the bones show signs of crushing and plastic distortion, limiting their utility for comparative purposes.

H.-D.S. has viewed the holotype of *Nearctylodon broomi* (USNM 317201; Lewis, 1986), a nearly complete articulated skeleton of a small, probably juvenile individual of *K. wellesi*, which is now on public display at the National Museum of Natural History (Washington, DC). The preliminary report by Lewis (1986) provided some details about the dentition of this and other specimens collected from the same quarry on Comb Ridge. This collection has yet to be fully described. These apparently immature tritylodontid skeletons, although useful for showing the overall body proportions of juveniles, are poorly preserved, and none appears to be fully ossified (Lewis, 1986, 299).

On several occasions both authors have examined the postcranial elements of *Oligokyphus* that were described by Kühne (1956) and are
housed in The Natural History Museum, London. Most of these bones are fragmentary and variously abraded, which accounts for Kühne’s use of multiple specimens to produce composite reconstructions for individual skeletal elements. Comparison of *Oligokyphus* and *Kayentatherium* elucidates various important postcranial features in these tritylodontids and necessitates modification of some of Kühne’s descriptions and reconstructions.

**Description**

**Postcranial Axial Skeleton**

The vertebral column is most completely documented in MCZ 8812, which preserves an articulated series of vertebrae from the atlas (including a possible fragment of a proatlas) to the posterior dorsal region, along with most of the dorsal ribs and a number of isolated caudal vertebrae. Most vertebrae are crushed and often considerably distorted. Well-preserved, dissociated vertebral centra from other specimens referable to *Kayentatherium* were also available for examination.

*Atlas.* The atlas is composed of paired, unfused atlantal neural arches and a centrum (fig. 5.1). The atlantal arch is composed of a thin dorsal plate, representing the lamina, and a robust ventral base that bears articular facets for the centrum and occipital condyles and represents the pedicle. The thin medial margins of the laminae appear not to have been in contact along the midline (fig. 5.1B), although they were probably ligamentously joined in life. The dorsolateral, or external, surface of each lamina is almost flat and bears no indication of any muscular process. The base of the lamina near its junction with the pedicle is thickened (fig. 5.1B). The two facets at the base of the neural arch (pedicle) are of unequal size, with the facet for the occipital condyle being more deeply concave and considerably larger. Each arch base supports a ventrolaterally projecting transverse process. A groove appears just behind the transverse process and continues as a deep sulcus passing dorsally between the process and the lateral aspect of the occipital facet. This groove, which extends between the anterior margin of the lamina and the dorsal rim of the occipital facet, presumably marked the course of the vertebral artery. The atlantal arches and intercentrum were presumably ligamentously joined.

The atlantal and axial centra are not suturally attached to each other, unlike the condition in *Oligokyphus* (BMNH R 7315; Kühne, 1956, fig. 43) and *Morganucodon* (Jenkins & Parrington, 1976, fig. 1G, H). A short
dents, which projects from the dorsal half of the anterior face of the centrum, is stout at its base but attenuates on all sides to a distinct apical point (figs. 5.1D–F, 5.2A). An obliquely inclined, anteroventrally facing facet for articulation with the first intercentrum is situated ventral to the dents. The contact areas for the atlantal arches are set off from the remainder of the dorsal surface of the centrum, which forms a broad concavity divided by a low median ridge.

**Axis.** The axial centrum is constricted at midlength and relatively short (fig. 5.2A). As in *Oligokyphus* (Kühne, 1956, fig. 43), the anteroposterior lengths of the atlantal and axial centra are about equal. The robust transverse process of the axis projects posterolaterally and has an expanded distal end. The prezygapophyses were apparently small. The large postzygapophyses bear ventrolaterally facing facets. As on all other vertebrae, anapophyses are absent. The tall, hatchet-shaped neural spine is mediolaterally compressed and thin except for anterior and posterior terminal tuberosities. The dorsal margin of the process is distinctly convex in lateral view (fig. 5.2A). The lateral face of the process, broad and gently concave, provided ample surface for suboccipital muscles, possibly M. obliquus capitis.

**Figure 5.1.** Atlantal elements of Tritylodontidae indet., MCZ 8839. (A–C) Right atlantal arch in (A) lateral, (B) anterior (with addition of left element), and (C) medial views. (D–F) Atlantal centrum with dens in (D) dorsal, (E) anterior, and (F) ventral views. Scale bar equals 1 cm. Abbreviations: d, dens; f.oc, facet for contact with occipital condyle; l.at, lamina of atlantal arch; s.v, vertebrarterial sulcus; t.p, transverse process.
Postaxial Cervical Vertebrae. MCZ 8812 has five postaxial cervical vertebrae (C3–7), for a total of seven cervicals. The disk-like, amphicoelous centra are about three times as wide as long (fig. 5.2B, C), unlike the cervicals of *Oligokyphus* in which the width of the centrum only slightly exceeds its length (Kühne, 1956). The centra bear midventral keels as do those of the atlas and axis. Their anterior and posterior articular surfaces have sharp ventral rims. The short, dorsally projecting neural spines taper toward slightly thickened apices. The prezygapophyses project more dorsally than those in *Oligokyphus* (cf. fig. 5.2B and Kühne, 1956, fig. 41C) and thus do not present the great transverse width seen in dorsal view of the cervicals in *Megazostrodon* (Jenkins & Parrington, 1976, fig. 6A). The pre- and postzygapophyseal facets are shallowly concave and convex, respectively, along a transverse plane and, as a whole, are inclined to within

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**Figure 5.2.** *Kayentatherium wellesi*, MCZ 8812. (A) Atlas-axis complex in right lateral view. Scale bar equals 1 cm. (B, C) Postaxial cervical vertebra in (B) anterior and (C) right lateral views. Scale bar equals 2 cm. Abbreviations: d, dens; f.at.a, facet for contact with atlantal arch; n.s, neural spine; p.z, prezygapophysis; po.z, postzygapophysis; t.p, transverse process.
about 30° of the vertical plane. The pedicles of the slender neural arches are narrow anteroposteriorly and enclose a very wide neural canal. The transverse processes are short and stout. The parapophyseal and diapophyseal facets are well separated. The parapophyses are positioned more ventrally on anterior cervical centra and are successively displaced dorsally on posterior cervicals; on C7, the parapophysis is located halfway up on the anterior rim of the centrum. As in *Massetognathus* (Jenkins, 1970) and *Oligokyphus* (Kühne, 1956), the cervical ribs were not intervertebral in position. Although Kühne (1956, 141) interpreted the cervical ribs in *Oligokyphus* as fused, his illustrations show that the diapophyses and parapophyses are broken (Kühne, 1956, fig. 44A–C). In *Kayentatherium*, the cervical ribs are not fused to the vertebrae.

**Dorsal Vertebrae.** The first dorsal vertebra (fig. 5.3) differs from the last cervical in having a slightly longer centrum and an anteroposteriorly broader neural spine, which is more or less triangular in transverse section.

