

LUO, Z.-X. 2015. Origin of the Mammalian Shoulder. Pp.167-187.  
In: K. P. Dial, N. H. Shubin and E. L Brainerd (eds.)  
Great Transformations: Major Events in the History of Vertebrate Life.  
Chicago: The University of Chicago Press.

## 10

# Origin of the Mammalian Shoulder

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### Introduction

The shoulder girdle connects the forelimb and the axial skeleton (fig. 10.1). Its structure has undergone significant changes through the origins of extant mammals from the pre-mammalian cynodonts, accompanied by evolution of locomotor function (Jenkins 1970a, 1971a, 1971b; Jenkins and Weijs 1979). Thanks to the newly discovered fossils and more extensive comparative studies in the last two decades, the shoulder girdle structure has become better known in a wide range of pre-mammalian cynodonts, stem mammaliaforms that are extinct relatives to modern mammals, and Mesozoic clades of the crown Mammalia defined by the common ancestor of monotremes, marsupials, and placentals, plus fossil mammals among these living groups (Krebs 1991; Rougier 1993; Sereno and McKenna 1995; Hu et al. 1997; Ji et al. 1999; Gow 2001; Luo and Wible 2005; Martin 2005; Hu 2006; Sereno 2006; Sues and Jenkins 2006; Luo, Chen, et al. 2007; Hurum and Kielan-Jaworowska 2008; Chen and Luo 2013). The better-preserved fossils have revealed more complex patterns of evolution of the shoulder girdles through the great transition from cynodonts to mammals.

Monotremes are different from marsupials and placentals, collectively known as the crown therians (or *Theria sensu* Rowe 1988), in patterns of embryogenesis, and

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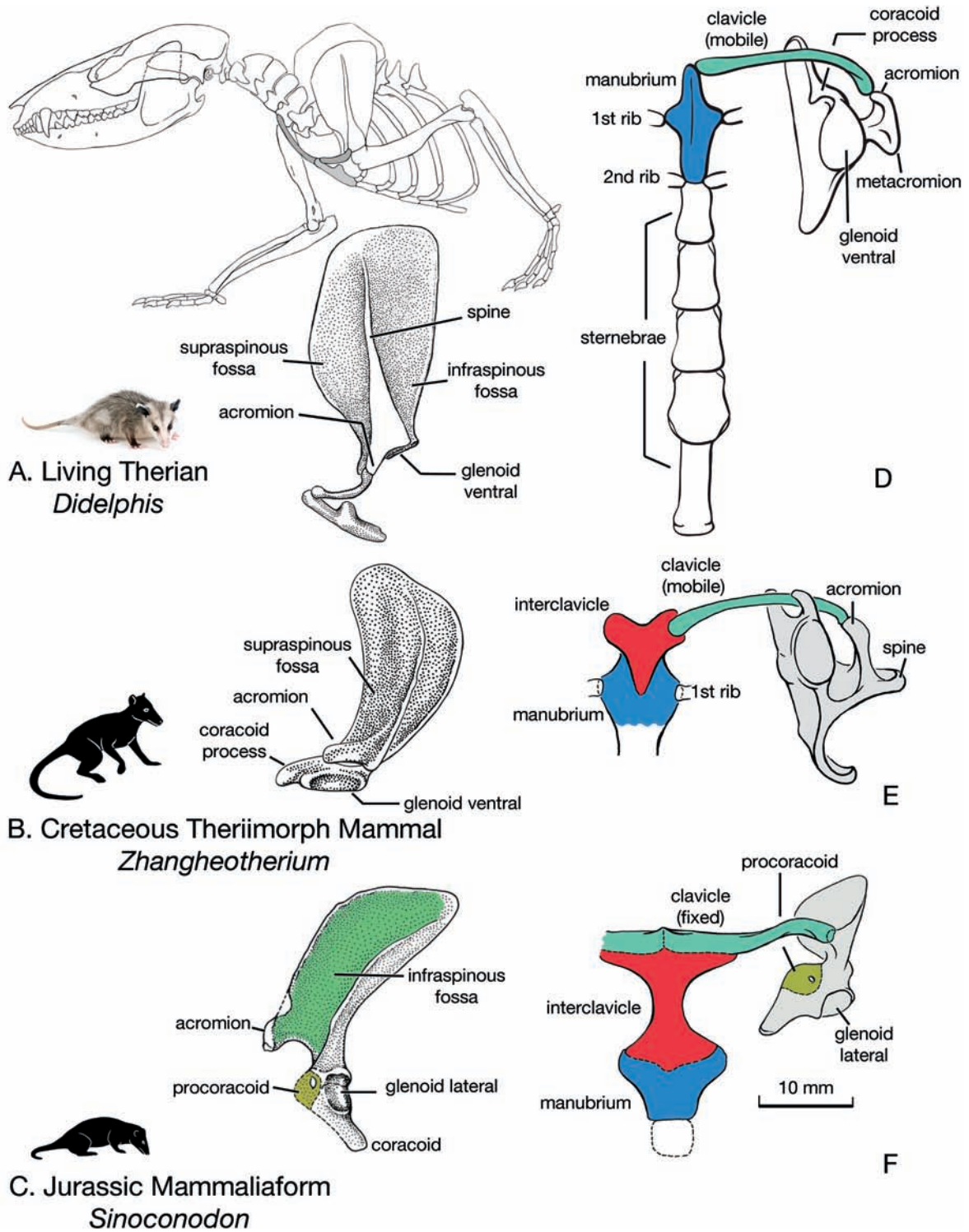


