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Shoulder Girdle and Forelimb in Multituberculates: Evolution of Parasagittal Forelimb Posture in Mammals

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Introduction

During the early evolution of mammals, the shoulder girdle and forelimb underwent a profound functional transformation: the rigid shoulder girdle and laterally divergent forelimb posture of the earliest mammals were transformed into the mobile shoulder girdle and more parasagittal forelimb posture that characterizes nearly all living therian (marsupial and placental) mammals (Gregory, 1912; Romer, 1922; Jenkins, 1970a, 1971a, 1973; Jenkins & Weijs, 1979). The fossil record has begun to yield decisive evidence of how and when this musculoskeletal reorganization occurred.

In 1984, I discovered a skull and partial skeleton of a cimolodontan multituberculate that preserve in articulation most of the ribcage and sternum, all elements of the shoulder girdle, and the major long bones of the forelimb. Sereno and McKenna (1995) briefly described this specimen, now referred to as *Kryptobaatar dashzevegi* (Sereno, in review) and suggested that its shoulder girdle and elbow joint provide key evidence for three related hypotheses:

1. Multituberculates, like therians, are characterized by a mobile shoulder girdle and a more parasagittal forelimb posture than that in monotremes and nonmammalian cynodonts.
2. A mobile shoulder girdle and more parasagittal forelimb posture arose once within Mammalia sometime before the Late Jurassic.
3. The shoulder girdle provides key character evidence placing multituberculates within crown mammals closer to therians than to monotremes.

Some authors have questioned these hypotheses, arguing that (1) the proposed postural interpretation is incorrect (Gambaryan & Kielan-Jaworowska, 1997; Kielan-Jaworowska, 1997, 1998); (2) the postural interpretation, if correct, arose more than once within Mammalia (Ji et al., 1999; Luo et al., 2002); and (3) the character evidence from the shoulder girdle is not decisive or compelling with regard to the alliance of multituberculates and therians (Rougier et al., 1996a; Gambaryan & Kielan-Jaworowska, 1997; Luo et al., 2002).

In this report, the phylogenetic significance of the shoulder girdle and elbow for early mammalian relationships is reevaluated, a task more easily accomplished with the recent publication of a data set for basal mammals that includes postcranial characters (Luo et al., 2002). Then, the posture and probable function of the shoulder and elbow joints in multituberculates are reconsidered, with special reference to cineradiographic data from recent mammals (Jenkins, 1970b; 1971a; Pridmore, 1985).

Taxonomic Framework

A phylogenetic taxonomic scheme is utilized here for basal mammalian clades that recognizes node-stem triplets with integrative phylogenetic definitions (for more discussion, see Sereno, in press). At present paleontologists are split over whether to adhere to a more inclusive, traditional definition of "Mammalia" (Hopson & Barghusen, 1986; Crompton & Jenkins, 1979; Kemp, 1982, 1983; Cifelli, 2001; Luo et al., 2002) or to adopt a less inclusive, crown group definition and erect new taxa at more inclusive levels (Rowe, 1988, 1993; Rowe & Gauthier, 1992). For clarity of meaning in the following paper, the rationale behind the choice of taxonomic definitions is briefly considered.

Traditional Mammalia

What may be termed the "traditional" concept of the taxon Mammalia was formulated by paleontologists. The definition included extinct genera, such as *Sinoconodon* and *Morganucodon,* with an advanced jaw joint that were regarded as basal, if not ancestral, to later mammals. These genera, however, are now widely accepted to lie outside crown mammals (i.e., the clade bounded by living monotremes, marsupials and placentals). Maintenance of a definition of Mammalia that extends beyond crown mammals to include stem genera has been based in good measure on (1) preference for an apomorphy-based definition featuring the jaw joint and/or (2) inclusion of basal taxa to mirror as much as possible traditional taxonomic content.

Kermack and Mussett (1958) identified the dentary-squamosal jaw joint as the necessary and sufficient key derived character (apomorphy) for Mammalia. As this joint was eventually discovered in tritheledontids, the concavoconvex form of the joint became the key apomorphy. Key apomorphies, however, inevitably require continued modification and, therefore, are of questionable utility in phylogenetic taxonomy (for a review, see Sereno, 1999). The jaw joint, in this particular case, is poorly described and/or preserved in critical immediate outgroups and basal ingroups, and homoplasy or further variation in the form of the jaw joint is possible, if not probable. Perhaps in recognition of these shortcomings, some authors who endorse the form of the jaw joint as a criterion for delineating Mammalia have chosen to *define* Mammalia on the basis of reference taxa (Luo et al., 2002, 19).

Because the phylogenetic meaning and taxonomic content of Mammalia has varied over the years (Rowe & Gauthier, 1992), it is difficult to isolate a single tradition. Some authors have viewed mammals as a grade or polyphyletic assemblage (Simpson, 1959; Kielan-Jaworowska, 1992) and others view them as a clade with monotremes in loose alliance with several extinct basal lineages as Prototheria (fig. 10.1; Kermack, 1967; Crompton & Jenkins, 1979). Only in the last twenty years has cladistic work supported specific phylogenetic hypotheses positioning taxa, such as *Sinoconodon* and *Morganucodon,* outside a clade comprising crown mammals (fig. 10.2B; Rowe, 1988; Crompton & Luo, 1993; Wible & Hopson, 1993).

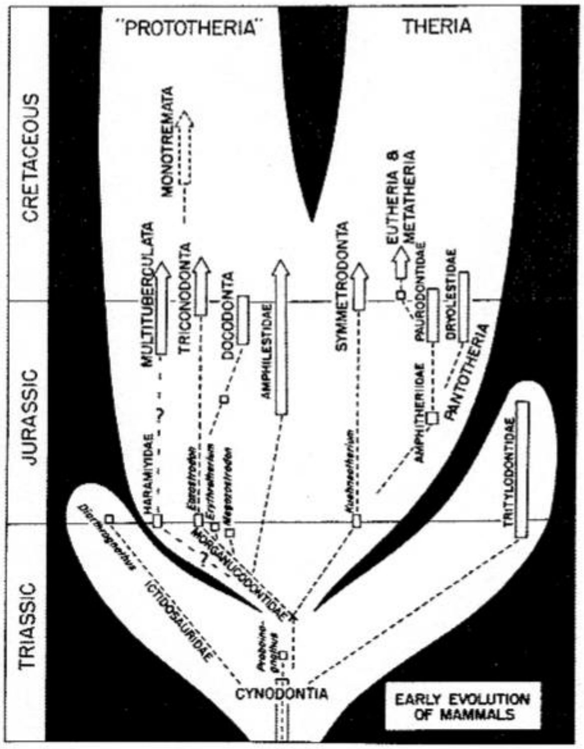

Figure 10.1. Phylogenetic diagram showing Mammalia as potentially monophyletic with a basal split along two lines, Prototheria and Theria (from Crompton & Jenkins, 1978, 1979).

That is why the important clade comprising crown mammals is left unnamed when Mammalia is used at a more inclusive level (Cifelli, 2001; Luo et al., 2002, 22).

The taxon Aves, in this regard, presents an instructive contrast to Mammalia. Traditionally, Aves was regarded as a monophyletic clade that comprised a recognized subclade of crown birds (Neornithes), outside of which were positioned several extinct stem taxa (e.g., *Archaeopteryx*). That century-long phylogenetic consensus provides the opportunity for phylogenetic definitions to maintain the traditional phylogenetic meaning and taxonomic content of both Aves and Neornithes (Sereno, 1998, in press). There is no such historical precedence for the taxon Mammalia and, as a result, no widely used alternative name for crown mammals.

Crown "Mammalia"

Rowe (1987, 209) proposed a crown definition of Mammalia as "the most recent common ancestor of its two principal divisions, Monotremata and Theria, and all of its descendants." Later definitions presented slight variations on this theme (Rowe, 1988, 247, 1993, 138). The definition of Mammalia presented here (table 10.1) is very similar but employs species as reference taxa, such as the genus *Ornithorhynchus* in place of "monotremes," to increase clarity of meaning and stability.

Recommended Revision

Given the foregoing, a crown group definition of Mammalia is preferred, because there appears to be little historical basis for a more inclusive phylogenetic definition of Mammalia. Available crown-group definitions of Mammalia, however, use vulgarizations of high-level clades as reference taxa (e.g., monotremes or therians) and are not linked by definition to subordinate stem-based taxa in node-stem triplets (Sereno, 1999). Stability of taxonomic content, nonetheless, is greatest when definitions (1) utilize formal lower-level, reference taxa that are phylogenetically remote from the node of concern and (2) are constructed for mutual stability in the face of new taxa or altered relationships (Sereno, 1999).

One solution outlines four node-stem triplets at the base of the mammalian clade (fig. 10.2A, table 10.1, Sereno, in review). Two of these comprise crown-total taxa defined by survivorship (Mammalia, Theria), and two are diversity-based node-stem triplets (Mammaliamorpha, Theriiformes) that link particularly diverse stem taxa (Tritylodontidae, Allotheria, respectively). Both tritylodontids (i.e., *Bienotherium*) and tritheledontids (i.e., *Pachygenelus*) are used as ingroup reference taxa for

Table 10.1. Indented taxonomic hierarchy and proposed phylogenetic definitions for four node-stem triplets among basal mammalian clades (see fig. 10.2A)

Taxonomic hierarchy	Phylogenetic definition
Mammaliamorpha Rowe, 1988	The least inclusive clade containing *Tritylodon langaevus* Owen,1884, *Pachygenelus monus* Watson, 1913, and *Mus musculus* Linnaeus, 1758.
Tritylodontidae Kühne, 1956	The most inclusive clade containing *Tritylodon longaevus* Owen, 1884, but not *Pachygenelus monus* Watson, 1913, *Mus musculus* Linnaeus, 1758.
Tritheledontidae Broom, 1912	The most inclusive clade containing *Pachygenelus monus* Watson, 1913 but not *Tritylodon longaevus* Owen, 1884, *Mus musculus* Linnaeus, 1758.
Mammaliaformes Rowe, 1988	The most inclusive clade containing *Mus musculus* Linnaeus, 1758 but not *Tritylodon longaevus* Owen, 1884 or *Pachygenelus monus* Watson, 1913.
Mammalia Linnaeus, 1758	The least inclusive clade containing *Ornithorhynchus anatinus* (Shaw, 1799) and *Mus musculus* Linnaeus, 1758.
Prototheria Gill, 1872	The most inclusive clade containing *Ornithorhychus anatinus* (Shaw, 1799) but not *Mus musculus* Linnaeus, 1758.
Monotremata Bonaparte, 1837	The least inclusive clade containing *Ornithorhynchus anatinus* (Shaw, 1799) and *Tachyglossus aculeatus* (Shaw, 1792).
Theriimorpha Rowe, 1993	The most inclusive clade containing *Mus musculus* Linnaeus, 1758 but not *Ornithorhynchus anatinus* (Shaw, 1799).
Theriiformes Rowe, 1988	The least inclusive clade containing *Mus musculus* Linnaeus, 1758 and *Taeniolabis taoensisn* (Cope, 1882).
Allotheria Marsh, 1880	The most inclusive clade containing *Taeniolabis taoensis* (Cope, 1882) but not *Mus musculus* Linnaeus, 1758 or *Ornithorhynchus anatinus* (Shaw, 1799).
Multituberculata Cope, 1884	The least inclusive clade containing *Taeniolabis taoensis* (Cope, 1882) and *Paulchofattia delgadoi* Kühne, 1961.
Trechnotheria McKenna, 1975	The most inclusive clade containing *Mus musculus* Linnaeus, 1758 but not *Taeniolabis taoensis* (Cope 1882) or *Ornithorhynchus anatinus* (Shaw, 1799).
Theria Parker & Haswell, 1897	The least inclusive clade containing *Mus musculus* Linnaeus, 1758 an *Didelphis marsupialis* Linnaeus, 1758.
Metatheria Huxley 1880	The most inclusive clade containing *Didelphis marsupialis* (Linnaeus, 1758) but not *Mus musculus* Linnaeus, 1758.

(continued)

Table 10.1. *(continued)*

Taxonomic hierarchy	Phylogenetic definition
Marsupialia Illiger, 1811	The least inclusive clade containing *Didelphis marsupialis* (Linnaeus 1758) and *Phalanger orientalis* (Pallas, 1766).
Eutheria Gill 1872	The most inclusive clade containing *Mus musculus* Linnaeus, 1758 but not *Didelphis marsupialis* Linnaeus 1758.
Placentalia Owen, 1837	The least inclusive clade containing *Dasypus novemcinctus* Linnaeus, 1758, *Elephas maximums* Linnaeus, 1758, *Erinaceus europaeus* (Linnaeus, 1758), *Mus musculus* Linnaeus 1758.

Note: Boldface indicates node-based definitions; regular typeface indicates stem-based definitions. Monotremata, Marsupialia, and Placentalia are best employed as node-based, crown taxa within more inclusive stem-based Allotheria, Metatheria, and Eutheria, respectively. Twelve deeply nested or type species are used as specifiers.

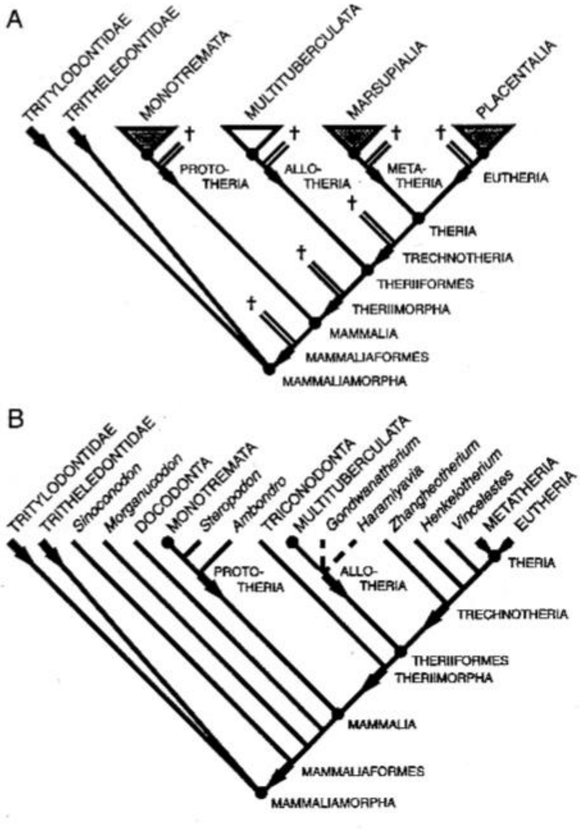

Figure 10.2. (A) Phylogenetic diagram at the base of Mammaliamorpha showing the arrangement of crown clades (shaded triangles), a diversity-based stem clade (empty triangle), extinct taxa (crosses), node-based taxa (dots), and stem-based taxon (arrows). (B) Phylogenetic diagram showing the arrangement of major groups at the base of Mammaliamorpha consistent with Luo et al. (2002) and others, utilizing phylogenetic definitions for higher-level taxa presented in this paper (table 10.1). Dashed lines indicate particularly weak support.