The neural spines of the first three dorsal vertebrae are tall, mediolaterally narrow, and distinctly inclined posterodorsally (fig. 5.3). The neural spine of the third thoracic has a slightly thickened apex. The neural arch of the first dorsal bears a small process, which, on the second dorsal, becomes a prominent tubercle and, starting at the third dorsal, a distinct, dorsally and slightly laterally projecting process. On the posterior dorsal vertebrae, the process changes into a more or less horizontal, increasingly laminar feature posteriorly. Kühne (1956, 102) noted that anterior dorsal vertebrae of *Oligokyphus* bear “a rather strong diapophysis, which is well
separated from the articulation of the rib.” Although situated just pos-
terodorsal to the tubercular facet, the process does not support the tuber-
culum and thus is musculotendinous rather than diapophyseal in origin. The robust prezygapophyses project beyond the anterior margin of the centrum. As on the cervical vertebrae, the parapophyseal and diapophyseal facets are confluent rather than separate. All dorsal vertebrae have distinct, irregular neurocentral sutures that join the pedicles of the neural arches to the centra. Intervertebral foramina for the exit of spinal nerves are largely intravertebral in position; deep notches are formed along the posterior margins of the pedicles, but corresponding notches on the anterior margins of successive pedicles are only slightly developed. The centra are constricted at mid-length and bear ventral keels.

A gradient in neural spine structure begins in the region of the fourth to sixth dorsal vertebrae (fig. 5.4A): the neural spines decrease in height posteriorly, and lateral exostoses appear on their apices. Starting at the sixth dorsal vertebra, the spines become more sharply inclined posteriorly, the lateral exostoses are prominent, and the posterior margins of the apices are extended as a pronounced lappet, producing a trident appearance in dorsal view (figs. 5.3, 5.4B). The posterior lappets presumably represent attachment sites for robust supraspinous and/or interspinous ligaments. Starting at the eleventh dorsal vertebra, the apices of the neural spines become much expanded and flattened to form distinct “spine tables” (fig. 5.3), and the neural spines become broad anteroposteriorly. Lewis (1986, 297) noted apical expansion of the neural spines on the dorsal vertebrae of the Comb Ridge specimens of *Kayentatherium*, where “transverse expansion [is] greatest in the posterior dorsals, especially in

**Figure. 5.4.** *Kayentatherium wellesi*, MCZ 8812. (A) Dorsal vertebrae four to six with associated ribs in left lateral view. (B) Dorsal vertebrae fifteen and sixteen with associated ribs in left lateral view. Scale bars equal 2 cm.
lumbers.” A similar differentiation of the dorsal neural spines is present in *Exaeretodon*, where the first four vertebrae have tall, slender spines, and the following twelve have spines with much expanded dorsal apices (Bonaparte, 1963).

Both pairs of zygapophyseal facets of the first dorsal vertebra and the prezygapophyseal facets of the second dorsal vertebra are steeply inclined at angles comparable to those of the cervical series. The postzygapophyseal facets of the second dorsal vertebra, however, appear to be more or less horizontal, a condition that persists through the ninth dorsal vertebra. A gradational return to an inclined orientation appears to occur from the tenth through twelfth dorsal vertebrae. The zygapophyseal facets of the posterior dorsal vertebrae are steeply inclined at about 40° from the vertical plane.

No abrupt structural transition exists between the thoracic and lumbar regions. Although a gradational change in zygapophyseal orientation is apparent, neither an antilinical nor a diaphragmatic vertebra is present. All dorsal neural spines are posterodorsally inclined. The centra of the dorsal vertebrae become increasingly longer and more massive toward the posterior end of the series (fig. 5.3). Starting at about the tenth dorsal vertebra, the parapophyseal facets shift increasingly posterodorsally.

Lewis (1986, 297) reported a count of nineteen dorsal vertebrae for the Comb Ridge specimens of *Kayentatherium*, of which “the last two could be called lumbar,” but did not specify any criteria for this distinction. The last “lumbar,” or nineteenth dorsal vertebra, thus appears to be missing in MCZ 8812. Jenkins (1971) distinguished thirteen thoracic and seven lumbar vertebrae in *Thrinaxodon*, with the thoracolumbar transition gradational and to some extent arbitrarily determined on the basis of costal structure.

**Caudal Vertebrae.** Comparison of the numerous isolated caudal centra with those of *Oligokyphus* demonstrates that the caudal vertebral column displays a similarly pronounced proximodistal gradation. On the basis of material available, caudal vertebrae can be described only by distinguishing proximal and distal centra. The tail in *Kayentatherium*, which comprised at least nineteen vertebrae (Lewis 1986), was apparently long and well developed.

Proximal caudal vertebrae (fig. 5.5A, B) have short centra and apparently robust neural arches, the pedicles of which are positioned anteriorly on the centrum (as in *Oligokyphus*; Kühne, 1956, fig. 47). On proximal centra, the ventral half of the posterior articular surface is recessed and
faces posteroventrally. The horizontal transverse processes arise variably from the sides of the centra, on some centra from near the neurocentral junction (fig. 5.5A) and on others from mid-centrum (fig. 5.5B). A longitudinal ventral groove presumably carried coccygeal vessels (Kühne, 1956). Distal caudal centra are more elongate. The neural spines and various other processes evidently became progressively smaller and eventually disappeared toward the distal end of the tail (fig. 5.5C). In these vertebrae, the neural canal is reduced to a narrow sulcus. Many caudal centra bear vascular foramina of various shapes and positions, especially on their ventral surfaces.

**Ribs.** The dorsal ribs lack the imbricating plates or processes present in many basal eucynodonts (fig. 5.3). In the more anterior dorsal ribs, the articular region of the proximal end is long, narrow, and relatively flat, with the capitular and tubercular facets separated by a mere constriction. The tuberculum is usually situated above and behind the capitulum. The shaft of a typical rib is anteroposteriorly flattened. Proximally, the shaft arches laterally and somewhat posteriorly; the distal half is straighter and directed ventrally. A distinct projection or rugosity is located a short distance distal to the tuberculum on the dorsal margin of the shaft and may mark the insertion of parts of longissimus dorsi. Distally, the shaft gradually attenuates and then expands again to support a ventrally facing, oval facet for a costal cartilage. The gentle curvature of the distal portion of the more anterior dorsal ribs indicates a rather deep thorax. The first dorsal rib differs from others in the great width of its shaft. The shafts of the seventh cervical ribs, which are distinctly more slender, are preserved bilaterally along the anterior margins of the first thoracic ribs in MCZ 8812.
Ribs nine and twelve on the left side as well as rib seven on the right side in MCZ 8812 exhibit fractures with nearthrotic formations (fig. 5.3). In each instance, both ends of the fractured shaft became expanded through callus formation and developed irregular articular facets, forming a secondary joint. One posterior dorsal rib bears a massive nodular growth just distal to its proximal head.

**Pectoral Girdle**

*Scapula.* The scapula is structurally complex. Viewed from medial aspect, the scapular blade without the acromion is more or less triangular in outline (figs. 5.6B, 5.8B), flaring broadly toward the convex vertebral margin. The smooth medial surface of the scapular blade has three confluent surfaces of different orientation; these surfaces are delimited by lines of pronounced flexure, which have been accentuated in MCZ 8812 by crushing during fossilization. An anteriorly facing surface is separated from a large medially facing area by a line of curvature extending from the anterior angle to the anteromedial region of the supraglenoid buttress. The posterior border of the scapula is thickened and supports a slightly concave, posteriorly and slightly laterally facing postscapular fossa (fig. 5.6C) below the posterior angle; in *Cynognathus*, a comparable fea-

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**Figure 5.6.** *Kayentatherium wellesi*, MCZ 8812. Left scapula in (A) posterior, (B) medial, and (C) lateral views. The anteroposterior width of the scapular blade has been somewhat exaggerated by crushing during fossilization. Scale bar equals 2 cm. Abbreviations: a.cl, area of attachment of clavicle; ac, acromion; f.is, infraspinous fossa; f.ps, postscapular fossa; f.ss, supraspinous fossa; i.t, insertion of M. triceps brachii (caput scapularis); s.gl, scapular glenoid facet; s.s, scapular spine.
ture was interpreted as representing the origin of M. teres major by Gregory and Camp (1918, 471).