FIG. 10.1 Shoulder girdles of mammaliaforms and therian mammals. Top, Extant marsupial *Didelphis virginiana*: shoulder girdle in lateral view (A) and ventral view (D). Middle, Early Cretaceous theriimorph (spalacotheroid) *Zhangheotherium quinquecuspedens*: scapulocoracoid in lateral view (B) and restoration of shoulder girdle in ventral view (E). Bottom, Early Jurassic mammaliaform *Sinoconodon rigneyi*: scapulocoracoid in lateral view (C), restoration of shoulder girdle in ventral view (F). Stylistic figures not on the same scale.

in adult structure and function of the shoulder girdle and forelimb (Lessertisseur and Saban 1967a; Jenkins 1970b; Klima 1973, 1985; Walter 1988). Among therians, marsupials differ from placentals in timing of embryonic development of the shoulder girdle (Sears 2004, 2005; Hübler et al. 2010), a difference that is attributable to gene patterning (Keyte and Smith 2010; Hübler et al. 2013). Marsupials have a more conserved pattern of variation of the scapula than placentals, which is related to an accelerated development of the shoulder girdle and forelimb (Sánchez-Villagra and Maier 2002; Sears 2004; Hübler et al. 2010; Keyte and Smith 2010). This ontogenetic feature is required for fetuses to climb to maternal tits after their premature birth, a life history constraint of all marsupials (Lillegraven 1975; Gemmell et al. 2002). Placental mammals have diverse morphologies, related to the fact that their shoulder girdle is unconstrained (relative to marsupials) and to their versatile locomotor adaptations (Kardong 1998; Hildebrand and Goslow 2001; Polly 2007).

Recent advances in developmental genetics of the mouse, a model organism in laboratory studies, have made it possible to trace the morphogenesis of some adult features of the shoulder girdle to gene networks and signaling pathways. Sternal, shoulder girdle, and forelimb characters of mice are now attributable, in an increasingly precise way, to gene patterning (Timmons et al. 1994; Matsuoka et al. 2005; McIntyre et al. 2007; Capellini et al. 2010). The understanding of the genetic control of morphogenesis is a good step toward the deciphering of the evolution, as it can offer a more explicit genetic underpinning for embryogenesis and on the mechanism of macroevolutionary transformation (Vickaryous and Hall 2006; Sears et al. 2013).