Mammaliamorpha, because opinion has varied as to which taxon is closer to Mammalia (Wible, 1991, Crompton & Luo, 1993, Wible & Hopson, 1993, Hopson & Kitching, 2001, Luo et al., 2002).

Two taxa in the proposed taxonomic framework have fallen from widespread use—Prototheria and Allotheria. Here they are revived as stem-based taxa that contain less inclusive node-based groups, Monotremata and Multituberculata, respectively (fig. 10.2A, table 10.1). Prototheria, so defined, specifically includes the extinct and often poorly known relatives of monotremes (e.g., *Steropodon* and *Obdurodon*), as the taxon was used in the earliest cladistic classifications of Mammalia (McKenna, 1974, 1975).

It should be noted that another taxon, Australophenida, has been erected recently with taxonomic content similar to Prototheria as defined above: "the common ancestor of *Ambondro, Ausktribosphenos,* living monotremes and all its descendants" (Luo et al., 2002, 22). Employing poorly known stem taxa (e.g., *Ausktribosphenos*) as reference taxa in a node-based definition, however, is a recipe for instability, because the relationships of genera based on such fragmentary material is likely to remain controversial (e.g., Rich et al., 2002). Archer et al. (1993), as one solution to this problem, included these extinct stem taxa within a stem-based Monotremata (Archer et al., 1993). The solution outlined here, in contrast, restricts Monotremata to a node-based crown clade and employs a stem-based Prototheria to gather together extinct, and often poorly known, stem taxa (fig. 10.2A, table 10.1).

Allotheria, like Prototheria, may be defined as a stem-based taxon more inclusive than Multituberculata, which has already been given a node-based definition (Simmons, 1993). A stem-based Allotheria includes a node-based Multituberculata and functions like Prototheria and Monotremata, respectively. Allotheria, as defined here, has the capacity to incorporate various poorly known extinct relatives of multituberculates, such as gondwanatherians and haramiyids, without basing its definition on such enigmatic forms (fig. 10.2A).

Metatheria and Eutheria, likewise, are defined here as stem-based taxa, following comments of similar intent by Novacek et al. (1997, 483) regarding the definition of Eutheria. Each includes its respective crown clade, Marsupialia and Placentalia (Archibald & Deutschman, 2001, 108), here explicitly defined (table 10.1). In the case of the crown clade Placentalia, the configuration of basal taxa is controversial; candidate clades include xenarthrans, afrotherians, or erinaceomorphs or some combination of the three (Waddell et al., 1999, Liu & Miyamoto, 1999, Liu et al., 2001, Cifelli, 2001). Using several representative genera as ingroup reference taxa (*Dasypus, Elephas, Erinaceus, Mus*) in the definition of Placentalia serves to identify the same common placental ancestor regardless of which hypothesis ultimately proves to be the most robust (table 10.1).

Thus, in this scheme, four familiar high-level taxa that comprise the bulk of mammalian diversity—Prototheria, Allotheria, Metatheria, and Eutheria—are given stem-based definitions. Nested within each of these clades is a widely used node-based taxon, three of which are crown groups (Monotremata, Marsupialia, Placentalia) and the last of which constitutes the most diverse mammalian clade of the Mesozoic (Multituberculata) (fig. 10.2A, table 10.1). Node-stem triplets stabilize the relationship between taxa; Theria, for example, equals Metatheria plus Eutheria in taxonomic content, regardless of the discovery of new basal therians or the repositioning of existing basal taxa. Crown groups, in addition, are associated with widely used names (Mammalia, Theria, Monotremata, Marsupialia, Placentalia).

The following institutional abbreviations are used: FMNH, Field Museum of Natural History, Chicago; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MCZ, Museum of Comparative Zoology, Cambridge; PSS-MAE, Paleontology and Stratigraphic Section of the Geologic Institute, Mongolian Academy of Sciences, Mongolian-American Museum Expedition, Ulaan Baatar/New York; UCPC, University of Chicago Paleontology Collection, Chicago; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Previous Work

Forelimb Posture in Multituberculates

Simpson (1928a) regarded the multituberculate shoulder girdle and forelimb as similar in design to that in therians, basing his observations on the proximal ends of the scapulocoracoid and humerus in *Ptilodus* and *Djadochtatherium.* About the ventral orientation of the glenoid, he remarked that it was "exactly that of higher mammals and fundamentally unlike that in monotremes" (1928a, 11). "The importance of the scapula," he continued with remarkable prescience, is that it demonstrates that multituberculates "cannot possibly have been ancestral or closely related to the monotremes." Simpson, however, did not further characterize multituberculate forelimb posture.

By manipulating isolated elements of Late Cretaceous multituberculates, Sloan and Van Valen (1965, 3) concluded, similarly, that in the shoulder joint "movement of the humerus is apparently in the same plane as the blade of the scapula." This orientation presupposes a more parasagittal forelimb posture. In the elbow joint, they continued, "movement of the ulna . . . is restricted to a single plane" by the shapes of opposing surfaces.

On the basis of a well-preserved skeleton of the Paleocene multituberculate *Ptilodus* and isolated girdle and forelimb bones from the Late Cretaceous, Krause and Jenkins (1983, 235) came to similar conclusions, noting that "multituberculate shoulder girdle posture and mobility were comparable to those of modern therians."

In marked contrast to previous authors, Kielan-Jaworowska and Gambaryan (1994) concluded that the forelimbs in multituberculates are significantly abducted (i.e., sprawling) and that their gate, when moving fast, "was different from those occurring in modern mammals" (1994, 82). Their model was based in large part on Late Cretaceous cimolodontan multituberculates from Mongolia. In midstride, the humerus was shown extending from the glenoid nearly perpendicular to the skeletal axis (Gambaryan & Kielan-Jaworowska, 1997, fig. 10, fig. 10.12). In contrast to previous studies of the mammalian elbow joint (Jenkins, 1973), they proposed a causal link between the trochlear elbow joint and the parasagittal posture of the forelimb in therians; the condylar elbow joint in multituberculates, they suggested to the contrary, is functionally consistent with a sprawling forelimb posture and "does not support multituberculate-therian sister-group relationship" (Gambaryan & Kielan-Jaworowska, 1997, 40).

Locomotor Specialization in Multituberculates

On the basis of fragmentary postcranial remains, Gidley (1909, 621) suggested, "the relatively large proportions of the pelvis and hind limbs strongly suggest that *Ptilodus* was saltatorial." Simpson (1926) challenged this interpretation on the basis of comparative limb proportions of recent mammals. In his view, multituberculate postcranial remains then available were insufficient to determine conclusively whether multituberculates were primarily terrestrial or arboreal herbivores. He concluded (1926, 247), "it would be remarkable if many of them were not at least semi-arboreal."

Jenkins and Krause (1983) and Krause and Jenkins (1983) described tarsal, pedal, and caudal features in *Ptilodus* that allowed significant rotational capability of the pes, enhanced pedal grasping with a divergent hallux, and a prehensile tail, all potentially assisting in headfirst descent within an arboreal habitat. They stated, nevertheless, that these "adaptations for climbing" do not imply that *Ptilodus* or other multituberculate genera were "exclusively arboreal" (Krause & Jenkins, 1983, 243).

More recently, Kielan-Jaworowska and Gambaryan (1994) argued, to the contrary, that these same osteological features are present in running and jumping mammals. On the basis of a more complete multituberculate pes in *Kryptobaatar,* they concluded that the hallux might not have been divergent, at least in Asian cimolodontans. Returning to Gidley's view of multituberculates as terrestrial saltators, they argued multituberculates used an asymmetrical jumping gait at fast speeds.

Forelimb Posture in Other Nontherian Mammals

Forelimb posture in other basal mammals that preserve at least part of the pectoral girdle and forelimb have been interpreted either as sprawling or more parasagittal. The triconodont *Gobiconodon* was reconstructed with the forelimb in a more parasagittal posture, based on the lower portion of the scapula and a partial forelimb (Jenkins and Schaff, 1988, fig. 1). A similar forelimb posture was regarded as probable based on the more complete remains of *Henkelotherium* (Krebs, 1991, fig. 12) and *Vincelestes* (Rougier, 1993, fig. 104), mammals usually placed closer to therians (fig. 10.2B).

Recent discoveries of nearly complete, albeit flattened, skeletons of the triconodont *Jeholodens* (Ji et al., 1999) and the more advanced mammal *Zhangheotherium* (Hu et al., 1997) have led to other interpretations. Regarding *Jeholodens,* Ji et al. (1999, 327, 330) proposed that the mobile shoulder girdle arose independently from that in therians and that, despite the advanced form of the girdle with its ventrally facing glenoid, it was associated with a "sprawling elbow." Similarly for *Zhangheotherium,* Hu et al. (1997, 141, fig. 5) argued that it possessed a mobile shoulder girdle, but that the humerus was "more abducted" than that in most living therians. The evidence for both of these interpretations of forelimb posture, however, is questioned below.

New Fossil Evidence

Kryptobaatar, a Multituberculate

The discovery of an articulated skeleton of *Kryptobaatar dashzevegi* (formerly tentatively referred to as *Bulganbaatar;* Sereno & McKenna, 1995) that preserves both shoulder girdles and forelimbs in articulation clarifies many details regarding the structure and function of the shoulder and elbow joints (s. 10.2–10.4, 10.7; Sereno, in review).

Shoulder Girdle. The shoulder girdle is composed of scapulocoracoids, clavicles and an interclavicle. Unlike most mammals, the scapulocoracoid is longer than the humerus and approximately five times longer than its greatest width. The blade is narrower than in other mammals and mammalian outgroups. Both dorsal and ventral edges project laterally, the former is usually regarded as the homolog of the therian scapular spine (figs. 10.3, 10.7). The long axis of the blade may have been oriented only about 60° above the horizontal, rather than vertical as in some mammals (fig. 10.8; Sereno, in review). The so-called "incipient supraspinous fossa" occurs as a subtle depression along the dorsal margin of the blade near the base of the acromial process (fig. 10.3). The large, thin, T-shaped acromial process is nearly completely preserved on the right scapulocoracoid. The large size of the acromial process effectively positions the acromioclavicular articulation lateral to the humeral head and glenoid (fig. 10.7A). The ventrally facing glenoid cavity forms an elongate, arched articular surface (fig. 10.7). It is broadest under the blade, where the surface is concave, and canted slightly laterally (fig. 10.4). The coracoid is completely

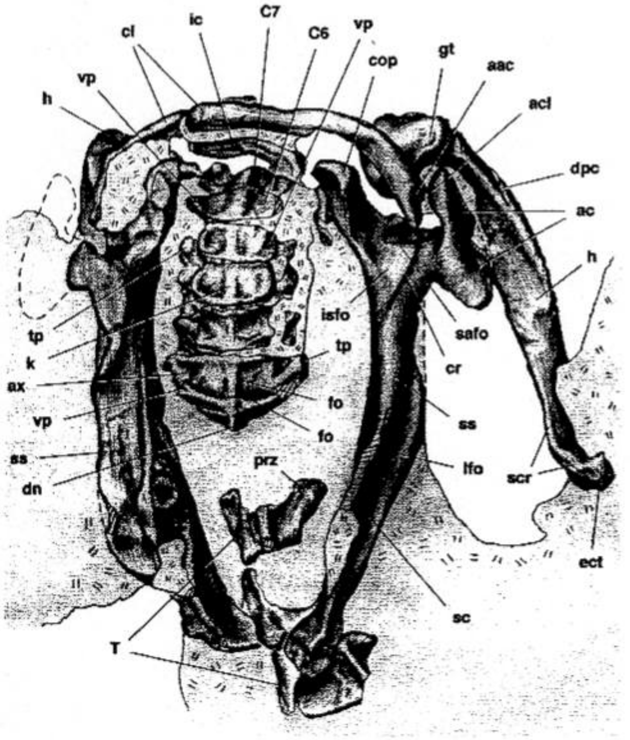

Figure 10.3. Partial skeleton of *Kryptobaatar dashzevegi* (PSS-MAE 103) in dorsal view. Scale bar equals 1 cm. Cross-hatching indicates broken bone surface. Abbreviations: 6,7, vertebral number; aac, articular surface for the acromion; ac, acromion; acl, articular surface for the clavicle; ax, axis; C, cervical; cl, clavicle; cop, coracoid process; cr, crest; dn, dens; dpc, deltopectoral crest; ect, ectepicondyle; fo, foramen; gt, greater tuberosity; h, humerus; ic, interclavicle; isfo, incipient supraspinous fossa; k, keel; lfo, lateral fossa; prz, prezygapophysis; safo, subacromial fossa; sc, scapula; scr, supinator crest; ss, scapular spine; T, thoracic vertebra; tp, transverse process; vp, ventral process.

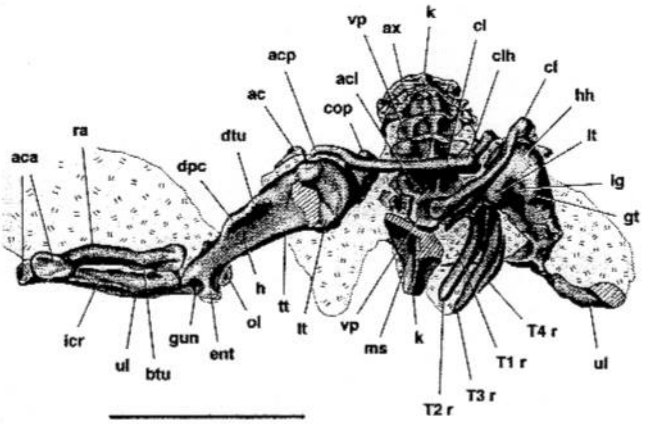

Figure 10.4. Partial skeleton of *Kryptobaatar dashzevegi* (PSS-MAE 103) in anterior view. Scale bar equals 1 cm. Cross-hatching indicates broken bone surface. Abbreviations: 1-4, rib number; ac, acromion; aca, articular surface for the carpus; acl, articular surface for the clavicle; acp, acromial process; ax, axis; btu, biceps tubercle; cl, clavicle; clh, clavicular head; cop, coracoid process; dpc, deltopectoral crest; dtu, deltoid tubercle; ent, entepicondyle; gt, greater tuberosity; gun, groove for the ulnar nerve; h, humerus; hh, humeral head; icr, interosseous crest; ig, intertubercular groove; k, keel; lt, lesser tuberosity; ms, manubrium sterni; ol, olecranon; r, rib; ra, radius; T, thoracic; tt, teres tuberosity; ul, ulna; vp, ventral process.

co-ossified with the scapula and has never been recovered as separate element in any multituberculate.