Viewed from lateral aspect, the anterior and posterior borders of the scapula are reflected laterally, enclosing a broad infraspinous fossa between them (fig. 5.6C). A groove above the supraglenoid buttress probably marks the origin of the caput scapularis of M. triceps brachii (fig. 5.6C; cf. Jenkins, 1971, fig. 18D). The ventral end of the posterior border is markedly thickened, where it forms a broad posterolateral area above the glenoid facet. The anterior border, which is homologous to the mammalian scapular spine, bears an expanded, rugose margin for muscular attachment, most likely M. deltoideus. The robust, anterolaterally projecting acromion bears a distinct clavicular facet (fig. 5.6B). It is undercut anteroventrally along its junction with the scapular base. An incipient, bilplanar supraspinous fossa is formed between adjacent surfaces of the scapular blade and spine at the anterior angle of the scapula (fig. 5.6C).

The scapular base supports a large, rounded, concave glenoid facet and bears narrow articular surfaces for the coracoid and procoracoid. The base forms a short process for contact with the procoracoid. The scapular facet of the glenoid faces ventrally rather than posterolaterally, as in other nonmammalian cynodonts. In contrast to more basal eucynodonts, the dorsal margin of the glenoid facet is more defined and overhangs the glenoid socket more extensively.

**Coracoid and Procoracoid.** The coracoid and procoracoid (fig. 5.7) are comparable to those in other nonmammalian cynodonts, but they are much smaller relative to the scapula (fig. 5.7; cf. Jenkins, 1971, fig. 17). The coracoid facet of the glenoid has a rather bulbous posterior termi-

**Figure 5.7.** *Kayentatherium wellesi*, MCZ 8812. Right coracoid and procoracoid in (A) medial and (B) lateral views. The relative orientation of bones differs in the two illustrations. Scale bar equals 2 cm. Abbreviations: co, coracoid; co.f, coracoid foramen; co.gl, glenoid facet of coracoid; pc, procoracoid.
nus (fig. 5.7B) and apparently faced posterolaterally and only somewhat dorsally. The procoracoid does not contribute to the formation of the coracoid facet of the glenoid, unlike the condition in most other known nonmammalian cynodonts with the exception of *Exaeretodon* (Bonaparte, 1963).

**Clavicle.** The clavicle is distinctly angular (fig. 5.9A, B), a feature that is also present in the derived probainognathian *Prozostrodon* (Bonaparte & Barberena, 2001). Its medial two-thirds comprise a slender shaft that expands proximally into a spatulate plate for articulation with the interclavicle. The plate bears prominent striations parallel to the long axis of the bone, principally on its dorsal surface; it is thickest along its long axis and is delimited by sharp margins, especially anteriorly. The lateral third of the clavicle, which is offset from the medial two-thirds at an almost right angle, is a fairly robust rod with a posterodorsal and slightly lateral orientation. A recess on the distal end, which is partially delimited by a distinct ridge, represents the articular contact with the acromion.

**Interclavicle.** The interclavicle, which is thin and dorsoventrally flattened, bears broad, anterolaterally projecting clavicular processes (fig. 5.9C). These processes are flat and were overlapped ventrally by the expanded proximal ends of the clavicles. The short posterior ramus is slightly expanded posteriorly. A ventromedial projection may mark the origin of a portion of M. pectoralis.

**Sternum.** As in *Bienotheroides* (Sun & Li, 1985, fig. 4), the manubrium of *Kayentatherium* comprises a pair of ossifications that presumably were
joined along the midline by cartilage in life. Only the left manubrial element is preserved in MCZ 8812 (fig. 5.10). The bone is thicker posteriorly than anteromedially. Its lateral margin is anteroposteriorly concave, the ventral surface is flat, and the dorsal surface is distinctly concave. The anterior margin is thin and rounded. A large, raised convex facet at the anterolateral corner faces anterolaterally. Kühne (1956, 113) interpreted the large facet on the manubrium in *Oligokyphus* as contacting the coracoid and a smaller one as contacting the first thoracic rib. In MCZ 8812, there is no evidence of facet development along the ventromedial margin of the coracoid that would indicate an articulation with the manubrium; a more plausible interpretation is that the large manubrial facet represents the articulation with the robust first thoracic rib. A second facet on the posterolateral corner of the manubrial element faces dorsally and posterolaterally and was probably for contact with the second thoracic rib.
In addition to the manubrium, the sternum of MCZ 8812 comprises three unfused sternebrae (fig. 5.10). The anterior two sternebrae are wider than thick and flare posteriorly; costal facets are situated on the posterior half of the lateral margins and face posterolaterally. The posterior sternebra is a massive, rounded element with deep anterolateral concavities for rib contact. The sternum of *Oligokyphus* is formed by four fused sternebrae (Kühne, 1956, fig. 51B).

**Forelimb**

*Humerus.* The humerus (fig. 5.11) is robust, with flaring proximal and distal ends and a proportionately short diaphysis, which is triangular in transverse section. The greatest width across the epicondyles is about sixty percent of humeral length in MCZ 8812 [compared with forty percent in *Massetognathus*, about fifty percent in *Thrinaxodon*, fifty-four percent in *Exaeretodon*, and fifty-eight percent in *Chiniquodon* (Jenkins, 1971); however, the ratio in *Megazostrodon* is only about thirty-two percent (Jenkins & Parrington, 1976, fig. 7d)]. The planes of the proximal and distal ends are offset relative to one another (cf. fig. 5.11A, C), with the result that the humerus has a twisted appearance. The angle between the planes is approximately $40^\circ$, comparable to that in other nonmammalian cynodonts (Jenkins, 1971).

The proximal end of the humerus is a continuous surface of unfinished, presumably cartilage-covered bone that extends from the areas of medial...
and lateral tuberosities. The bulbous articular surface of the central area, representing the head of the humerus, is directed anteromedially as well as dorsally. The head is raised above the adjacent dorsal surface of the shaft; ventrally, the head is delineated from the ventral surface by a slight ridge. The articular surface of the humeral head is confluent with adjoining areas where medial and lateral tuberosities would be expected; the texture of these areas, however, suggests that they were covered by cartilage and incorporated into the joint. A distinct lesser tuberosity is not developed. At the proximomedial end of the humerus, where the insertion of M. subscapularis might be expected (lesser tuberosity), the bulbous and somewhat expanded articular surface intersects with a broad surface that extends distally to about the middle of the shaft (fig. 5.11C). A distinct projection near its distal end may represent an attachment of M. triceps (as in monotremes; Howell, 1937, fig. 2G).

