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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

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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,

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 (Mammaliomorpha, 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
Mammalia Rowe, 1988	The least inclusive clade containing <i>Tritylodon langae-vus</i> Owen, 1884, <i>Pachygenelus monus</i> Watson, 1913, and <i>Mus musculus</i> Linnaeus, 1758.
Tritylodontidae Kühne, 1956	The most inclusive clade containing <i>Tritylodon longae-vus</i> Owen, 1884, but not <i>Pachygenelus monus</i> Watson, 1913, <i>Mus musculus</i> Linnaeus, 1758.
Tritheledontidae Broom, 1912	The most inclusive clade containing <i>Pachygenelus monus</i> Watson, 1913 but not <i>Tritylodon longae-vus</i> Owen, 1884, <i>Mus musculus</i> Linnaeus, 1758.
Mammaliaformes Rowe, 1988	The most inclusive clade containing <i>Mus musculus</i> Linnaeus, 1758 but not <i>Tritylodon longae-vus</i> Owen, 1884 or <i>Pachygenelus monus</i> Watson, 1913.
Mammalia Linnaeus, 1758	The least inclusive clade containing <i>Ornithorhynchus anatinus</i> (Shaw, 1799) and <i>Mus musculus</i> Linnaeus, 1758.
Prototheria Gill, 1872	The most inclusive clade containing <i>Ornithorhynchus anatinus</i> (Shaw, 1799) but not <i>Mus musculus</i> Linnaeus, 1758.
Monotremata Bonaparte, 1837	The least inclusive clade containing <i>Ornithorhynchus anatinus</i> (Shaw, 1799) and <i>Tachyglossus aculeatus</i> (Shaw, 1792).
Theriomorpha Rowe, 1993	The most inclusive clade containing <i>Mus musculus</i> Linnaeus, 1758 but not <i>Ornithorhynchus anatinus</i> (Shaw, 1799).
Theriformes Rowe, 1988	The least inclusive clade containing <i>Mus musculus</i> Linnaeus, 1758 and <i>Taeniolabis taoensis</i> (Cope, 1882).
Allotheria Marsh, 1880	The most inclusive clade containing <i>Taeniolabis taoensis</i> (Cope, 1882) but not <i>Mus musculus</i> Linnaeus, 1758 or <i>Ornithorhynchus anatinus</i> (Shaw, 1799).
Multituberculata Cope, 1884	The least inclusive clade containing <i>Taeniolabis taoensis</i> (Cope, 1882) and <i>Paulchofattia delgadoi</i> Kühne, 1961.
Trechnotheria McKenna, 1975	The most inclusive clade containing <i>Mus musculus</i> Linnaeus, 1758 but not <i>Taeniolabis taoensis</i> (Cope 1882) or <i>Ornithorhynchus anatinus</i> (Shaw, 1799).
Theria Parker & Haswell, 1897	The least inclusive clade containing <i>Mus musculus</i> Linnaeus, 1758 and <i>Didelphis marsupialis</i> Linnaeus, 1758.
Metatheria Huxley 1880	The most inclusive clade containing <i>Didelphis marsupialis</i> (Linnaeus, 1758) but not <i>Mus musculus</i> Linnaeus, 1758.

(continued)