The clavicles are slender rod-shaped elements that curve from the acromion to the midline, where they presumably articulate in a pair of shallow fossae on the anterior face of the interclavicle (fig. 10.3). The left and right clavicle have been dislodged ventrally and dorsomedially, respectively (fig. 10.4). The fossae are broadly open, and the joint, for this reason, appears to have allowed pivoting movement of the clavicle in several directions. The lateral half of the clavicle is dorsoventrally flattened and curves posteriorly toward the acromion and over the bulbous head of the humerus. There does not appear to be any contact between the clavicle and humeral head.

The interclavicle is shaped like a three-leaf clover. The interclavicle is strongly bowed posteriorly, unlike the more flattened interclavicle in other mammals and mammalian outgroups. Its shape and curvature are unique to multituberculates (figs. 10.4, 10.5, 10.7). The posterior margin of the ventral flange rests against the anterior margin of the manubrium sterni.

Girdle Joints. Although the glenoid has been described as teardrop-shaped (McKenna, 1961, 6) or pear-shaped (Kielan-Jaworowska and

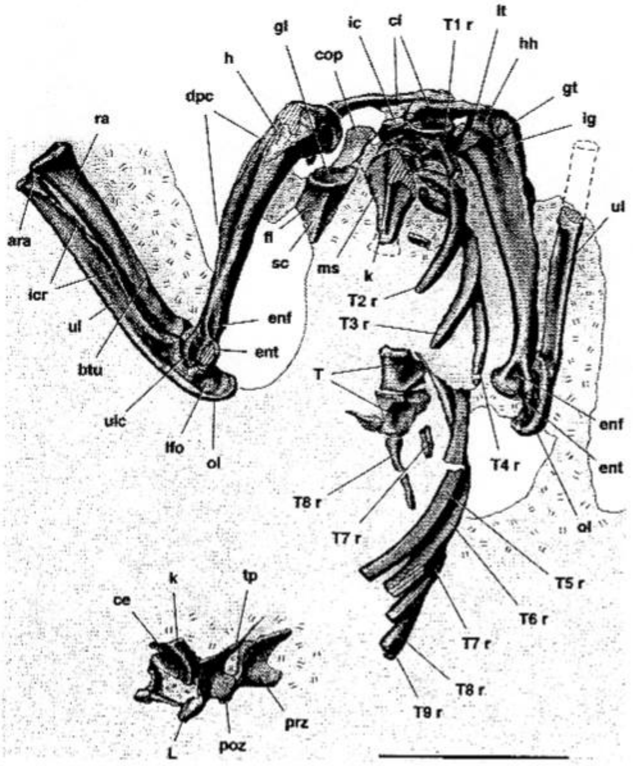

Figure 10.5. Partial skeleton of *Kryptobaatar dashzevegi* (PSS-MAE 103) in ventral view. Scale bar equals 1 cm. Cross-hatching indicates broken bone surface. Abbreviations: 1-9, rib number; ara, articular surface for the radius; btu, biceps tubercle; ce, centrum; cl, clavicle; cop, coracoid process; dpc, deltopectoral crest; enf, entepicondylar foramen; ent, entepicondyle; fl, flange; gl, glenoid; gt, greater tuberosity; h, humerus; hh, humeral head; ic, interclavicle; icr, interosseous crest; ig, intertubercular groove; k, keel; lfo, lateral fossa; lt, lesser tuberosity; L, lumbar vertebra; ms, manubrium sterni; ol, olecranon; poz, postzygapophysis; prz, prezygapophysis; r, rib; ra, radius; sc, scapula; T, thoracic vertebra; tp, transverse process; ul, ulna; ulc, ulnar condyle.

Gambaryan, 1994, 22) in multituberculates, this may be based on incomplete specimens. In PSS-MAE 103, the glenoid is narrow and subrectangular; it is approximately four times longer than wide and is longer than the diameter of the humeral head (fig. 10.7F). The form of the glenoid appears very similar in other multituberculate species. The posterior (scapular) portion is transversely broader, more concave, and faces ventrally. The scapular portion of the glenoid is offset laterally (figs. 10.5, 10.7F). The anterior (coracoid) portion of the glenoid extends to the end of the coracoid process and is transversely flat. In lateral view, it arches anteroventrally (fig. 10.7A) and extends between the greater and lesser trochanters (fig. 10.7F). In this region, the glenoid is one-third the width of the humeral head, allowing considerable transverse mobility of the humeral head at the shoulder joint. The anteroposterior length of the glenoid, in contrast, exceeds that of the humeral head. During maximum extension, anteriormost and posteriormost portions of the glenoid extend beyond the humeral head. The longer length of the glenoid does not appear to limit anteroposterior flexion-extension at the shoulder joint (Jenkins, 1971b).

The right acromioclavicular joint is slightly disarticulated (fig. 10.3). The smooth, narrow joint surface suggests that the clavicular brace may have had a somewhat flexible attachment at the shoulder. The medial end of each clavicle is disarticulated from the interclavicle (fig. 10.4). The medial one-third of the clavicle has a subcylindrical shaft and a rounded medial head that appears to have articulated in a shallow fossa on the interclavicle (figs. 10.4, 10.7B). This joint doubtless allowed some movement, as there are no ligament striae, deeply contoured articular surfaces, or fusion, as occurs in monotremes or immediate mammalian outgroups (Jenkins and Parrington, 1976, fig. 3).

Forelimb. The humeral head has been described as hemispherical, but the medial portion of the head (closer to the lesser trochanter) is the most convex and has the greatest contact with the glenoid (fig. 10.7). Greater and lesser trochanters are nearly identical in size. The lesser trochanter is slightly lower in position than the greater trochanter, and its perimeter is better demarcated from the articular surface of the head (fig. 10.4; Kielan-Jaworowska & Qi, 1990; Kielan-Jaworowska & Gambaryan, 1994), as in *Morganucodon* (Jenkins & Parrington, 1976). The deltopectoral crest develops from the ridge below the greater trochanter and extends distally to an apex located near the midpoint of the humeral shaft (figs. 10.4, 10.7D). The distal end is only moderately expanded (ten percent) compared with humeral length. The transverse axis of the distal end of the humerus, as measured against an axis through the lesser and greater trochanters, exhibits torsion of only about 15° (fig. 10.7G). The entepicondyle is more expanded transversely than the ectepicondyle, and the radial condyle is broader than the ulnar condyle, as seen in ventral view (figs. 10.6C, 10.11B; Kielan-Jaworowska & Qi, 1990; Kielan-Jaworowska and Gambaryan, 1994). The asymmetry of the ulnar condyle is of particular interest. In proximal or distal view, the ventral surface of the condyle is beveled strongly, so that the entire surface faces ventrolaterally toward the radial condyle (figs. 10.6, 10.11B). The anterior portion of the ulnar condyle, thus, might better be described as a "hemicondyle," because it lacks a median eminence and symmetrical (ventromedially facing) articular surface. This asymmetric articular surface resembles the ulnar portion of the therian trochlear joint (Sereno & McKenna, 1995). In dorsal view, the articular surface narrows to form a keel-shaped condyle (fig. 10.11B). The prominent, hemispherical radial condyle is surrounded by a nonarticular trough, the radial fossa (figs. 10.6C, 10.7D). The radial condyle flattens as it passes under the humerus and becomes transversely concave in dorsal

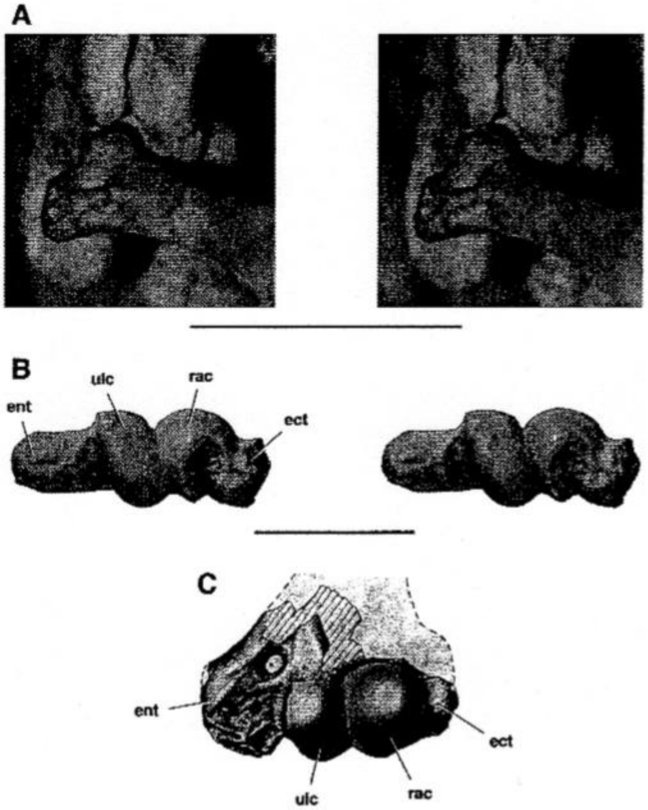

Figure 10.6. (A) Stereopair of right elbow joint of *Kryptobaatar dashzevegi* (PSS-MAE 103) in ventromedial view. (B) Stereopair in distal view and (C) drawing in ventral view of the distal end of left humerus of *Lambdopsalis bulla* (IVPP V7151.150). Scale bar in (A) equals 5 mm; scale bar in (B) and (C) equals 1 cm. Abbreviations: ect, ectepicondyle; ent, entepicondyle; rac, radial condyle; ulc, ulnar condyle.

view (figs. 10.6B, 10.11B). The dorsal portion of the radial condyle, thus, also bears a strong resemblance to the therian trochlear joint.

The olecranon process of the ulna is well developed and the semilunar notch forms a deep articular trough with raised proximal and distal lips (fig. 10.11B). The semilunar notch is divided by an intercondylar crest into a larger medial socket for the ulnar condyle and a smaller, more strongly beveled, lateral socket for the radial condyle of the humerus. An oval concave articular facet—the radial notch—truncates the distal margin of the semilunar notch and accommodates the head of the radius. A crescentic interosseous crest builds from a ridge at midshaft to a well-developed flange on the distal one-third of the shaft (fig. 10.5). The small distal end of the ulna is nearly circular with a concave distal articular surface for the carpus (fig. 10.4).

The expanded head of the radius has a subquadrate contour in proximal view (figs. 10.4, 10.6A). Its concave proximal articular surface rotates

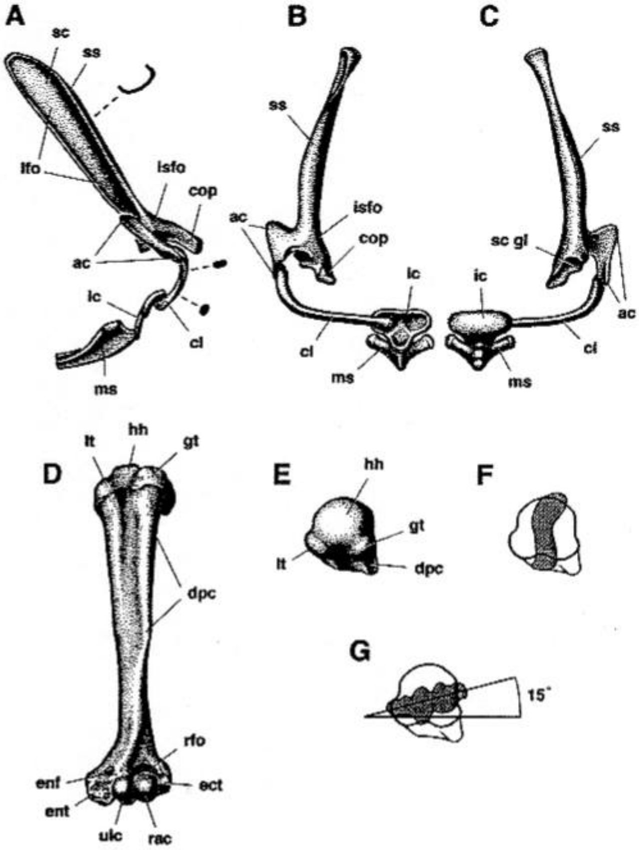

Figure 10.7. Reconstruction of the pectoral girdle, manubrium sterni, and humerus of *Kryptobaatar dashzevegi* (PSS-MAE 103) (D–G enlarged by twenty percent relative to A–C). (A) Pectoral girdle and manubrium sterni in right lateral view with cross sections of the scapular blade and clavicle; (B, C) pectoral girdle and manubrium sterni in anterior and posterior views; (D) left humerus in ventral view; (E) left humerus in proximal view; (F) left humerus in proximal view and left glenoid (shaded); (G) left humerus in proximal view and left distal end (shaded). Abbreviations: ac, acromion; cl, clavicle; cop, coracoid process; dpc, deltopectoral crest; ect, ectepicondyle; ent, entepicondyle; enf, entepicondylar foramen; gl, glenoid; gt, greater tuberosity; hh, humeral head; ic, interclavicle; isfo, incipient supraspinous fossa; lfo, lateral fossa; lt, lesser tuberosity; ms, manubrium sterni; rac, radial condyle; rfo, radial fossa; sc, scapula; ss, scapular spine; ulc, ulnar condyle.

against the hemispherical radial condyle on the humerus. During such long-axis rotation, the swollen rim on the medial aspect of the head of the radius slides against the concave radial notch on the ulna (fig. 10.11B; Krause & Jenkins, 1983, fig. 15). The shaft narrows in width distal to the head and then is slightly swollen again by the biceps tubercle (fig. 10.4). The distal two-thirds of the shaft is flattened transversely, and the distal end flares to twice the width of that of the ulna. In distal view, the long axis of the distal articular ends of the radius and ulna is oriented anteroposteriorly, at approximately 90° to the transverse axis of the elbow joint (fig. 10.5).

Elbow Joint. The right and left forearms are flexed to angles of approximately 20° and 60°, respectively, to the long axis of the humerus (fig. 10.5). Extension to an angle of approximately 180° appears to have been possible, given the dorsal continuation of the ulnar condyle and deep olecranon fossa on the humerus. During extension, the elbow operates as a transverse hinge joint that is slightly skewed from a transverse axis. A small amount of abduction of the manus occurs with extension at the elbow joint due to the spiral form of the ulnar condyle (figs. 10.4, 10.6B, 10.11B; Jenkins, 1973). The anterior portion of the ulnar condyle of the humerus forms a cam for the ulna that is flattened and beveled posteromedially (Jenkins, 1973). When the elbow is flexed (fig. 10.6A), the ulna articulates only on the flattened lateral aspect of the condyle. The bulbous radial condyle and prominent biceps tubercle suggest that considerable long-axis rotation of the radius was possible.