There is no distinct demarcation for a greater tuberosity. The proximolateral end of the humerus, where this tuberosity might be expected, is an angular and slightly dorsally reflected intersection between the proximal articular surface and the deltopectoral crest. The length of the robust deltopectoral crest is about fifty-three percent of the total humerus length, compared with about forty-one percent in *Thrinaxodon* (Jenkins, 1971, fig. 28E) and thirty-five percent in *Megazostrodon* (Jenkins & Parrington, 1976, fig. 7d). Set at a distinct angle to the adjacent proximal portion of the shaft, the crest borders a wide bicipital depression and is thickest distally. In MCZ 8812, the deltopectoral crest bears distinct stria-

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**Figure 5.11.** *Kayentatherium wellesi*, MNA V3141. Right humerus (slightly reconstructed) in (A) ventral, (B) dorsal, and (C) lateral views. Scale bar equals 2 cm. Abbreviations: c.dp, deltopectoral crest; cap, capitulum; ec.c, ectepicondyle; en.c, entepicondyle; en.f, entepicondylar foramen; f.bc, bicipital fossa; g.t, greater tuberosity; h.h, head of humerus; l.t, lesser tuberosity; u.c, ulnar condyle.
The medial edge of the deltopectoral crest continues posterodistally as a low, rounded ridge that forms a bar across the large entepicondylar foramen. There is no ectepicondylar foramen.

The entepicondyle is thicker and broader than the ectepicondyle. The former is farther from the radioulnar articulation than the latter, an asymmetry that increases the relative moment arm of the antebrachial flexors over the extensors (Jenkins, 1973). The broad ulnar condyle wraps around the distal end and extends onto both the dorsal and ventral aspects of the humerus, although the condyle is less extensive ventrally than dorsally. The radial condyle (*sensu* Jenkins, 1973) also wraps around the distal end. The intercondylar groove is relatively broad. The surficial texture of the bone on both condyles extends medially and laterally across the entire distal end of the humerus. Thus, the free margins of the epicondyles appear to have been cartilaginous.

**Ulna.** The olecranon process is long relative to the total length of the ulna (fig. 5.12). Measured from the center of the well-defined semilunar...
The gently sigmoidal shaft of the ulna is transversely narrow. Either side of the shaft bears a longitudinal groove, especially near the proximal end, representing the areas of attachment of extensor and flexor muscles.
There is a well-developed anteromedial crest on the ulna for anchoring the radioulnar interosseous ligament. The distal portion of the ulnar shaft is flat anteriorly. The distal end of the ulna has its largest diameter in an anteroposterior direction. The distal articular facet is convex, with no trace of a styloid process.

Radius. The radius (fig. 5.13) has a slightly sigmoidal curvature, comparable to that of the ulna. The expanded proximal and distal ends are linked by a cylindrical shaft. The radial head bears an oval, concave articular facet (fig. 5.13D). The posterior margin of the head extends more proximally than does the anterior margin, with the result that the facet is inclined slightly anteriorly (fig. 5.13A). On the posteromedial aspect of the radial head is a broad, anteriorly tapering facet for contact with the ulna (fig. 5.13A). The extent of the facet indicates only modest capability for antebrachial pronation and supination (contra Kühne, 1956). A distinct ridge extends from the ulnar facet distally and posteromedially along the shaft; this feature is associated with a medial depression (fig. 5.13A). The ridge may represent the attachment of the radioulnar interosseous ligament; alternatively, a distinct crest on this ridge (fig. 5.13A) may represent a bicipital tuberosity, the point of attachment for M. biceps brachii.

The distal end of the radius is widest mediolaterally. The concave distal articular facet is delimited by sharp bony edges. The radius of MNA V3141 preserves a small but distinctly protuberant facet on the posterolateral margin of the distal end that articulates with the ulna. The size of

Figure 5.13. Kayentatherium wellesi, MCZ 8812. Left radius in (A) posteromedial, (B) anterolateral, and (C) medial views. (D) Proximal articular surface of left radius. Scale bar equals 2 cm. Abbreviations: cr, crest; d.f, facet for distal contact with ulna; f.u, facet for proximal contact with ulna; fo.ra, radial fossa.
this facet and the opposing area on the ulna, which is correspondingly narrow, indicate that movement at the distal radioulnar joint was modest and involved pivoting of the radius on the ulna. A styloid process is absent.

*Manus.* Both forefeet are preserved in MCZ 8812 (fig. 5.14). The bones were slightly disarticulated, especially those of the left manus, and some elements are missing. MNA V3141 also includes a partial manus.

The carpus comprises four proximal elements, two centralia, and at least three distal carpals (preserved on the right side of MCZ 8812).

The ulnare (fig. 5.15A), the largest proximal carpal, has a convex lateral margin and a medial margin that bears two raised facets separated by a notch for a perforating vessel. The more proximal facet, which is large and triangular, contacted the intermedium; the smaller distal facet presumably articulated with the lateral centrale. The ulnare is anteroposteriorly longer along its lateral margin than along its medial edge, and its dorsoventral thickness is greater medially than laterally. Its proximal end bears a large facet for articulation with the distal end of the ulna. The ventral surface of the ulnare is concave, whereas the dorsal face is saddle shaped.
The thick intermedium (fig. 5.15D) has a saddle-shaped dorsal surface and a notched lateral margin that corresponds to the notched medial margin of the ulnare. The nearly straight medial margin of the intermedium forms an extensive facet for contact with the radiale. The proximal and distal facets for the ulna and lateral centrale, respectively, are well developed. On the ventral surface of the intermedium, a proxi-modistal ridge separates two concavities.

The rather flat distal face of the nodular radiale (fig. 5.15B) is divided by a groove into two distinct facets. The rounded proximal surface contacted the distal end of the radius.

The pisiform is represented only by a fragmentary element on the left side (fig. 5.15C). The more or less triangular bone is flat and thin except for the area that bears an articular facet for the ulnare.

The two centralia (fig. 5.15E, F) may have been aligned transversely to the long axis of the manus as reconstructed for *Thrinaxodon* by Jenkins (1971, 128). One of the bones is slightly flattened dorsoventrally and possibly represents the medial centrale. The other, with an irregularly nodular shape, may be the lateral centrale. Three bones in the right carpus represent distal carpals (fig. 5.14), but their relative positions are uncertain due to postmortem disturbance of their articular context.

The metacarpals are broadly expanded proximally and distally (fig. 5.14). Metacarpal I is the shortest and relatively widest in overall dimensions; the bone also differs from other metacarpals in having an asymmetric proximal end with the greatest expansion transversely. The proximal ends of all metacarpals are dorsoventrally deeper than the distal ends. A depression in the lateral side of the proximal end of each of metacarpals II–IV accommodates the adjoining metacarpal.

The phalanges are robust. At the interphalangeal joints, the distal condyles are dorsoventrally asymmetric; the articular facets extend further proximally onto the flexor aspect than onto the extensor surface, an
asymmetry that indicates a modest degree of digital flexion. The proximal ends of the ungual phalanges bear large flexor tubercles ventrally (fig. 5.14). The distal portions of the manual unguals are distinctly flattened, unlike the tapering, cone-like unguals in other nonmammalian cynodonts (e.g., Jenkins, 1971, fig. 35A-D), and have sharp lateral and medial edges. The phalangeal formula of the manus is 2-3-3-3-3 in the Comb Ridge material referable to *Kayentatherium* (Lewis, 1986), and this is probably also the case in MCZ 8812.

**Pelvic Girdle**

The pelvis of *Kayentatherium* is best known from the still-undescribed Comb Ridge specimens (Lewis, 1986, fig. 2). MCZ 8812 preserves only the anterior portion of the left iliac blade. Incomplete pelvic elements, including an ilium of a small indeterminate tritylodontid (MCZ 8835) and an ischium of *Dinnebitodon*, are represented in the MCZ-MNA collections and provide the basis for the following observations.