### Shoulder Girdle and Musculature of Extant Mammals

The transformation in the shoulder girdle in early mammal evolution is evident from the prominent differences between extant therians and stem mammaliaforms (fig. 10.1), and from the distinctive patterns among Mesozoic mammal groups phylogenetically intermediate between therians and monotremes (figs. 10.2–10.4). Extant therians have fewer bony elements in the shoulder girdle and the sternum than stem mammaliaforms, through an evolutionary reduction and eventual loss of

the interclavicle bone, a membranous element in the sternal series. With exception of those of flying and burrowing adaptations, therians have proportionally smaller sternal elements than those of monotremes and mammaliaforms (fig. 10.4). This is especially evident in the manubrium, the anterior-most sternal element developed embryonically from the endochondral sternbrae. Therians and Mesozoic theriomorph (“therian-like”) mammals lost the procoracoid that is a primitive character of some mammaliaforms and monotremes. Therians and their theriomorph relatives show a simplified scapulocoracoid, with the much-diminished embryonic coracoid (also known as metacoracoid *sensu* Vickaryous and Hall 2006) integrated into the glenoid of the adult scapula.

**Extant therians (figs. 10.1–10.3)**—The scapulas of marsupials and placentals have two topographical areas: a ventral region of the coracoid process, the glenoid and the acromion, and a dorsal region of the plate-like blade that has the septal part of the scapular spine, a crest-like septum dividing the lateral surface of the scapular blade into the supraspinous muscle fossa and the infraspino-*s* muscle fossa.

The ventral part of the spine bears the acromion (thus called here the acromiospine). The acromion is projected ventrally or anteroventrally to articulate with the lateral (distal) end of the clavicle, forming the acromioclavicular joint. The acromial part of the spine can have a metacromion in some (although not all) therians, and it marks the separation of the spino-deltoid part from the acromio-clavicular part of the deltoid muscle (Jenkins and Weijs 1979; Evans 1993; Großmann et al. 2002). The part of the spine dorsal to the acromion is a simple crest, herein called the septal part of the spine, or the septospine, which separates the supraspinous fossa and the infraspino-*s* fossa.

The acromiospine and septospine have distinctive embryonic development: the former developed endochondrally, while the latter developed as appositional bone without cartilaginous precursor (Sánchez-Villagra and Maier 2002, 2003) (fig. 10.5). More recently, genetic studies show that the coraco-gleno-acromial area has different gene patterning, from the plate-like blade and the septospine in mouse (Timmons et al. 1994; Dietrich and Gruss 1995; Pellegrini et al. 2001; Capellini et al. 2010, 2011). The relative independence of the