Jeholodens, a Triconodont

Recent discovery of an articulated triconodont skeleton from China, *Jeholodens jenkinsi* (Ji et al., 1999), supplements previous information on the triconodont shoulder girdle and forelimb, (*Gobiconodon ostromi;* Jenkins & Schaff, 1988). Ji et al. (1999) believed that the shoulder joint in *Jeholodens* was mobile but that the elbow joint was abducted into a sprawling posture. They described a small interclavicle with loose attachment to the clavicle and an "incipient ulnar trochlea" at the distal end of the humerus resembling that in therians.

Reexamination of the specimen, however, reveals that the medial ends of the clavicles, the interclavicle, and the manubrium sterni are completely hidden from view by other elements and matrix. It is not possible, likewise, to verify the presence of an incipient trochlea at the distal end of the humerus, which has a somewhat convex distal articular margin. As this portion of the humerus is preserved and exposed in dorsal view, it resembles neither a trochlea nor well-formed distal condyles.

In *Jeholodens,* the broad supraspinous fossa, ventrally positioned acromion, and ventrally facing glenoid of the scapula are clearly derived, as established in *Gobiconodon* (Jenkins & Schaff, 1988). The clavicle in *Jeholodens* is strap-shaped but more robust than in *Kryptobaatar.* The elbow joint in triconodonts is best exposed in *Gobiconodon* (Jenkins & Schaff, 1988, figs. 14, 15). A distal trochlea on the humerus has been reported but not figured. The proximal end of the ulna has a deep semilunar notch with an intercondylar crest, similar to that in multituberculates and therians (fig. 10.11B, 10.C). The elbow joint appears to have been designed for considerable flexion-extension. Based on *Jeholodens* and *Gobiconodon,* therefore, triconodonts appear to have an advanced mobile shoulder girdle with a fully developed supraspinous fossa. The

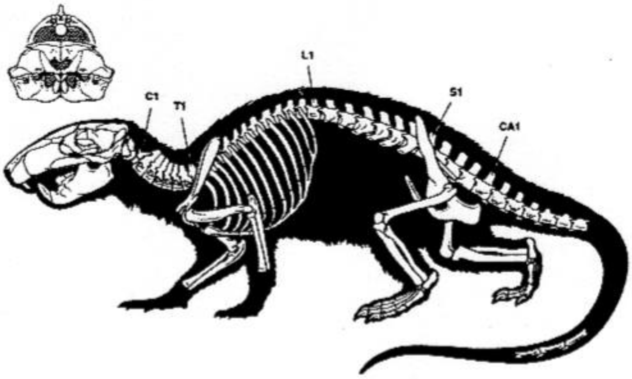

Figure 10.8. Skeletal reconstruction of *Kryptobaatar dashzevegi*. Skull, neck, ribcage, pectoral girdle, and forelimbs based on PSS-MAE 103; lumbar and proximal and midcaudal vertebrae, pelvic girdle, and hind limbs based on ZPAL MgM-I/41. Lumbar vertebrae also based on *Nemegtbaatar gobiensis* (ZPAL MgM-I/81). Top drawing shows the skull and the broadest rib in the ribcage. Abbreviations: C1, atlas; T1, first thoracic vertebra; L1, first lumbar vertebra; S1, first sacral vertebra; CA1, first caudal vertebra.

forelimb appears to have had a more parasagittal than sprawling posture (*contra* Ji et al., 1999) that emphasized hinge-like flexion-extension at the elbow, as previously shown in a skeletal reconstruction of *Gobiconodon* (Jenkins & Schaff, 1988, fig. 1).

Zhangheotherium, a Symmetrodont

Recent discovery of an articulated symmetrodont skeleton from China, *Zhangheotherium quinquecuspidens* (Hu et al., 1997), provided information on the symmetrodont shoulder girdle and forelimb. Like Ji et al. (1999), Hu et al. (1997) concluded that the shoulder girdle of *Zhangheotherium* was mobile, with a pivotal clavicle-interclavicle joint, but that the elbow joint is more primitive than that in therians, based on three features of the humerus: the "incipient trochlea for the ulna," "large lesser tubercle relative to the greater tubercle," and more pronounced torsion (30°) in the humeral shaft. Later in the same report, however, they observed the reverse about the size of the humeral tuberosities (tubercles), stating that the greater tuberosity is "slightly wider" than the lesser. Likewise, they noted a "weakly developed ulnar condyle" in addition to the trochlea at the distal end of the humerus (Hu et al., 1997, 140–141).

The holotypic skeleton of *Zhangheotherium* is preserved in ventral view, exposing the entire pectoral girdle (Hu et al., 1997, fig. 1), opposite the condition in the holotypic skeleton of *Jeholodens*. Reexamination of the specimen has revealed new information. Several derived features are present in the pectoral girdle including the supraspinous fossa, ventrally facing glenoid, ventrally positioned acromioclavicular articulation, and reduced size of the interclavicle. There is ample evidence for mobility in the pectoral girdle but no evidence that the humerus was held in a subhorizontal, or sprawling, posture, as proposed by Hu et al. (1997). Both forelimbs are preserved, although neither fully exposes either the proximal or distal articular ends of the humerus. The relative size of the humeral tuberosities, thus, is a moot point (*contra* Hu et al., 1997). The prominence and relative size of the tuberosities, in any case, have been shown to vary considerably within subgroups of extant mammals (e.g., Argot, 2001, fig. 8.1) and are not indicative of erect versus sprawling postures. The same is true regarding humeral torsion and forelimb posture. The torsion reported in *Zhangheotherium* (30°) is a rough approximation at best, because the proximal axis across the tuberosities cannot be precisely established. And the form of the elbow joint remains uncertain, because the lateral portion of the distal end of the humerus is not fully exposed.

Thus, on the basis of *Zhangheotherium,* symmetrodonts appear to have an advanced mobile shoulder girdle with a fully developed supraspinous fossa. The great capacity for hinge-like flexion-extension at the elbow joint is shown on the right side of the skeleton, where flexion at the elbow has brought the forearm against the humerus. The forelimb may well have had a more parasagittal than sprawling posture that emphasized hinge-like flexion-extension at the elbow, as in *Jeholodens.*

Phylogenetic Comparisons

Specializations in the Pectoral Girdle and Forelimb

Multituberculata. Six features in the pectoral girdle and forelimb of *Kryptobaatar* are unusual compared with other mammals and mammalian outgroups and appear to characterize all multituberculates, including both Late Cretaceous and Paleocene multituberculates (Krause & Jenkins, 1983; Kielan-Jaworowska & Gambaryan, 1994).

1. Scapular blade convex with C-shaped cross section. The transversely convex scapular blade in multituberculates contrasts with that in therians, monotremes, and mammalian outgroups, in which the central portion of the blade is relatively flat (figs. 10.9, 10.10).
2. Coracoid glenoid subrectangular (Sereno & McKenna, 1995). The elongate, subrectangular shape of the anterior portion of the glenoid in multituberculates (fig. 10.7E) is easily distinguished

from the subtriangular shape that characterizes therians, monotremes, and mammalian outgroups (figs. 10.9, 10.10).

3. Coracoid posterior process absent (Sereno & McKenna, 1995). In multituberculates, there is no development of a discrete posterior process on the coracoid, which presumably forms the narrow anterior extension of the glenoid. The prominent anteromedial corner of the coracoid process is likely the much reduced homolog of the posterior process of therians, monotremes, and mammalian outgroups.
4. Interclavicle clover-shaped (Sereno & McKenna, 1995). The interclavicle in multituberculates has a unique three-leaf clover shape. The presence of a clover-shaped interclavicle in the fossorial Paleocene taeniolabidoid *Lambdopsalis* (IVPP, unnumbered, articulated clavicle and manubrium sterni) suggests that this bone, like much of the multituberculate skeleton, differs little in size and shape. In therians, the interclavicle is reduced in size and fused to the manubrium sterni (Klima, 1987). In monotremes and mammalian outgroups, the ventral process is usually longer than the lateral process and has a distinctive shape (Jenkins & Parrington, 1976; Kemp, 1982).
5. Interclavicle dorsoventrally arched (Sereno & McKenna, 1995). In multituberculates the interclavicle is dorsoventrally bowed, with the concave anterior surface articulating with the clavicle (figs. 10.7). The interclavicle in monotremes, in contrast, is transversely arched (fig. 10.9B). In immediate mammalian outgroups, the interclavicle is flat (Jenkins & Parrington, 1976; Sun & Li, 1985).
6. Ulnar distal articular end approximately one-third the area of that of the radius. The distal end of the ulna tapers significantly in diameter. The radius, in contrast, expands in width so that the articular surface of its distal end is three times the area of that of the ulna (fig. 10.4). A marked size differential of the articular ends of the bones of the forearm may well occur in all multituberculates (e.g., Krause & Jenkins, 1983, fig. 14). In monotremes, the triconodonts *Jeholodens* and *Gobiconodon* (Ji et al, 1999; Jenkins & Schaff, 1988), *Henkelotherium* (Krebs, 1991), and the basal eutherian *Eomaia* (Ji et al., 2002), the distal ends of the radius and ulna appear to be subequal. In many other mammals and mammalian outgroups, however, the distal end of the radius is larger, although not to the degree observed in *Kryptobaatar* (e.g., *Morganucodon;* Jenkins & Parrington, 1976; *Kayentatherium,* MCZ 8812).

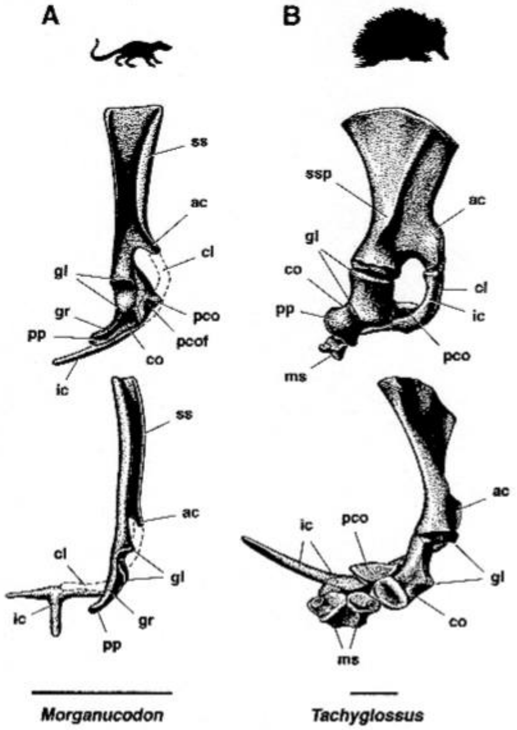

Figure 10.9. Pectoral girdle of (A) *Morganucodon watsoni,* a basal mammaliaform, and (B) *Tachyglossus aculeatus* (UCPC, recent collection), an extant monotreme in lateral (above) and posterior (below) views. The distal scapular blade of *Morganucodon* based on the closely related trithelodotid *Pachygenelus.* Scale bars equal 1 cm. Abbreviations: ac, acromion; cl, clavicle; co, coracoid; gl, glenoid; gr, groove; ic, interclavicle; ms, manubrium sterni; pco, procoracoid; pcof, procoracoid foramen; pp, posterior process; ss, scapular spine; ssp, secondary scapular spine.

Monotremata. Among living mammals, the fixed pectoral girdle in monotremes is strikingly primitive. Nevertheless, six derived features, all possible fossorial adaptations, appear to have been present in the common monotreme ancestor.

1. Glenoid facing laterally. In monotremes, the glenoid faces almost directly laterally rather than posterolaterally as in mammalian outgroups (Jenkins & Parrington, 1976) or posteroventrally as in theriimorphs (fig. 10.10). In the echidna *Tachyglossus,* the glenoid is angled very slightly posteriorly, so that the edge of the glenoid is visible in posterior view (fig. 10.9). In the platypus *Ornithorhynchus,* the glenoid is angled very slightly anteriorly, so that the edge of the glenoid is visible in anterior view.
2. Coracosternal contact (Sereno & McKenna, 1995). In *Ornithorhynchus* and *Tachyglossus,* a synovial joint is present between a transverse process on the coracoid and the manubrium sterni (fig. 10.9B). Contact between these bones is unknown elsewhere among synapsids.

3. Coracoid and procoracoid overlap of interclavicle (Sereno & McKenna, 1995). In monotremes, the pectoral girdle is strengthened in the midline by overlapping articulations between the coracoid and procoracoid and between the opposing procoracoids (fig. 10.9B). In other mammals and mammalian outgroups, opposing pectoral girdles never contact, and contact between the pectoral girdle and axial skeleton is limited to the claviculosternal joint.
4. Clavicle-interclavicle fusion (Sereno & McKenna, 1995). These bones fuse only in monotremes. Complete fusion occurs late in development and characterizes fully grown adults.
5. Interclavicle lateral process long, contacting acromion (Sereno & McKenna, 1995). The lateral process of the interclavicle is long enough to contact the acromion only in monotremes among tetrapods (fig. 10.9B).
6. Interclavicle posterior process fan-shaped (Sereno & McKenna, 1995). In monotremes, the posterior process of the interclavicle has an unusual fan shape. It expands in width toward its posterior contact with the manubrium sterni. A unique low median keel is also present on the ventral aspect of the interclavicle in both *Ornithorhynchus* and *Tachyglossus*. In multituberculates (fig. 10.7), basal mammaliamorphs (fig. 10.9A; Jenkins & Parrington, 1976; Sun & Li, 1985), and more distant outgroups (Jenkins, 1971b), the posterior process is tongue-shaped or parallel-sided and does not expand in width distally.

Synapomorphies in the Pectoral Girdle and Forelimb

This section describes synapomorphies in the pectoral girdle and forelimb among basal mammalian clades (fig. 10.15, tables 10.2, 10.3). The authors cited after a synapomorphy (also table 10.2) were the first to use the character in a phylogenetic analysis (for a more detailed discussion, see Sereno, in review).

Mammalia. Four synapomorphies from the pectoral girdle and forelimb characterize mammals.