**Ilium.** The elongate iliac blade (fig. 5.16A, B) was oriented anterodorsally in life (Lewis, 1986, fig. 2) and gradually expands to its greatest depth anteriorly (fig. 5.16C). A longitudinal ridge on the lateral surface (crista lateralis *sensu* Kühne, 1956) defines dorsal and ventral surfaces, which

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*Figure 5.16.* (A, B) Tritylodontidae indet. (MCZ 8835), left ilium in (A) lateral and (B) medial views. Note that the dorsal and ventral margins of the preacetabular portion are damaged. (C) *Kayentatherium wellesi* (MCZ 8812), partial left ilium in lateral view. Hatched areas denote broken surfaces. (D) *Dinnebitodon amarali* (MNA V3232), right ischium in lateral view. Scale bars each equal 1 cm. Abbreviations: ac.f, acetabular facet; d.p, posterodorsal process of ilium; f.pu, facet for contact with pubis; gr, groove; s.il, sacroiliac facet.
face dorsolaterally and ventrolaterally, respectively. In MCZ 8835, the ventral margin of the blade is a thin, slightly everted flange, and the surface between the ventral margin and the longitudinal ridge is slightly concave. The medial surface of the iliac blade is extensively marked by parallel striae and rugosities representing a well-developed sacroiliac syndesmosis; as in *Oligokyphus* (Kühne, 1956, 124), this surface is divided by a longitudinal ridge. Behind the sacroiliac articulation, the neck of the ilium is approximately triangular in transverse section (MCZ 8835). Any evidence of a pit below the lateral longitudinal ridge, which Kühne (1956, 124) interpreted as the origin of M. rectus femoris in *Oligokyphus*, has been obscured by crushing in this region in MCZ 8835. A dorsally and slightly posteriorly directed, spine-like process arises from the dorsal margin of the ilium at the level of the posterior end of the sacroiliac facet (fig. 5.16A); most of the process has been broken off in MCZ 8835, but the process is completely preserved in USNM 317201 (Lewis, 1986, fig. 2). Kühne’s (1956, fig. 57) reconstruction depicts no dorsal process on the ilium of *Oligokyphus* but does show a step-like increase in the depth of the iliac blade at a location similar to that of the process. Examination of Kühne’s collection of *Oligokyphus*, however, reveals two ilia in which a prominent, flange-like posterior process is more or less completely preserved (BMNH R 7445, 7448); on several other ilia (BMNH R 7442-7444, 7446, and 7447), the process has been broken off but its base is evident. The ilium of *Exaeretodon* has a posteriorly directed process (Bonaparte, 1963, fig. 9).

The large, concave acetabular facet of the ilium is oriented perpendicular to the long axis of the bone and faces posterolaterally (fig. 5.16A) rather than ventrally as in basal eucynodonts (e.g., Jenkins, 1971, figs. 45A, 46A). A triangular articular surface is situated on the ventral process for contact with the pubis. As in *Oligokyphus* (BMNH R 7441) and *Exaeretodon* (Bonaparte, 1963, fig. 9), a dorsal acetabular rim is absent, with the resulting marginal gap between the ilial and ischial facets of the acetabulum presumably filled by fibrocartilage in life. The acetabular facets of the ilium and ischium form slightly protruding lateral margins. Kühne’s (1956, fig. 57) reconstruction of the pelvis of *Oligokyphus* depicts the bony acetabulum as an elongated socket with the greatest diameter in an anteroposterior direction.

**Ischium.** The acetabular portion of the ischium (fig. 5.16C) is separated from the plate-like, ventromedially directed ischial plate by a slight constriction. The acetabular facet faces dorsally and anterolaterally; as noted above, the dorsal margin of the acetabulum was not completed in bone.
A distinct medial facet contacted the ilium. A ridge extends from the center of the lateral rim of the acetabular facet posterodorsally, gradually attenuating toward the ischial tuberosity; a shallow sulcus is present just dorsal to the ridge. Comparable features are present in basal eucynodonts (Jenkins, 1971, figs. 45A, 47A). The thin anteroventral edge of the ischial plate contributes to the margin of an apparently large obturator foramen. The acetabular notch between the acetabular facet and the pubic process is shallow in MNA V3232 but deep in MNA V3235.

**Hind Limb**

The hind limb is represented in the MCZ-MNA collections only by the nearly complete left femur of an indeterminate tritylodontid (MCZ 8838) as well as parts of the left femur and the proximal ends of both tibiae in MNA V3141.

*Femur.* The bulbous femoral head is reflected slightly dorsomedially relative to the long axis of the shaft (fig. 5.17A, C). The articular surface as a whole is a slightly asymmetric ovoid and extends laterally onto the ridge between the head and greater trochanter (fig. 5.17D). The shape of the femoral head, which is also present in *Oligokyphus* (Kühne, 1956, fig. 58), differs from the symmetrically hemispheroidal head in *Morganucodon* (Jenkins & Parrington, 1976, figs. 12, 13e). The area of the femoral neck is only faintly defined by a slight constriction. The deep intertrochanteric fossa occupies the entire broad surface between the trochanters and the head and extends farther distally than in either basal eucynodonts (Jenkins, 1971, figs. 48B, 49B) or *Morganucodon* (Jenkins & Parrington, 1976, fig. 12c).

The robust, triangular trochanters arise from the femoral shaft in relatively ventral positions. They diverge at angles of about 40° relative to the long axis of the shaft in MCZ 8838 and are more or less aligned in the same transverse plane. The lesser trochanter is reflected dorsally and is thicker than the ridge connecting it to the femoral head.

The femur of MCZ 8838 closely resembles that of *Bienotherium* (Young, 1947, fig. 20A). Kühne’s (1956, fig. 58) reconstruction of the femur of *Oligokyphus* resembles the femur of MCZ 8838 in the shape of the femoral head and the relative positions of the trochanters on contralateral sides of the shaft. However, other details shown in Kühne’s reconstruction, notably a ridge on the dorsal side of the greater trochanter, the cylindrical shape of the greater trochanter, and an acute notch between the greater trochanter and femoral head, appear to represent major differences.
The shaft of the femur is oval in transverse section, with the smaller diameter between the dorsal and ventral surfaces. A crest along the posteroverentral margin of the shaft (fig. 5.17B) is comparable to a ridge in basal eucynodonts (Jenkins, 1971, 172). The lateral condyle of the femur is considerably wider transversely than the medial one (fig. 5.17B) and forms a gently convex articular surface; the medial condyle has a more sharply curved articular surface and projects further ventrally than the lateral one. These features are already present in basal eucynodonts (Jenkins, 1971, 172) and are retained among some extant mammals (Jenkins & Parrington, 1976, 424). There is no distinct patellar groove.

Tibia. The narrowest dimension of the oval shaft is mediolateral rather than anteroposterior as in basal eucynodonts (Jenkins, 1971, figs. 56, 57). The proximal end, which is expanded anteriorly and laterally, bears two condylar facets that are separated by a low ridge (fig. 5.18). The slightly concave facet for the medial condyle is inclined anteromedially; the long axis of the facet extends almost transversely. The posterolateral facet for the lateral femoral condyle is elongate, and its long axis extends posteromedially. A projection on the anteromedial margin of the articular surface appears to represent a tibial tuberosity for the insertion of M. quadriceps.

Figure 5.17. Tritylodontidae indet., MCZ 8838. Left femur (slightly reconstructed) in (A) dorsal, (B) ventral, and (C) medial views. (D) Proximal view of the proximal end. Outline of greater trochanter restored from MCZ 8832. Scale bar equals 2 cm. Abbreviations: cr, crest; g.tr, greater trochanter; h.f, head of femur; it.f, intertrochanteric fossa; l.c, lateral condyle; l.tr, lesser trochanter; m.c, medial condyle.
femoris; similarly positioned tubercles are present in other nonmam-
malian cynodonts (Jenkins, 1971, 186). The cnemial crest, which extends
distally from the tibial tuberosity, is not as prominently developed as in
Oligokyphus (Kühne, 1956, fig. 60). A distinct excavation along the prox-
imomediaimal aspect of the tibial shaft may mark the origin of M. tibialis an-
terior, as suggested for Oligokyphus (Kühne, 1956, 128). A prominent lat-
eral groove on the flexor aspect possibly relates to the origin of a plantar
flexor muscle. The slightly convex distal end of the tibia is irregular in out-
line, and its articular surface has a pitted texture suggestive of cartilagi-
inous covering in life. An elliptical scar of uncertain identity is present on
the medial aspect of the tibial shaft in MCZ 8838.

Discussion

The partial skeleton of Kayentatherium (MCZ 8812) and other trity-
lodontid postcranial remains from the Kayenta Formation offer a basis
for reassessing the allegedly mammalian postcranial features that have
been ascribed to this group of nonmammalian eucynodonts. The com-
posite reconstruction of the skeleton of Kayentatherium (fig. 5.19), based
primarily on MCZ 8812, depicts a stockily built animal with a large head,
stout vertebral column, and robust girdles and limbs. Do postcranial fea-
tures provide persuasive evidence in support of a sister-group relation-
ship between Tritylodontidae and Mammalia?

Postcranial Axial Skeleton

The cervical vertebrae exhibit features that were already present, in-
cipiently developed among basal eucynodonts, or appear to be not closely
similar to the respective condition in basal mammals. The unfused paired neural arches and the intercentrum of the atlas in *Kayentatherium* are structurally similar to those in basal eucynodonts and represent a pattern that is retained in *Morganucodon*. Although small, the axial prezygapophyses are likewise a plesiomorphic feature. The axial centrum is longer than the atlantal centrum in basal eucynodonts; these proportions are retained among mammals, but the length of the two centra is more or less equal in *Oligokyphus* (Kühne, 1956, fig. 43) and *Kayentatherium*. The presence of a distinct dens is a mammal-like feature, but, in fact, this structure originated among basal eucynodonts (Jenkins, 1971). The dens in *Kayentatherium* (MCZ 8812) is short, stout, and anteriorly attenuated. Its dorsal surface, however, is slightly inclined anteroventrally (figs. 5.1E, 5.2A) and unlike the horizontal dorsal surface of the dens in *Morganucodon*, which bears a facet for the transverse ligament of the atlas (Jenkins & Parrington, 1976, fig. 1f, g). There is no evidence of such a facet in *Kayentatherium*, and the inclination of the dorsal surface of the dens is mechanically unsuited to sustain a transverse ligament of the atlas, which is a major component of the osseoligamentous check mechanism constraining atlanto-axial flexion in mammals (Jenkins, 1969). Instead, the dens in *Kayentatherium* may have served for attachment of the apical and alar ligaments (as in mammals). Our interpretation that *Kayentatherium* lacked a transverse atlantal ligament is corroborated by the presence of axial prezygapophyses that supported the atlantal arches and effectively
reinforced the atlanto-axial joint against flexure (Jenkins, 1969). The dorsal surface of the dens of *Oligokyphus* as illustrated by Kühne (1956, fig. 43; BMNH R 7315) also is anteroventrally inclined. This specimen, however, is not as well preserved as BMNH R 7316, in which the structure of the sloping dorsal surface of the dens is patently evident; as in *Kayentatherium*, there is no facet for a transverse atlantal ligament.

The structure of other cervical intervertebral articulations likewise distinguishes tritylodontids and mammals. In *Kayentatherium*, the cervical zygapophyses are dorsally directed and the facets are steeply inclined (to within about 30° of the vertical plane), which is comparable to the condition in the basal eucynodont *Thrinaxodon* (Jenkins, 1971, fig. 12C) but differs from the more horizontally inclined zygapophyses and facets in *Megazostrodon* (Jenkins & Parrington, 1976, fig. 6a, b). The only features shared by tritylodontid and mammalian cervical vertebrae are the reduced height of the neural spines and the anteroposterior narrowness of the pedicles; both may be related to an elevated (i.e., slightly extended) posture of the neck.

The dorsal vertebrae of *Kayentatherium* have almost no features that might be characterized as mammal-like. Typically in mammals, the orientation of anterior thoracic zygapophyseal facets exhibits a marked shift to a horizontal orientation at the cervicothoracic junction. In *Thrinaxodon*, the cervicodorsal boundary is delineated by a distinct zygapophyseal facet reorientation at C7; however, the shift is toward a more vertical orientation (from 55° to 15° relative to a sagittal plane through the pre- and postzygapophyses, respectively) (Jenkins, 1971, 53). In contrast, a reorientation of facet angle occurs at the second dorsal vertebra in *Kayentatherium*; the facets shift to a more or less horizontal orientation, as in mammals. The elongate and posteriorly inclined neural spines on the anterior dorsal vertebrae in *Kayentatherium* indicate a well-developed nuchal ligament and M. semispinalis for suspension of the large head (as in some mammals), and yet these features appear to be but a slight elaboration of the same fundamental pattern present in the cervicodorsal column of *Thrinaxodon* (Jenkins, 1971, fig. 12C).

An important distinguishing feature of mammals is thoracolumbar differentiation that occurs as the result of a relatively abrupt shift in the orientation of the zygapophyses and neural spines (at the diaphragmatic and antclinal vertebrae, respectively). There is definitive evidence from a single specimen referable to *Morganucodon* that distinct thoracolumbar differentiation was already present in basal mammals (Jenkins & Parrington, 1976, fig. 6D, E). *Kayentatherium*, however, clearly lacks any
such differentiation. Although the orientation of the posterior dorsal zygapophyseal facets does not preclude some axial flexion and extension in this region, strong supra- and interspinous ligaments (as indicated by the shape of the apices of the neural spines) probably would have restricted flexibility. Whereas a number of distinctive features are evident among the dorsal vertebrae and ribs, the structural transitions along the truncal series are entirely gradational.

The exostoses on the neural spines of mid- and posterior dorsal vertebrae of Kayentatherium are comparable to those in Exaeretodon (Bonaparte, 1963), but exostoses appear to be absent in Oligokyphus. The median exostosis, which projects posteriorly, most likely represents the site of attachment for well-developed supraspinous and/or interspinous ligaments. The posterolateral projections, commencing at the tenth dorsal and elaborated as “spine tables” more posteriorly along the dorsal column, appear to be indicative of hypertrophied epaxial musculature, particularly M. transversospinalis, which bridges adjacent vertebrae or short, contiguous series of vertebrae. Together these features most plausibly are interpreted as contributing additional rigidity to the back and are yet another example of the diverse axial features among nonmammalian cynodonts for reinforcement of the lumbar region [for discussions of this problem, see Jenkins (1971, 86–91) and Kemp (1980, 232–235).