1. Scapulocoracoid suture fused (Sereno & McKenna, 1995). With rare exception among fossil and recent mammals (McKenna, 1961; Klima, 1987; Jenkins & Schaff, 1988), the scapulocoracoid suture fuses at some point during development. In monotremes (*Ornithorhynchus, Tachyglossus*), fusion occurs only in older individuals (e.g., unfused in fig. 10.15B). In therians, fusion may

Table 10.2. Characters and character-states in the pectoral girdle and forelimb among basal mammals and mammalian outgroups, listed by clade (A) and anatomical region (B)

A. Listed by Clade

Mammalia

1. Scapulocoracoid suture: open (0); fused (1). (Sereno & McKenna, 1995)
2. Coracoid groove: present (0); absent (1). (Sereno & McKenna, 1995)
3. Coracoid posterior process, length: longer or subequal to (0), or shorter than (1), maximum glenoid diameter. (modified from Sereno & McKenna, 1995)
4. Procoracoid foramen: present (0); absent (1). (Sereno & McKenna, 1995)

Theriimorpha

5. Acromion position: dorsal (0), or lateral (1), to the glenoid. (Rowe, 1988)
6. Supraspinous fossa along anterior margin of scapular blade: absent or rudimentary (0); present (1). (Rowe, 1988)
7. Glenoid width: subequal to (0), or approximately 60% of (1), transverse width of the humeral head. (Sereno & McKenna, 1995)
8. Coracoid glenoid, orientation: posterolateral (0); lateral (1); posteroventral (2). (Sereno & McKenna, 1995)
9. Coracoid glenoid, form: convex (0); concave (1). (Sereno & McKenna, 1995)
10. Procoracoid: present (0); reduced/fused with manubrium sterni (1). (Rowe, 1988)
11. Clavicular head, form: tongue-shaped (0); rod-shaped (1).
12. Interclavicle size: larger (0), or smaller (1), than the sternum (anteroposterior and transverse dimensions). (modified from Rowe, 1988)
13. Humeral ulnar condyle, form: condylar (0); hemicondylar (1); trochlear (2). (Rowe, 1988)
14. Ulnar olecranon process length: less (0), or equal to or more (1), than the length of the semilunar notch.
15. Ulnar semilunar notch, intercondylar crest (anterior view): absent or rudimentary (0); present (1).
16. Ulnar anconeal process: absent (0); present (1).

Trechnotheria

17. Acromion, form: perpendicular (0), or recurved to lie parallel (1), to scapular blade. (Sereno & McKenna, 1995)

Vincelestes + Theria

18. Interclavicle-sternum coossification: absent (0); present (claviculosternal contact) (1). (Rowe, 1988)

B. Listed by anatomical region

Pectoral Girdle

1. Scapulocoracoid suture: open (0); fused (1).
5. Acromion position: dorsal (0), or lateral (1), to the glenoid.
18. Acromion form: perpendicular (0), or recurved to lie parallel (1), to scapular blade.
6. Supraspinous fossa along anterior margin of length of scapular blade: absent or rudimentary (0); present (1).

(continued)

Table 10.2. *(continued)*

7. Glenoid width: subequal to (0), or approximately 60% of (1), transverse width of the humeral head.
4. Coracoid posterior process, length: longer or subequal to (0), or shorter than (1), the maximum diameter of the glenoid.
8. Coracoid glenoid, orientation: posterolateral (0); lateral (1); posteroventral (2).
9. Coracoid glenoid, form: convex (0); concave (1).
2. Coracoid groove: present (0); absent (1).
10. Procoracoid: present (0); reduced/fused with manubrium sterni (1).
4. Procoracoid foramen: present (0); absent (1).
11. Clavicular head, form: tongue-shaped (0); rod-shaped (1).
12. Interclavicle size: larger (0), or smaller (1), than the sternum (anteroposterior and transverse dimensions).
18. Interclavicle-sternum coossification: absent (0); present (claviculosternal contact) (1).

Humerus

13. Humeral ulnar condyle, form: condylar (0); hemicondylar (1); trochlear (2).

Radius and Ulna

14. Ulnar olecranon process length: less (0), or equal to or more (1), than the length of the semilunar notch.
15. Ulnar semilunar notch, form (anterior view): shallow, subrectangular (0); deep, hourglass-shaped (1).
16. Ulnar anconeal process: absent (0); present (1).

Note: 0, primitive state; 1, 2, derived states; ?, not preserved or exposed; X, too transformed to score; multistate character 13 is ordered, because the derived states are cumulative. Embryological evidence is used to score relevant characters in terminal taxa with living representatives.

occur in neonates or subadults, and, in a few cases, the suture remains open in adults (e.g., xenarthrans). Mammalian outgroups (*Morganucodon,* tritheledontids, tritylodontids) invariably show an open scapulocoracoid suture (fig. 10.9A; Jenkins & Parrington, 1976; Sun & Li, 1985).

2. Coracoid groove absent (Sereno & McKenna, 1995). The groove, or trough, on the posterior margin of the coracoid in mammalian outgroups (fig. 10.9A) is not present on the coracoid in monotremes (fig. 10.9B) or on the reduced, co-ossified coracoid in multituberculates and therians (fig. 10.10).
3. Coracoid posterior process shorter than glenoid diameter (modified from Sereno & McKenna, 1995). In monotremes, the robust coracoid has a posterior process that is shorter than the glenoid diameter (fig. 10.9B). In *Jeholodens* and *Zhangheotherium,* the posterior process is not fully exposed but appears to have been

Table 10.3. Taxon-by-character matrix

Taxon	Character-States			
	5	**10**	**15**	
Tritylodontidae	00000	00000	00000	000
Tritheledontidae	00000	00000	00000	000
Morganucodon	00000	00000	00000	000
Monotremata	11110	00000	00000	000
Gobiconodon	1???1	11??1	???11	10?
Jeholodens	1?1?1	11111	???1?	???
Multituberculata	1X111	01111	11111	100
Zhangheotherium	111?1	11111	11?0?	?10
Henkelotherium	11111	111?1	?1?11	?10
Vincelestes	11111	11111	?1211	111
Metatheria	11111	11111	11211	111
Eutheria	11111	11111	11211	111

Note: Abbreviations as in Table 10.2.

short as in *Henkelotherium.* This process has been completely reduced in multituberculates. In therians, the posterior process is usually reduced to a relatively small anteromedially projecting protuberance (fig. 10.10B). In mammalian outgroups, in contrast, the posterior process is equal to, or longer than, glenoid diameter (fig. 10.9A; Jenkins, 1971b; Sun & Li, 1985).

4. Procoracoid foramen absent (Sereno & McKenna, 1995). The procoracoid foramen has not been recorded at any developmental stage in mammals (Klima, 1987). Mammalian outgroups (*Morganucodon,* tritheledontids, tritylodontids), in contrast, invariably retain the foramen for transit of the supracoracoideus nerve and associated vasculature (fig. 10.9A; Jenkins & Parrington, 1976; Sun & Li, 1985).

Theriimorpha. Twelve synapomorphies in the pectoral girdle and forelimb characterize theriimorphs (table 10.2).

5. Acromioclavicular joint positioned lateral to the glenoid (modified from Rowe, 1988). In theriimorphs, the acromion extends ventrally from the lateral aspect of the scapula, so that the joint with the clavicle is positioned lateral to the glenoid (fig. 10.10). This condition is clearly present in triconodonts (*Gobiconodon, Je-*

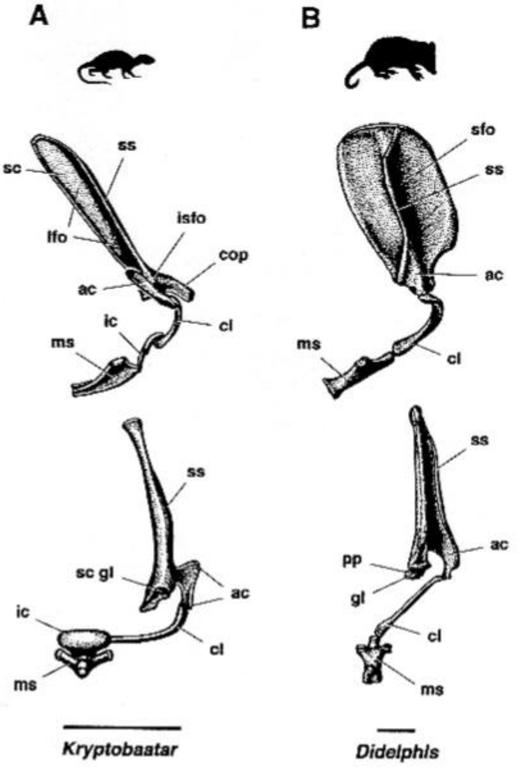

Figure 10.10. Pectoral girdle of (A) *Kryptobaatar dashzevegi* and (B) *Didelphis virginiana* (UCP, recent collection) in lateral (above) and posterior (below) views. Scale bars equal 1 cm. Abbreviations: ac, acromion; cl, clavicle; cop, coracoid process; gl, glenoid; ic, interclavicle; isfo, incipient supraspinous fossa; lfo, lateral fossa; ms, manubrium sterni; pp, posterior process; sc, scapula; sfo, supraspinous fossa; ss, scapular spine.

holodens; Jenkins & Schaff, 1988; Ji et al., 1999), symmetrodonts (*Zhangheotherium;* Hu et al., 1997), and the basal trechnotherian *Vincelestes* (Rougier, 1993). The complete multituberculate acromial process, seen for the first time in *Kryptobaatar* (figs. 10.3, 10.7), is particularly long and places the acromioclavicular joint immediately lateral to the midpoint of the arc of the glenoid. In this position, the acromion and scapular spine lie along an axis passing through the glenoid, so that muscles attaching to either side of the scapular spine may now be involved in the mobilization and/or stabilization of the shoulder joint. In monotremes and mammalian outgroups (fig. 10.9), the acromion projects from the anterior margin of the scapular blade and does not descend to the level of the glenoid (Jenkins, 1971b; Jenkins & Parrington, 1976; Sun & Li, 1985).

6. Supraspinous fossa along anterior margin of scapular blade (Rowe, 1988). In all theriimorphs except multituberculates, a well-marked

supraspinous fossa extends along the anterior margin of the scapular blade, anterior to the scapular spine and base of the acromial process (fig. 10.10B; Jenkins & Schaff, 1988; Krebs, 1991; Rougier, 1993; Hu et al., 1997; Ji et al., 1999, 2002). Multituberculates, a notable exception among theriimorphs, are similar to outgroups, in which the protruding anterior edge of the blade has been interpreted as the homolog of the therian scapular spine (figs. 10.9, 10.10A).

7. Glenoid width only approximately sixty percent of transverse width of the humeral head (Sereno & McKenna, 1995). In theriimorphs, the maximum width of the glenoid (transverse width of scapular portion) is approximately one-half the maximum diameter of the opposing surface of the humeral head (fig. 10.7E). The marked differential width of the articular surfaces is present in multituberculates (fig. 10.11E) and *Vincelestes* (Rougier, 1993) and appears to be present in triconodonts, symmetrodonts, and basal trechnotherians (Jenkins & Schaff, 1988; Krebs, 1991; Hu et al., 1997; Ji et al., 1999). In theriimorph outgroups, in contrast, the scapular glenoid more closely approximates the size of the opposing surface of the humeral head, as in monotremes (Jenkins, 1971b; Sun & Li, 1985).
8. Coracoid glenoid with posteroventral orientation (Sereno & McKenna, 1995). In theriimorphs, the coracoid glenoid faces posteroventrally. In lateral view, little of the surface of the coracoid glenoid is exposed, because it is positioned parallel to the line of sight (fig. 10.10). In theriimorph outgroups, in contrast, the coracoid glenoid faces either laterally (monotremes) or posterolaterally (basal mammaliamorphs, basal synapsids). As a result, the coracoid glenoid is broadly exposed in lateral view but largely hidden in posterior view (fig. 10.9).
9. Coracoid glenoid concave (Sereno & McKenna, 1995). In theriimorphs, the glenoid is anteroposteriorly concave and transversely flat (multituberculates) or very slightly concave (e.g., *Vincelestes;* Rougier, 1993, fig. 82). In triconodonts and symmetrodonts, the coracoid process is also anteroposteriorly concave (Hu et al., 1997: Ji et al., 1999). In theriimorph outgroups, in contrast, the coracoid glenoid is concavoconvex (fig. 9; Jenkins, 1971b; Jenkins & Parrington, 1976).
10. Procoracoid reduced/fused with the manubrium sterni (Rowe, 1988). In theriimorphs, the procoracoid fails to ossify as a separate

element. In the embryos of living marsupials, a procoracoid condensation is occasionally retained as a small cartilaginous element (praeclavium) at the medial end of the clavicle (Klima, 1987). In placentals, the procoracoid anlagen of the procoracoid is incorporated into the manubrium sterni (Klima, 1987). In theriimorph outgroups such as monotremes, *Morganucodon,* and tritylodontids, the procoracoid is an ossified element sutured to the coracoid and scapula (fig. 10.9).

11. Clavicular head rod-shaped (Sereno & McKenna, 1995). The medial end of the clavicle in theriimorphs is rod-shaped rather than flattened, presumably to allow more flexibility at the claviculointerclavicle joint. A clavicle of this type is known in multituberculates, the triconodont *Jeholodens,* the symmetrodont *Zhangheotherium,* and *Henkelotherium.* In theriimorph outgroups, the clavicle has a flattened, fluted medial end that is firmly attached to the interclavicle (Jenkins, 1971b).
12. Interclavicle smaller than the sternum (anteroposterior and transverse dimensions) (modified from Rowe, 1988). In theriimorphs, the interclavicle is reduced in size, either as a small ossification (fig. 10.7; Hu et al., 1997) or as embryological condensation (Klima, 1987). The interclavicle appears to be partially co-ossified to the manubrium sterni in *Vincelestes* (Rougier, 1993, fig. 83). In theriimorph outgroups, the interclavicle is larger than the manubrium sterni.
13. Humeral ulnar hemicondyle (modified from Rowe, 1988). In theriimorphs, the anterior portion of the humeral ulnar condyle takes the form of a hemicondyle, in which only the lateral, intercondylar portion of the primitive hemispherical condyle is developed. The hemicondyle, thus, has an asymmetrical cam shape (Jenkins, 1973, 290). In multituberculates the cam is developed only on the anterior half of the ulnar condyle adjacent to the bulbous, hemispherical portion of the radial condyle (fig. 10.11B). In therians, the ulnar condyle is cam-shaped posteriorly as well, which, together with the broadened intercondylar groove, forms the trochlea (fig. 10.11C). An ulnar condyle that is, at least in part, cam-shaped is transitional to a fully developed therian trochlea. In theriimorph outgroups, the ulnar condyle is more symmetrically developed, although somewhat variable in its convexity.
14. Ulnar olecranon exceeds the length of the semilunar notch. In theriimorphs, the long olecranon process increases the lever arm

of the triceps musculature, reflecting the increased activity of the elbow joint in the stride in a forelimb with a more parasagittal posture (fig. 10.11B, C). In theriimorph outgroups, the olecranon is somewhat shorter than the semilunar notch (Jenkins, 1976; Jenkins & Parrington, 1976; Sun & Li, 1985). In monotremes, the olecranon is subequal to the length of the semilunar notch and may have gained this length secondarily as a fossorial adaptation.