**Appendicular Skeleton**

Major features of the pectoral girdle, notably the supraspinous and postscapular fossae, orientation of the glenoid, position of the scapular spine, and shape of the clavicle, invite consideration as mammal-like features, but comparisons are somewhat limited by the fact that the shoulder girdle in basal mammals is still incompletely known.

The presence of a biplanar supraspinous fossa, between an anterior extension of the scapular blade and the scapular spine, might be considered a patently mammalian feature were it not for two counterindications. The first is that a supraspinous fossa was already present among basal eucynodonts. In Kayentatherium, the fossa is restricted to the dorsal half of the scapula and is thus only an incomplete expression of this feature in the area where, in basal eucynodonts, there is an incipient anterior shelf (Jenkins, 1971, fig. 17A; Kemp, 1980, fig. 10). The second problem is that there is no evidence for the presence of a biplanar supraspinous fossa in basal mammals. The vertebral end of the scapula in Megazostrodon, albeit damaged in the only known specimen, apparently did not possess this feature, and there is no indication of a biplanar fossa on the known incomplete
scapulae referable to *Morganucodon* (Jenkins & Parrington, 1976, figs. 4, 7a). Among mammals, monotremes and multituberculates (Krause & Jenkins, 1983; Sereno & McKenna, 1995) apparently never developed a biplanar supraspinous fossa, although the putative equivalent of M. supraspinatus may be identified or reconstructed as originating from the anterior surface of the laterally reflected scapular spine. Complete supraspinous fossae are known only in later Mesozoic mammals, such as Early Cretaceous triconodontids (Jenkins & Crompton, 1979; Ji et al., 1999).

A postscapular fossa is not a universal mammalian feature. It occurs principally as a fossorial specialization (e.g., in some edentates) but also in forms with a powerful forelimb stroke (such as bears and pinnipeds) in which M. teres major, a humeral retractor, is hypertrophied. A similar functional inference may be made for the postscapular fossa of *Kayentatherium*. The feature is incipiently developed in more basal eucynodonts (e.g., Jenkins, 1971, fig. 17).

The overall configuration of the glenoid and coracoid region in *Kayentatherium*, including the reduction in the relative size of the procoracoid and coracoid and the exclusion of the procoracoid from the glenoid (fig. 5.8), is comparable to that in basal mammals with one notable exception. The primarily ventral, and only slightly posterolateral, orientation of the scapular facet of the glenoid in *Kayentatherium* is closely similar to the ventral orientation generally present in more derived mammals (in which the procoracoid has been lost and the coracoid has been reduced to a small process for muscle attachment).

The scapula of *Kayentatherium* diverges from the pattern seen in basal mammals. The two most salient differences are the size and orientation of the scapular spine and the position of the infraspinous and supraspinous fossae relative to the glenoid (fig. 5.20A). In basal eucynodonts, the anterior margin of the scapula—homologous to the mammalian scapular spine—is reflected anterolaterally and situated anterior to the shoulder joint (fig. 5.20B). In basal mammals such as *Morganucodon*, the lateral reflection is relatively accentuated, so that the margin of the scapular spine is approximated to the anterior margin of the glenoid (fig. 5.20C). In more derived mammals, the scapular spine is positioned above the shoulder joint, bisecting the supra- and infraspinous fossae in a manner that provides a symmetrical approach of supra- and infraspinatus muscle fibers to the greater tuberosity of the humerus. *Kayentatherium*, in contrast, has a large, anterolaterally directed scapular spine that is situated well away from the glenoid (fig. 5.20A). Kemp (1982, 246) likewise
recognized this unusual feature in *Oligokyphus*, which he characterized as “the extreme eversion of the acromion process of the scapula.” A second unusual feature in *Kayentatherium* is the relative anterolateral displacement of the infraspinous fossa; the long axis of the central sulcus of the fossa extends anterolateral to the glenoid (fig. 5.20A) rather than dorsally through the glenoid as in basal mammals (fig. 5.20C). As a result, the supraspinatus muscle also is displaced anteriorly, away from the glenoid, rather than posteriorly and closer to the joint as in basal mammals. The development of a massive M. supraspinatus in direct line between the acromion and interclavicle may account for the distinctively angular form of the clavicle in *Kayentatherium*.

There are major differences between the humerus of *Kayentatherium* and those of basal mammals in the configuration of the tuberosities and humeral head. In *Kayentatherium*, the areas representing the greater and lesser tuberosities are confluent with the humeral head and not developed as distinct features (although they may have been more prominent as part of a cartilaginous ‘epiphyseal’ cap); the configuration of the bony tuberosities is comparable to that in basal eucynodonts. The articular surface of the head is ovoid with the long axis extending mediolaterally (i.e., between the tuberosities); the dorsoventral curvature is only slightly more extensive than that seen in basal eucynodonts (Jenkins, 1971, fig. 26A). In contrast, the humeri of basal mammals have distinct bony tuberosities and a hemispheroidal humeral head, a pattern retained in more derived mammals.

Kühne’s (1956, fig. 55) reconstruction of the ulna in *Oligokyphus*, based on five incomplete specimens, depicts a more gracile, elongate bone than the ulna of (*the much larger*) *Kayentatherium*. As Kühne (1956, 120) noted, “if the humerus and the ulna [of *Oligokyphus*] are compared, the
preponderance of mammalian features in the ulna is overwhelming.” The basic configuration of the tritylodontid ulna, however, is already present in basal eucynodonts (Jenkins, 1971, figs. 31, 32)—sigmoidal curvature, anteroposteriorly narrow shaft, and longitudinal sulci; these features are retained in morganucodontids (Jenkins & Parrington, 1976, fig. 10).

The most widely cited feature of the ulna is the ossified olecranon process, which Hopson and Kitching (2001) scored as either present or absent in their cladistic analysis. Other authors have recognized intermediate conditions (Kemp, 1983; Rowe, 1988) or used degrees of ossification (Sidor & Hopson, 1998). Whereas tritylodontids and basal mammals both have ossified olecranon processes, more basal eucynodonts almost certainly had cartilaginous processes (Jenkins, 1971, 123). The presence of a large, ossified olecranon in _Kayentatherium_ contrasts with the extensively cartilaginous ‘epiphyseal’ ends of other long bones, notably the humerus and femur, which represent the plesiomorphic condition for cynodonts. A large, ossified olecranon on a short ulna in a robust animal is consistent with other features (postscapular fossa, extensive deltopectoral crest on the humerus, large flexor tubercles on the ungual phalanges) that are indicative of a powerful forelimb employed in activities other than locomotion, such as digging. The relative length of the olecranon in _Kayentatherium_ (MCZ 8812) is about thirty-six percent that of the distal segment of the ulna, falling well within the range of proportions (twenty to seventy-five percent) determined by Hildebrand (1995) for twenty-seven genera of present-day fossorial mammals. In _Megazostrodon_, the only basal mammal for which a complete ulna is currently known, the length of the olecranon is only about fifteen percent that of the distal segment of the ulna. We find no unambiguous phylogenetic signal in the ossification of the olecranon among eucynodonts.

The extent of the proximal radioulnar facets provides evidence for only a modest degree of antebrachial pronation and supination. With respect to the distal radioulnar articulation, Kühne (1956, 123) made the perceptive observation that in _Oligokyphus_ “the distal end of the ulna bears a concavity for accommodation of the radius. In the mammals it is always the radius which has a concavity for the convex articular surface of the ulna.” Although the shape of the distal ulnar articular facet in _Kayentatherium_ is not known, the surface of the distal end of the ulna that contacted the radius is narrow and flat. The radial facet is also small and protuberant. Pronation-supination thus would appear to have been limited to a simple pivoting of the radius on the ulna. In typical mammals, as Kühne (1956, 123) pointed out, the radius translates about a curvilinear
facet of the ulna. In *Morganucodon* (MCZ 19944), the distal end of the ulna for radial contact is distinctly rounded, and the corresponding facet on the radius is a small planar facet. Translation at the distal radioulnar joint thus appears to have been possible in basal mammals, but a comparable movement was absent in tritylodontids.

The fragmentary nature of the available tritylodontid ilia from the Kayenta Formation constrains our comparisons to relatively few observations. A juvenile skeleton of *Kayentatherium* (USNM 317201) has a dorsally and slightly posteriorly directed, spine-like process on the dorsal margin of the blade (Lewis, 1986, fig. 2); the base of a similar process is preserved on the ilia of *Kayentatherium* (MCZ 8812, fig. 5.16C) and of an indeterminate tritylodontid (MCZ 8835, fig. 5.16A, B). We interpret this process as a vestige of the more extensive posterior projection of the iliac blade in basal eucynodonts. In mammals, this process is absent or structurally modified. In *Megazostrodon*, as well as in ilia attributed to *Morganucodon*, there is no trace of a projection; the posterior half of the dorsal margin of the blade exhibits an elongate, slightly laterally reflected flange (Jenkins & Parrington, 1976, figs. 11a, 13a, d). In *Tachyglossus*, however, there are two low tuberosities along the posterior margin of the blade (Jenkins & Parrington, 1976, fig. 20d). The medial (sacral) surface of the ilium also appears to differ between tritylodontids and mammals. The incomplete anterior end of the blade of the partial ilium of MCZ 8812 reveals that the sacroiliac joint extended nearly to the anterior terminus. The incomplete ilium of MCZ 8835 (fig. 5.16B) shows that the joint surface extended posteriorly to the level of the dorsal process, in close proximity to the acetabulum. The sacroiliac joint thus occupied most of the medial surface of the iliac blade, in contrast to morganucodontids in which the articular area is situated on the anterior half of the ilium, well separated from the acetabulum by a “neck” that is circular in transverse section (Jenkins & Parrington, 1976, fig. 11b).

The anterodorsally oriented, relatively narrow iliac blade of tritylodontids has been cited as a synapomorphy shared with mammals. Kühne’s (1956, fig. 57) reconstruction of the pelvis of *Oligokyphus* has been particularly influential, especially his rendition of a very narrow, rod-like, and tapering iliac blade. Examination of the original material, however, reveals that all ilia referred to *Oligokyphus* are fragmentary; in none of the specimens is the anterior end of the ilium preserved, nor are the dorsal and ventral margins complete. We found no compelling evidence in support of Kühne’s (1956, fig. 57) reconstruction. Although a posterior process of the ilium is now recognized as present in *Oligokyphus* and
Kayentatherium, the anterior end of the tritylodontid ilium is still imperfectly known. On the basis of the partial ilium of MCZ 1812 (fig. 5.16C), the iliac blade appears to be somewhat spatulate, with its greatest dorsoventral dimension near the anterior terminus. Such an interpretation is consistent with the substantial evidence concerning the diversity of iliac shapes among nonmammalian eucynodonts that has been documented since the publication of Kühne's (1956) study. The ilia of more basal eucynodonts, such as Thrinaxodon and Cynognathus, have an expanded blade with both anterior and posterior projections, but even in basal forms the anterior portion of the blade has a larger surface area, indicating an anterior shift in muscular preponderance (Jenkins, 1971). In more derived eucynodonts, including the gomphodont Exaeretodon (Bonaparte, 1963, fig. 9) and the probainognathian Prozostrodon (Bonaparte & Barberena, 2001, fig. 15A), the iliac blade is composed almost entirely of an expanded anterior projection, with the posterior part reduced to a small process. Although incompletely known, the ilium of the probainognathian Therioherpeton has an entirely preacetabular, parallel-sided blade with no trace of a posterior process (Bonaparte & Barberena, 2001, fig. 5B). In view of the aforementioned evidence, the mammal-like pattern in tritylodontids appears far less extraordinary than it did several decades ago. In the context of the phylogenetic analysis by Hopson and Kitching (2001), which hypothesized a dichotomy between Probainognathia and Gomphodontia, a predominantly preacetabular iliac blade must have evolved independently at least twice (cf. Bonaparte & Barberena, 2001).

Tritylodontid femora, although approximating a mammalian pattern, differ in several important respects from those of basal mammals. As in more basal eucynodonts, the outline of the femoral head in MCZ 8838 is ovoid; the long axis, which passes from anterodorsal to posteroventral, is about twenty percent longer than the perpendicular short axis. In Morganucodon, the femoral head is very nearly if not perfectly hemispherical, with an axial differential estimated to be about six percent. The intertrochanteric fossa in MCZ 8838 is enormous, extending distally about one-third the length of the femur; in Morganucodon, the fossa is relatively restricted in extent, extending distally no more than twenty percent of the length of the femur.

The configuration of the femoral trochanters in Kayentatherium differs in several respects from that in basal eucynodonts and Morganucodon. In basal eucynodonts, the lesser trochanter is situated ventral and distal to the greater trochanter. In tritylodontids, the lesser trochanter has shifted medially but remains distal to the greater trochanter.
(cf. Young, 1947, fig. 20A); in terms of proximodistal placement, its apex is distal to that of the greater trochanter. In morganucodontids, the lesser trochanter has migrated proximally so that the apices of the trochanters are nearly aligned on the same transverse axis (Jenkins & Parrington, 1976, figs. 12a, 13b). The femur of MCZ 8838 thus exhibits an intermediate condition in that the trochanter is medially, but not proximally, displaced. Kühne (1956, 126) and, more recently, Hopson and Kitching (2001, 31) cited the presence of a notch separating the femoral head from the greater trochanter as an apomorphic feature; in basal eucynodonts, however, a slight indentation is present (Jenkins, 1971, fig. 48A, B), and the extent to which separation is apparent seems to reflect the degree of ossification of the proximal end. Finally, the greater trochanter in tritylodontids retains a plesiomorphic, flange-like structure, although it has a discernable apex. The greater trochanter of basal mammals, in contrast, is a proximally directed process with a pronounced apex; the proportional length of the base of the trochanter adjoining the shaft is decreased, and thus the flange-like appearance of the trochanter is reduced.

In conclusion, we find few features in the postcranial skeleton of tritylodontid cynodonts that could be interpreted as potential synapomorphies in support of a sister-group relationship between tritylodontids and mammals. In the preceding section, we demonstrated that most of the alleged postcranial similarities are only superficial in nature, and scoring them as representing the same character-state in phylogenetic analyses obscures the real structural differences in these features between tritylodontids and basal mammals. Finally, certain mammal-like features of the postcranial skeleton of the Tritylodontidae (e.g., large, ossified olecranon process) appear to represent autapomorphies for this group and thus are not useful for determining its phylogenetic relationships.

Acknowledgments

It is with the greatest pleasure that we contribute our study to a volume honoring our dear friend and colleague, James A. Hopson. Not only has Jim always been supportive of our own work in the diverse directions we have taken, but symbolically laying a large tritylodontid on his doorstep has special significance, for Jim is the veritable Dean of Cynodontia.

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**Literature Cited**