15. Ulnar intercondylar crest present. In theriimorphs, the semilunar notch of the ulna is divided by an intercondylar crest separating articular surfaces for the radial and ulnar condyles of the humerus (fig. 10.11B). The intercondylar crest is present in multituberculates (fig. 10.11B), *Vincelestes* (Rougier, 1993), and therians (fig. 10.11C) but is poorly documented in other basal theriimorphs. There is no intercondylar crest and, consequently, no articular surface on the ulna for the radial condyle of the humerus in monotremes, tritylodontids (fig. 10.11A), or more distant theriimorph outgroups (Jenkins, 1971b).
16. Ulnar anconeal process present. In theriimorphs, a distinct anconeal process is present at the posteriormost end of the intercondylar crest on the ulna in multituberculates (fig. 10.11B), triconodonts (Jenkins & Schaff, 1988, fig. 15), *Vincelestes* (Rougier, 1993, fig. 87), and therians (fig. 11C). In theriimorph outgroups, the ulnar cotylus for the humerus is broad with little development of its posterior rim, as seen in monotremes, tritylodontids (fig. 10.11A; Sun & Li, 1985, fig. 10), and more basal synapsids (Jenkins, 1971b).

Trechnotheria. One synapomorphy in the pectoral girdle characterizes trechnotherians (table 10.2). This synapomorphy eventually may be shown to have a broader distribution among basal theriimorphs.

17. Acromion recurved to lie parallel to scapular blade (Sereno & McKenna, 1995). In *Vincelestes* (Rougier, 1993, fig. 82) and therians (fig. 10.10B), the acromial process curves posteriorly so that the expanded portion of the process lies in a plane parallel to that of the scapular blade. In *Henkelotherium,* the acromial process may be developed in a similar manner (Krebs, 1991, fig. 7). The condition is poorly preserved in basal theriimorphs such as triconodonts and symmetrodonts. In multituberculates (figs. 10.3, 10.7) and *Morganucodon* (fig. 10.15A; Jenkins & Parrington, 1976, fig. 4), the acromial process curves laterally to a lesser degree, positioned perpendicular rather than parallel to

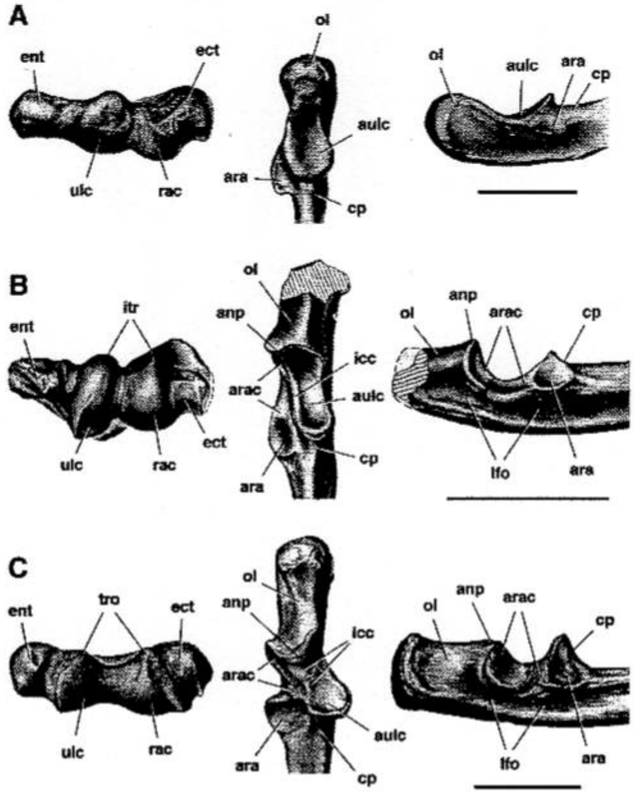

Figure 10.11. Distal right humerus in ventral view (anterior toward bottom) and proximal right ulna in anterior (left) and medial (right) views in (A) *Bienotherium yunnanense* (FMNH CUP 2286, 2291, 2300), (B) Cretaceous multituberculates from North America and Asia (*Nemegtbaatar gobiensis*), and (C) *Didelphis virginiana* (UCPC, recent collection). Distal right humerus and proximal right ulna in (B) drawn from stereophotographs in Jenkins (1973, fig. 19) and (Kielan-Jaworowska & Gambaryan, 1994, fig. 14D, E), respectively. Scale bars equal 2 cm, 5 mm, and 1 cm, respectively, for (A), (B), and (C). Abbreviations: anp, anconeal process; ara, articular surface for the radius; arac, articular surface for the radial condyle; aulc, articular surface for the ulnar condyle; cp, coronoid process; ect, ectepicondyle; ent, entepicondyle; icc, intercondylar crest; itr, incipient trochlea; lfo, lateral fossa; ol, olecranon; rac, radial condyle; tro, trochlea; ulc, ulnar condyle.

the scapular blade. In monotremes (fig. 10.9B), tritylodontids (Sun & Li, 1985, fig. 7), and more basal synapsids (Jenkins, 1971b, fig. 17), the acromial process projects anteriorly from the scapular blade.

Vincelestes plus Theria.

One synapomorphy from the pectoral girdle characterizes *Vincelestes* plus Theria (table 10.2).

18. Interclavicle and sternum co-ossified, claviculosternal contact (Rowe, 1988). In *Vincelestes* (Rougier, 1993, fig. 83) and therians (fig. 10.16B), the interclavicle fails to ossify as a separate element, and, as a result, the clavicle articulates with the manubrium sterni. In therians the endochondral portion of the interclavicle forms the anteromedian portion of the manubrium sterni (Klima, 1987, fig. 29). Among outgroups, the presence of a separate interclavicle remains uncertain in *Henkelotherium* and triconodonts. In multituberculates (figs. 10.11A–C) and *Zhangheotherium* (Hu et al., 1977), the interclavicle is present as a separate element, albeit reduced in size.

Phylogenetic Significance

Multituberculates as Theriimorph Mammals

The dentition in multituberculates, monotremes, and several other basal mammalian taxa is so modified that dental characters have had limited impact in sorting their relationships at the root of Mammalia. Likewise, the composition of the sidewall of the braincase was once viewed as key to resolving multituberculate relationships (Broom, 1914; Kielan-Jaworowska, 1971). A recent review of basicranial evidence (51 characters), however, proved indecisive; multituberculates were joined with therians in the shortest trees but linked with prototherians with one additional step (Rougier et al., 1996b, 24).

Sereno and McKenna (1995), elaborating on earlier results by Rowe (1988), suggested that postcranial characters, especially those from the shoulder girdle and forelimb, decisively link multituberculates and therians within Mammalia. Rougier et al. (1996a; 406) countered that "evaluation of the competing phylogenetic hypotheses of multituberculate relationships must await the inclusion of additional taxa and characters," a reasonable caution. Now we are in a position to reevaluate.

Luo et al. (2002) presented the most comprehensive analysis for basal mammalian phylogeny (275 characters, forty-six taxa). Using *Probainognathus* as an outgroup, they generated forty-two equally parsimonious trees from 271 informative characters [935 steps, consistency index (CI) = 0.499, retention index (RI) = 0.762; Luo et al., 2002, 6]. Rerun of their data yielded similar results (273 informative characters, forty-two trees, 933 steps, CI = 0.498, RI = 0.762, multistate taxa scored as polymorphic) and the same strict consensus tree (Luo et al., 2002, fig. 1).

Despite significant character support in their data placing multituberculates within crown mammals (Mammalia) as a sister-taxon to Theria (figs. 10.2A, B), Luo et al. (2002) regarded their position outside crown mammals as equally likely. Regarding postcranial support, Luo et al. (2002, 33) stated that only "four synapomorphies for multituberculates and trechnotherians are unambiguous." In their shortest trees, however, ten postcranial synapomorphies provide unambiguous support for this node. A total of twenty-one unambiguous characters (dental, cranial, postcranial) reside at Mammalia or nodes within that include multituberculates.

To test the significance of this result, Luo et al. (2002, fig. 2) constrained multituberculates plus *Haramiyavia* to a position outside Mammalia (crown mammals), generating trees seven steps longer (942 steps). Rerunning the analysis with similar constraints yielded similar results. With multituberculates and *Haramiyavia* as a clade outside Mammalia (crown mammals), length increases seven steps (933 to 940 steps). A similar result is obtained by constraining only multituberculates to a position outside crown mammals; in this case, *Haramiyavia* returns to the base of the tree (rather than as a sister-taxon to Multituberculata), reducing tree length by one step to 939 steps, or six steps beyond minimum length (933 steps). Regarding the most parsimonious and constrained positions for multituberculates, Luo et al. (2002, 33) reasoned, "this is a small difference between these two contrasting tree topologies," and further, "nonparametric tests . . . show that the difference is not significant." Thus, they concluded, "we do not favor one interpretation over the other."

Why do multituberculate relationships deserve this special six-step moratorium from phylogenetic interpretation? Is this another expression of the traditional viewpoint that holds that apomorphic resemblances between multituberculates and therians *must* be homoplastic? Luo et al. (2002, 32–33) regard the phylogenetic position of multituberculates especially difficult to determine because they (1) exhibit a mosaic of primitive and derived character states, (2) exhibit many masticatory and dental autapomorphies, and (3) lack a good early fossil record. This is not clear in the data set at hand or in current stratigraphic ranges (fig. 10.16). Multituberculates are not particularly unusual among Mesozoic mammaliaforms regarding missing data (via lack of preservation or transformation) or missing stratigraphic range.

Decay analysis shows that few nodes derived from the data presented by Luo et al. (2002) have as many unambiguous synapomorphies as those linking multituberculates and therians within Mammalia. Hundreds of trees exist at just one step beyond minimal length (934 steps), and thousands of trees exist at two steps beyond minimal length (935 steps). The strict or semistrict consensus of trees at 935 steps breaks down all nodes except two within Trechnotheria. If character support placing multituberculates within Mammalia (crown mammals) is deemed insignificant, then little significance resides elsewhere in this data set.

The decisiveness of characters from the shoulder girdle and forelimb regarding the affinities of multituberculates is real and documents a major transition in mammalian locomotor function and posture that occurred sometime during the Jurassic (fig. 10.15, node 2). In the data set of Luo et al. (2002), most of the twelve unambiguous characters linking multituberculates and trechnotherians are postcranial; fifty percent come from the pectoral girdle and forelimb. These data, furthermore, do not include six synapomorphies in the pectoral girdle and forelimb outlined above (7, 11, 12, 14–16, table 10.2). The structure of character data from the pectoral girdle and forelimb presented here is very simple (table 10.2). Several taxa are actual or potential taxonomic equivalents (Wilkinson, 1995) with identical, or potentially identical, character states, respectively (Tritylodontidae/Tritheledontidae/*Morganucodon;Gobiconodon*/*Jeholodens;Vincelestes*/Metatheria/Eutheria).

Problematic Characters in the Pectoral Girdle and Forelimb

Twenty characters from the pectoral girdle and forelimb from previous analyses (Rowe, 1988; Luo et al., 2002) are rejected or regarded as uninformative for nodes at the root of Mammalia (for more discussion, see Sereno, in review). Three are uninformative with the present terminal taxa (fig. 10.1B) or after rescoring character states (Rowe, 1988: radial condyle form; radial styloid process; Luo et al., 2002: supinator ridge with rectangular extension). One is a functional interpretation (Luo et al., 2002: claviculosternal apparatus joint) and another is clearly redundant (Luo et al., 2002: interclavicle-manubrium sterni contact/relationship). Most of the rejected characters are ill-defined or quite variable and, thus, are difficult to interpret and score (humeral head shape/inflection; bicipital (intertubercular) groove; lesser tuberosity muscle insertions; greater and lesser tuberosities form pronounced ridges; radial/ulnar condyle size (Rowe, 1988); cranial margin of interclavicle; curvature of the clavicle; acromioclaviclular joint; fossa for teres major muscle; medial surface of the scapula; lesser tuberosity size; deltopectoral crest length; humeral torsion; epicondylar robustness (Luo et al., 2002).

Functional Evolution

Multituberculates as Sprawling Saltators?

Unique Locomotor Model. There are no living quadrupedal mammalian saltators with a sprawling forelimb posture, nor have any extinct species been so interpreted previously. Thus, the functional model proposed for multituberculates by Gambaryan and Kielan-Jaworowska (1997) (fig. 10.12)—here termed the "sprawling saltator" model—is unique. The proposed stride sequence for multituberculates, furthermore, differs from locomotor patterns in living mammals—including the sprawling monotremes.

First, during the stride in living mammals, the elbow joint moves only slightly in a transverse direction (Jenkins, 1973) and is located either close to the thorax, as in therians (Jenkins, 1971a, 1979), or strongly abducted, as in monotremes (Pridmore, 1985)—but not transient in transverse position, moving from one to the other, as shown in the sprawling saltator

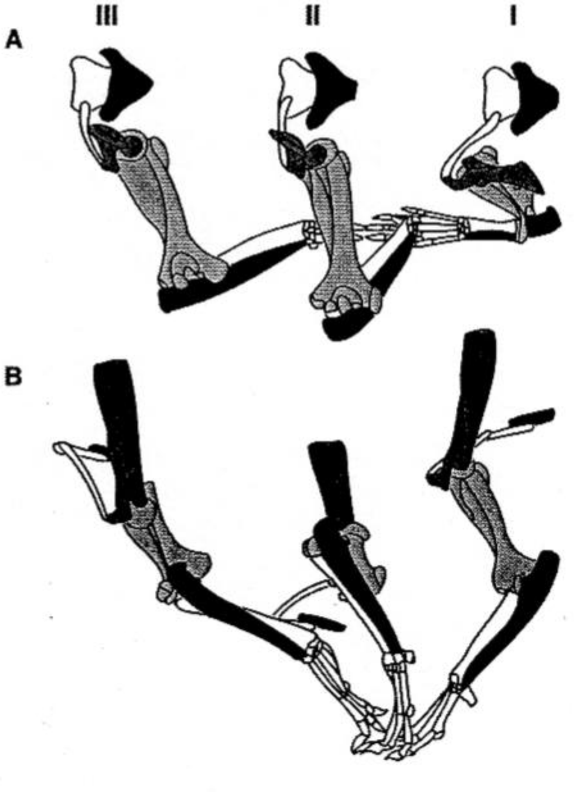

Figure 10.12. Reconstruction of phase I–III of the walking step of a multituberculate in (A) dorsal and (B) lateral views as proposed by Gambaryan and Kielan-Jaworowska (1997; after their fig. 10). Bones are differentiated by shading (not in the original).

model (fig. 10.12A, I, II). In this regard, Kielan-Jaworowska and Gambaryan (1997) stated, "the main difference between the abducted (sprawling) and parasagittal limbs does not concern the angle of humeral or femoral abduction from the sagittal plane, but the positions of hands and feet in the propulsive phase with respect to this plane." This is not true for the forelimb of living mammals as documented by cineradiography. Therian mammals with a more erect posture show far less humeral abduction than sprawling monotremes (figs. 10.13C, D).

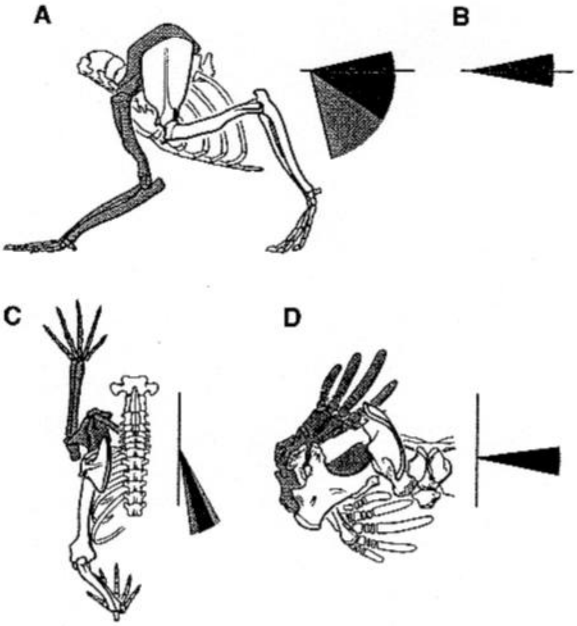

Figure 10.13. Lateral (A, B) and dorsal (C, D) views of the walking step in the eutherian *Didelphis virginiana* (A, C) and monotreme *Tachyglossus aculeatus* (B, D), showing the posture of the forelimb bones during the initiation (shaded, phase I) and completion (unshaded, phase III) of propulsion, as interpreted from cineradiography. Associated excursion arcs for the humerus show usual range of movement (dark shading) and occasional deviations beyond that range (light shading), with the apex of the arc located at the shoulder joint (after Jenkins 1970b, 1971b). (A) *Didelphis virginiana* in lateral view showing the posteroventral excursion of the shoulder joint, posture of the forelimb, and usual humeral arc of depression/elevation (about 50°; dark shading) during the walking step. (B) Smaller observed range of humeral depression/extension (about 20°) in the monotreme *Tachyglossus aculeatus* that is not synchronized with the step cycle. (C) *Didelphis virginiana* in dorsal view showing the posterior excursion of the shoulder joint, posture of the forelimb, and usual angle of humeral adduction from the sagittal plane (about 20°; dark shading) during the walking step. (D), *Tachyglossus aculeatus* in dorsal view showing the posture of the forelimb and usual angle of humeral adduction from the sagittal plane (about 90°; dark shading) during the walking step.

Second, movement of the shoulder joint relative to the trunk in therian mammals follows a short arc during propulsion, from a position anterodorsal to the manubrium sterni near the dorsal margin of the thoracic outlet to a position lateral to the manubrium near the ventral margin of the thoracic outlet (fig. 10.13A; Jenkins, 1979, fig. 5). In the sprawling saltator model, in contrast, the shoulder joint is shown originating in a position anteroventral to the manubrium, relocating to a position posterodorsal to the manubrium, and then returning far ventral to the manubrium and the associated thoracic outlet (fig. 10.12B, I–III).

Finally, the forearm assumes a vertical, or near vertical, posture toward the end of propulsion in both erect and sprawling mammals (Jenkins, 1970b, 1971a, 1979; Pridmore, 1985). In the sprawling saltator model, in contrast, the forelimb is oriented at approximately 60° from the vertical (fig. 10.12A, III). All these aspects of the proposed model for multituberculate locomotion are without parallel in extant mammals.

Other Discrepancies. Dorsal and lateral views of the sprawling saltator model differ in significant ways from each other and from preserved multituberculate skeletons. In dorsal view of phase I of the stride, the rotational axis of the elbow joint is shown as nearly transverse; in lateral view, the same axis is angled anterolaterally. In dorsal view of phase II, the clavicle is transversely oriented, and the interclavicle is located medial to the scapula; in lateral view, the clavicle is shown angling posterolaterally, and the interclavicle is positioned anterior to the scapula. In dorsal view of phase III, the interclavicle/manubrium and the olecranon process of the ulna are positioned farther anteriorly and posteriorly, respectively, than in lateral view.

Other proportions or articulations do not match preserved skeletal material. The scapula is shown as shorter, rather than longer, than the humerus; the interclavicle is shown as flat rather than strongly arched; the clavicle is shown articulating with the dorsal, rather than ventral, side of the interclavicle; and the claviculoacromial joint is positioned anterior, rather than lateral, to the glenoid (figs. 10.7A, B).

The form of the elbow joint in multituberculates clearly suggests that significant rotation occurred. In the sprawling saltator model for multituberculate locomotion, however, flexion-extension at the elbow is as limited as in monotremes (figs. 10.12, 10.13B). Gambaryan and Kielan-Jaworowska (1997, 38), nevertheless, stated that enhanced flexion-extension at the elbow joint also characterizes their model: "When during landing the forelimbs were stretched anteroventrally, the elbow joint extended and the olecranon fitted into a deep fossa olecrani on the dorsal side of the humerus." During this, or any other, phase of their model, however, the olecranon is not close to the olecranon fossa, and flexion-extension at the elbow is limited (fig. 10.12, II). Likewise, they reported "strong flexion of the elbow joint during the middle of the propulsive phase" that required "a deep coronoid fossa on the ventral side of the humerus, into which fitted the radial head." In their model, however, the elbow never flexes at an angle much less than 90°, which keeps the radial head far from the radial fossa. In *Kryptobaatar* (PSS-MAE 103), for example, it is clear that flexion of the elbow at an angle as tight as 50° still does not engage the radial fossa (fig. 10.5). The radial fossa comes into play under situations of much greater flexion, as preserved in the left forelimb of PSS-MAE 103 (fig. 10.5).

Evidence for Sprawling Forelimb Posture. In the sprawling saltator model (Gambaryan & Kielan-Jaworowska, 1997), movement of the humerus is closest to that observed in monotremes, which have a rigid pectoral girdle, laterally facing glenoid, strong muscles attached to hypertrophied tuberosities for humeral rotation and retraction, and limited flexion-extension at the elbow joint (figs. 10.13B, D; Pridmore, 1985). In multituberculates, in contrast, the shoulder joint is surely mobile during the stride, judging from its construction; the glenoid faces ventrally; the humeral epicondyles are much less expanded relative to humeral length, even in the presumed fossorial genus *Lambdopsalis* (less than fifty percent humeral length); and flexion-extension at the elbow joint is greatly enhanced, judging from the arc of the ulnar condyle of the humerus and other features. These attributes characterize therians with a more parasagittal forelimb posture.

Gambaryan and Kielan-Jaworowska (1997) largely sidestepped these fundamental, functionally relevant differences among extant mammals, basing their argument for sprawling posture instead on attributes of the humerus—namely, the (1) increased size and/or prominence of the lesser tuberosity compared with the greater tuberosity, (2) broad width of the intertubercular (bicipital) groove, (3) high degree of humeral torsion, and (4) condylar structure of the distal end. None of these characterize multituberculates, in particular, or provides convincing evidence for sprawling forelimb posture, as discussed below.

In multituberculates, the lesser tuberosity is subequal to the greater tuberosity in size and prominence (figs. 10.4, 10.7E); there is no significant size differential. The relative size of the tuberosities, furthermore, is not indicative of a particular forelimb posture. In *Tachyglossus* and some mammalian outgroups, in contrast, the lesser tuberosity can be as much as twice the dimensions of the greater tuberosity (Jenkins, 1971b, figs. 27, 28). In some extant therians, the reverse proportions obtain (MacPhee, 1994, fig. 26). Among therians, the lesser tuberosity can be smaller, subequal, or larger than the greater tuberosity, depending on the species examined. All three proportions, for example, occur among didelphimorphs (Argot, 2001, fig. 8.1). In fossorial therians, either tuberosity may be enlarged (MacPhee, 1994; *contra* Gambaryan & Kielan-Jaworowska, 1997, 30). In sum, the humeral tuberosities in multituberculates, which are subequal in size, do not provide evidence favoring a sprawling forelimb posture.

The depression between the humeral tuberosities (i.e., the intertubercular or bicipital groove) is developed as a broad, open trough in monotremes (Gambaryan & Kielan-Jaworowska, 1997, fig. 3C), basal mammaliamorphs such as *Morganucodon* (Jenkins & Parrington, 1976, fig. 5C), and mammaliamorph outgroups (Jenkins, 1971b, fig. 26B). In multituberculates and therians, the proximal end of the humerus is proportionately narrower, and the space between the tuberosities is much reduced. Gambaryan and Kielan-Jaworowska (1997, 30) suggested that the reduction in width—from a trough to a groove—is correlated with a reduction in musculature passing from the coracoid to the humerus, the groove occupied only by the tendon of the biceps brachii caput longum (in some therians, a slip of the coracobrachialis may also pass along the groove; Argot, 2001, 59).

Differentiating "broad" versus "narrow" regarding the space between the tuberosities, however, was not well specified. Kielan-Jaworowska and Gambaryan (1994, 61) stated, "the intertubercular groove is very wide in multituberculates; it is thirty-two percent of the width of the proximal epiphysis in *Nemegtbaatar* and twenty-eight to thirty-one percent in ?*Lambdopsalis,* while in modern small rodents it is only fourteen to twenty-three percent." Later they reported a groove width of thirty percent in *Nemegtbaatar,* forty percent in *Chulsanbaatar,* and forty percent in an unidentified Asian multituberculate (Gambaryan and Kielan-Jaworowska, 1997, 31). In *Kryptobaatar* (PSS-MAE 103), the groove constitutes approximately twenty-five percent of the width across the tuberosities and is narrower than the width of either tuberosity (figs. 10.4, 10.7E). In fact, a range of twenty to thirty percent appears to characterize all the Asian genera mentioned above including *Lambdopsalis* (see photographs in Kielan-Jaworowska & Gambaryan, 1994, and Gambaryan & Kielan-Jaworowska, 1997).

In the basal trechnotherian *Vincelestes,* the groove appears to be proportionately broader than in multituberculates (Rougier, 1993, 295, fig. 84). In the opossum *Didelphis,* the groove occupies fifty percent that of the width across the tuberosities and is subequal in width to the largest tuberosity (UCP, recent collection). Among extant didelphimorphs, the width of the groove relative to that across the tuberosities varies by as much as a factor of two (Argot, 2001, fig. 8.1). Among extant fossorial therians with various forelimb postures, likewise, the width of the groove varies from extremely narrow or partially enclosed (*Myospalax,* Gambaryan & Kielan-Jaworowska, 1997, fig. 6B; *Euphractus,* MacPhee, 1994, fig. 26) to more broadly open (*Manis,* MacPhee, 1994, fig. 26).

In sum, the space between the tuberosities in multituberculates takes the form of a groove and more closely resembles the bicipital groove in therians (with various forelimb postures) than it does the broadly open trough that characterizes monotremes and mammalian outgroups. The groove in multituberculates, therefore, does not provide evidence favoring a sprawling forelimb posture.

Torsion in the humeral shaft—i.e., the angle between the axis across the tuberosities proximally and the axis through the distal condyles and epicondyles distally (Simpson, 1928b; Kielan-Jaworowska & Gambaryan, 1994, fig. 46)—varies among mammals and mammalian outgroups. Among mammalian outgroups, torsion is 20–30° in the tritylodontid *Bienotherium* (FMNH CUP2286, 2300) and more distant taxa (Jenkins, 1971b, figs. 27, 28). Jenkins and Schaff (1988, 15) reported similar torsion (about 33°) in the triconodont *Gobiconodon.* Hu et al. (1997, 140), likewise, reported torsion of about 30° in the symmetrodont *Zhangheotherium,* although the proximal end of the humerus is not fully exposed (see above). Humeral torsion in extant fossorial mammals is sometimes greater (45° in Tachyglossidae; 60° in Chrysochloridae), although considerable variation exists (MacPhee, 1994, fig. 26).

Humeral torsion in *Kryptobaatar* is approximately 15°, as measured in both humeri of PSS-MAE 103 (fig. 10.7G). Other estimates of torsion for this genus (30°) are based on separate proximal and distal ends (Gambaryan & Kielan-Jaworowska, 1997) or on a humerus that is not fully exposed proximally (Kielan-Jaworowska, 1998, fig. 2). In the latter case, the preserved landmarks on this humerus in ventral view closely match those in PSS-MAE 103 (fig. 10.7D), and thus it would be very surprising if its torsion is greater by a factor of two. In *Lambdopsalis,* torsions of 24° and 38° were measured from two specimens; fractures in the shaft of each specimen, however, may well have artificially increased the apparent range of torsion in this genus (Gambaryan & Kielan-Jaworowska, 1997, fig. 9). Humeral torsion in multituberculates probably falls within a range of 15–30°.

In the metatherian *Didelphis,* humeral torsion measures 20–25°, and this range is typical of many therians (UCP, recent collection). Rougier (1993, 298) reported stronger torsion (40°) in the basal trechnotherian *Vincelestes.* Humeral torsion may have decreased somewhat from 20–30° in theriimorph outgroups to 20° or less among theriimorphs. But it is clear, first, that *Kryptobaatar* and perhaps other slender-limbed multituberculates have less than 20° of humeral torsion and, second, that humeral torsion among living and fossil theriimorphs with a variety of forelimb postures is more variable than previously was assumed. For these reasons, humeral torsion in multituberculates does not substantiate a sprawling forelimb posture.

Detailed study of the elbow joint in extinct mammalian outgroups has shown that during propulsion the primitive spiral condylar form of the distal humerus "maintains the forearm in a sagittal plane as the humerus adducts, elevates and medially rotates" (Jenkins, 1973, 288), much as does the asymmetrical trochlea of basal extinct therians or the living opossum (fig. 13B). Contrary to statements by Gambaryan and Kielan-Jaworowska (1997), the spiral condylar structure of the multituberculate humeroulnar joint does not support a sprawling forelimb posture. Krause and Jenkins (1983, 235) concluded, "as similar excursions are accommodated by the spiral trochlear humeroulnar joint of primitive therians, the significance of the difference between the condylar and trochlear joint types is unclear." Sloan and Van Valen (1965, 222) stated that ulnar movements in multituberculates are "restricted to a single plane by the shapes of the trochlea and semilunar notch" (fig. 10.11B). This is strongly corroborated in this study and is preserved *in situ* by comparing the articulated positions of left and right forelimbs in PSS-MAE 103 (figs. 10.4, 10.5).

In multituberculates, the ulna was not free to slide transversely across a broadly convex ulnar condyle on the humerus, as shown by Gambaryan and Kielan-Jaworowska (1997, fig. 1A). Rather, the ventral portion of the ulnar condyle in multituberculates is cam-shaped (fig. 10.6), the transitional form of the ulnar condyle predicted to have occurred during evolution of the therian trochlea (Jenkins, 1973, 290). The narrow dorsal half of the ulnar condyle is fitted to an arcuate fossa in the semilunar notch and is bounded laterally and dorsally by an intercondylar crest and anconeal process, respectively (fig. 10.11B). In sum, there is no evidence from the multituberculate humeroulnar joint that supports a sprawling forelimb posture.

Evidence for Saltatory Locomotion. The argument for saltatory locomotion in multituberculates was based on a single feature—the reconstructed length of the spinous processes of the lumbar vertebrae in *Nemegtbaatar* (Kielan-Jaworowska & Gambaryan, 1994, fig. 36B). The length of the lumbar transverse processes, in turn, was cited as an indicator of an asymmetrical gait, in which both forelimbs move before the hind limbs (Kielan-Jaworowska & Gambaryan, 1994, 65, 72). Hypotheses regarding the steepness of the trajectory of the jump, the shock-absorbing function of the forelimbs, and others stemmed from the initial conjecture of saltatory habits in multituberculates based on lumbar neural spine length.

The length of the lumbar neural spines in multituberculates, however, is not greater than that in other basal mammals relative to either the centrum or transverse processes. In lumbar vertebrae of *Eucosmodon* (Granger & Simpson, 1929, fig. 26A; Krause & Jenkins, 1983, fig. 28A), a complete spine measures fifty to seventy percent of the length of the centrum or transverse processes and is approximately subequal to the height of the centrum. The lumbar spines are erect, rather than anterodorsally inclined, and are either subquadrate or somewhat subrectangular in shape (Krause & Jenkins, 1983, fig. 28).

In *Kryptobaatar* (PSS-MAE 103), an anterior lumbar vertebra is preserved with all processes intact. The spine is proportionately shorter, measuring only 1 mm in height. The centrum of this vertebra has a height of 1.8 mm and the transverse processes measure 2 mm in length. Like *Nemegtbaatar,* the spine is narrower than in *Eucosmodon* and is anterodorsally inclined.

In *Nemegtbaatar,* all the spines in the single available lumbar series are broken and have been reconstructed at twice their preserved length (Kielan-Jaworowska & Gambaryan, 1994, fig. 36B). The evidence from *Kryptobaatar* brings into question this reconstruction.

In the triconodont *Gobiconodon,* the lumbar neural spines and transverse processes are longer than centrum length and thus relatively longer than in multituberculates (Jenkins & Schaff, 1988, fig. 12C, E, G). Relatively long lumbar transverse processes and spines, furthermore, are present in many nonsaltatory mammals (MacPhee, 1994, fig. 18). In fact, there are few skeletal correlates among the less modified vertebrate saltators that are not also present in fossorial or cursorial mammals (Emerson, 1985; Hildebrand & Goslow, 2001).

In sum, the evidence from the lumbar vertebrae of multituberculates suggests that significant variation might exist, some species with subquadrate, erect spines and others with somewhat narrower, anterodorsally inclined spines. There is no evidence at present to suggest that the lumbar spines of multituberculates are inordinately long or that increased length of the lumbar neural spines is correlated with saltatory habits alone. Two features common among habitual mammalian saltators, in fact, are absent in multituberculates—namely, significant lengthening and strengthening of the hind limb and a posterior, rather than anterior, centered body mass (Emerson, 1985; Sereno, in review). New evidence is needed if a plausible case is to be made for habitual saltatory locomotion in multituberculates.

Checklist for Forelimb Posture

Three major, biomechanically significant features in shoulder girdle and forelimb architecture in living mammals may best constrain the range of possible forelimb postures in extinct relatives: shoulder girdle orientation and shoulder and elbow joint mobility.

Shoulder Joint Orientation. In the sprawling monotremes and in extinct mammalian outgroups long held to have a semierect forelimb posture, the glenoid faces laterally or posterolaterally and the coracoid forms a significant portion of the articular socket (fig. 10.9). In sprawling or semierect postures, the forelimbs and position of the manus are farther from the body axis, which necessarily generates a significant transverse, or compressive, force acting against a laterally facing shoulder socket (figs. 10.13D, 10.14A; Gray, 1944; Jenkins, 1970b, 1971a, 1971b). In living therians and their extinct theriimorph relatives, in contrast, the forelimbs operate in a parasagittal plane closer to the body axis (Jenkins & Weijs, 1979). Consequently, most of the glenoid faces ventrally, the coracoid contribution is reduced, and the manus is positioned ventral to the glenoid (figs. 10.10, 10.14B, C). The glenoid is designed to oppose the humeral force vector, and its orientation, therefore, appears to be an excellent predictor of forelimb posture.

Shoulder Joint Mobility. In the sprawling monotremes and in extinct mammalian outgroups long held to have a semierect forelimb posture, opposing pectoral girdles are joined by rigid articulations of the clavicle, interclavicle, and (in monotremes) procoracoid to form a stable platform for the shoulder socket (figs. 10. 9, 10.14A). This stable shoulder joint is so designed to "sustain the compressive forces generated by sprawling limb posture" (Jenkins, 1971b, 135). In living therians and their extinct theriimorph relatives, in contrast, the shoulder joint participates in stride

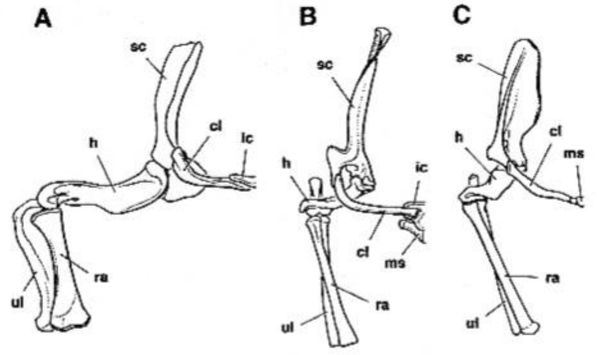

Figure 10.14. Anterior view of pectoral girdle and forelimb in a multituberculate compared with more basal and derived synapsids. (A) Cynodont based on *Cynognathus* and *Thrinaxodon* (Jenkins, 1971b). (B) *Kryptobaatar dashzevegi* based on PSS-MAE 103. (C) *Didelphis virginiana* (after Jenkins & Weijs, 1979). Abbreviations: cl, clavicle; ic, interclavicle; h, humerus, ms, manubrium sterni; ra, radius; sc, scapula; ul, ulna.

generation (fig. 10.13A, C), the clavicular articulations are reduced to allow such movement of the shoulder joint, and the clavicle and interclavicle are reduced or lost (figs. 10.10, 10.14B, C; Jenkins & Weijs, 1979). The stability of the union between opposing pectoral girdles depends on the humeral force vector and the presence of substantial transverse compressive stresses. Mobility of the shoulder joint, therefore, appears to be an excellent predictor of forelimb posture.

Elbow Joint Mobility. Flexion-extension at the elbow joint is minimal during terrestrial locomotion in the sprawling monotremes (fig. 10.13B) and in extinct mammalian outgroups (fig. 10.14A; Jenkins, 1971b, fig. 42). In monotremes, the ulnar portion of the distal humeral condyle is received in a shallow semilunar notch in the ulna. In tritylodontids, the ulnar condyle of the humerus is nearly flat and does not round onto either the anterior or posterior sides of the distal end (fig. 10.11A). In multituberculates and therians, in contrast, flexion-extension is clearly greatly enhanced. The bulbous ulnar condyle of the humerus has a dorsoventral articular arc of 180° or more (figs. 10.6B, 10.11B). The ulna, likewise, shows adaptations for increased flexion-extension, such as a distinct anconeal process and intercondylar crest, lengthened olecranon process, and marked radial and ulnar fossae. Enhanced flexion-extension at the elbow joint is linked with generating stride length in a parasagittal, or near parasagittal, plane (Jenkins 1971b, 1973) and thus appears to be an excellent predictor of forelimb posture.

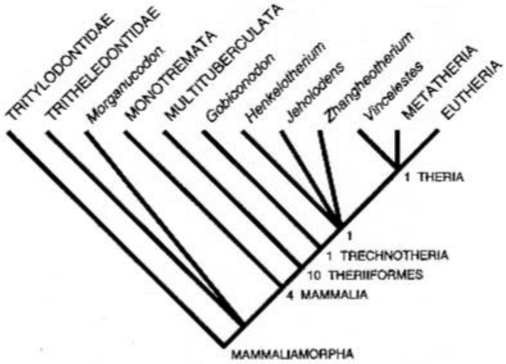

Figure 10.15. Semistrict consensus tree summarizing twenty-two minimum-length trees of twenty steps generated from eighteen characters in the pectoral girdle and forelimb across select mammaliamorph taxa (Tritylodontidae and Tritheledontidae as outgroups). Numbers show the distribution of unambiguous synapomorphies (consistencey index = 0.95, retention index = 0.98). Character support linking multituberculates and basal trechnotherians with Theria is strong and overwhelms available data from the skull and dentition regarding placement among crown mammal clades.

Evolution of Shoulder and Elbow Joints

From the available fossil record, it is possible to visualize three major stages in the evolution of mammalian shoulder and elbow joints. The skeletal changes associated with each stage appear to have evolved only once in mammalian history, an interpretation based on phylogenetic analysis (figs. 10.15, 10.16). The onus now is on the oft-repeated hypothesis of parallel evolution of these functional attributes in several mammalian lineages. Defending this hypothesis requires an alternative phylogenetic arrangement and/or a significant amount of new and contradictory character information to that summarized in this paper.

Girdle Simplification. Reduction and coossification of the coracoid with the scapula occurred at the base of Mammalia probably sometime during the Jurassic (fig. 10.16, node 1). In living mammals, fusion of the scapulocoracoid suture is nearly universal, but it often occurs quite late in posthatching/postnatal development. A second round of simplification occurred before the close of the Jurassic among basal therians involving fusion of the procoracoid and interclavicle to the manubrium sterni. The fossil record shows the loss of the procoracoid and interclavicle; the proposed fusions are deduced solely from embryological evidence in living therians (Klima, 1987).

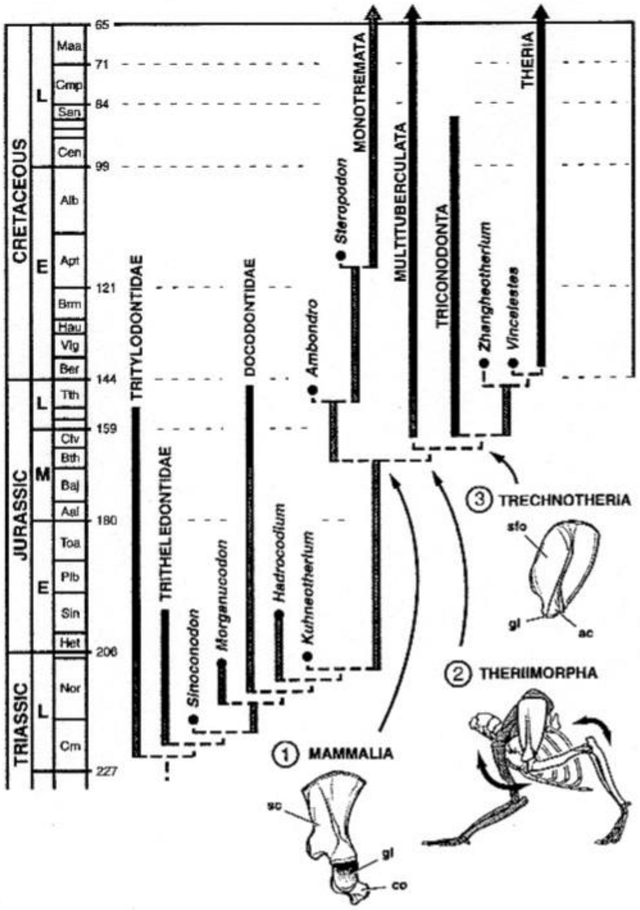

Figure 10.16. Temporally calibrated phylogeny for key early mammalian taxa showing major functional and skeletal innovations in the shoulder and elbow (1, girdle coossification; 2, enhanced shoulder/elbow joint mobility during locomotion; 3, girdle simplification). Known age estimates (dots), temporal durations (solid bars), and missing ranges (shaded bars) are shown. Time scale is based on Gradstein et al. (1999). Abbreviations: ac, acromion; co, coracoid; gl, glenoid; sc, scapula; sfo, supraspinous fossa.

Shoulder and Elbow Joint Mobility Mobility of the shoulder joint and enhanced flexion-extension of the elbow joint both appear to have evolved once, possibly in concert, among basal theriimorphs sometime before the close of the Jurassic (fig. 10.16, node 2). In living quadrupedal therians with a mobile shoulder joint, the elbow joint is located posterior to the shoulder joint near the thorax wall and, therefore, is subject to a greater degree of flexion and extension than in forms with sprawling or semierect forelimb postures. At present, phylogenetic evidence and the fossil record suggest that these two critical functional attributes of parasagittal forelimb posture in mammals evolved once over the same temporal interval before the close of the Jurassic.

Joint Stabilization. The evolution of the therian (humeroulnar) trochlear joint from the more primitive spiral condylar joint also appears to have occurred once and before the close of the Jurassic (fig. 10.16, node 3). The functional significance of this transition remains speculative, as the spiral condylar joint in multituberculates (and possibly other basal mammals) and the primitive therian trochlea (fig. 10.11B, C) both appear to generate the same forearm movement (Jenkins, 1973). Joint stabilization may be the most plausible explanation for evolution of the therian trochlea, but it is a hypothesis in need of supporting empirical data from living mammals.

Conclusions

1. The taxon Mammalia may best be defined phylogenetically as a node-based crown group. More inclusive definitions that incorporate extinct stem taxa have little historical basis, and apomorphy-based definitions utilizing the form of the jaw joint invite future ambivalence.
2. Taxonomic definitions for clades at the base of Mammalia are stabilized by node-stem triplets (e.g., Theria = Metatheria + Eutheria) delineated by complementary phylogenetic definitions that employ well-preserved recent and/or extinct genera (e.g., Ornithorhynchus, Taeniolabis).
3. The multituberculate pectoral girdle is characterized by several specializations not seen in other early mammals such as the unusual length of the scapular blade, loss of the coracoid posterior process, and clover-shaped interclavicle.
4. Character evidence from the pectoral girdle and forelimb plays a major role in establishing phylogenetic arrangements at the base of Mammalia, in particular positioning Multituberculata and several other Mesozoic clades within Mammalia in alliance with Theria.
5. Skeletal evidence from fossils and modern mammalian analogs does not support a sprawling forelimb posture or habitual saltatory locomotion in multituberculates. Evidence in favor of a more parasagittal forelimb posture in multituberculates includes the small ventrally facing glenoid, mobile shoulder joint, cam-shaped ulnar condyle of the humerus, and elbow joint with enhanced flexion-extension capability.
6. A mobile shoulder joint, an elbow joint with enhanced flexion-extension, and parasagittal forelimb posture appear to have evolved once, possibly in concert, among basal theriimorphs near the close of the Jurassic.

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