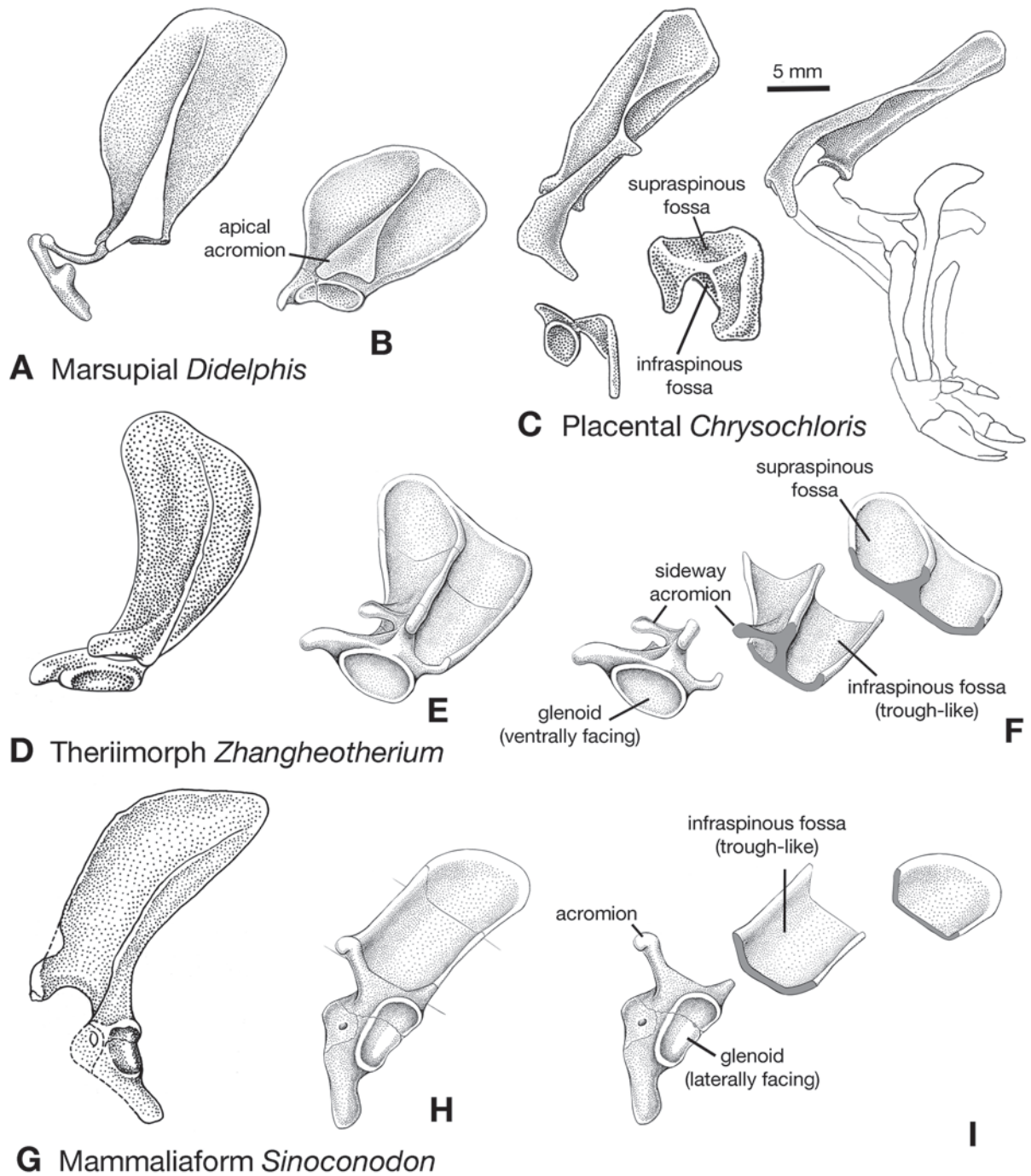


FIG. 10.2 Scapulocoracoid of mammaliaforms and mammals: offset acromion of stem therians and apical acromion of extant therians. A and B, Marsupial *Didelphis* left scapula in (A) lateral and (B) oblique (ventrolateral) views showing the acromion stemming from the top of the spine. C, Placental *Chrysochloris asiaticus* (African golden mole, a fossorial mammal), left scapula in lateral, ventral, and dorso-posterior views, and in articulation with the forelimb. D, E, and F, Early Cretaceous spalacotheroid *Zhangheotherium*, (a theriimorph) left scapula in lateral view (D), and oblique (ventrolateral) view (E), showing the acromion arising from the sidewall of the scapular spine, and the trough-like infraspinous fossa, and (F), reconstruction in cross-sections. G, H, and I, Early Jurassic mammaliaform *Sinoconodon rigneyi*, left scapula in lateral view (G), oblique (ventrolateral) view (H), and cross-sectional reconstruction (I). Sources: *Chrysochloris* redrawn from Lessertisseur and Saban (1967a), Asher et al. (2007), Wible et al. (2009), and public domain image from [www.digimorph.org](http://www.digimorph.org) (accessed in June 2012). Stylistic figures not on the same scale.

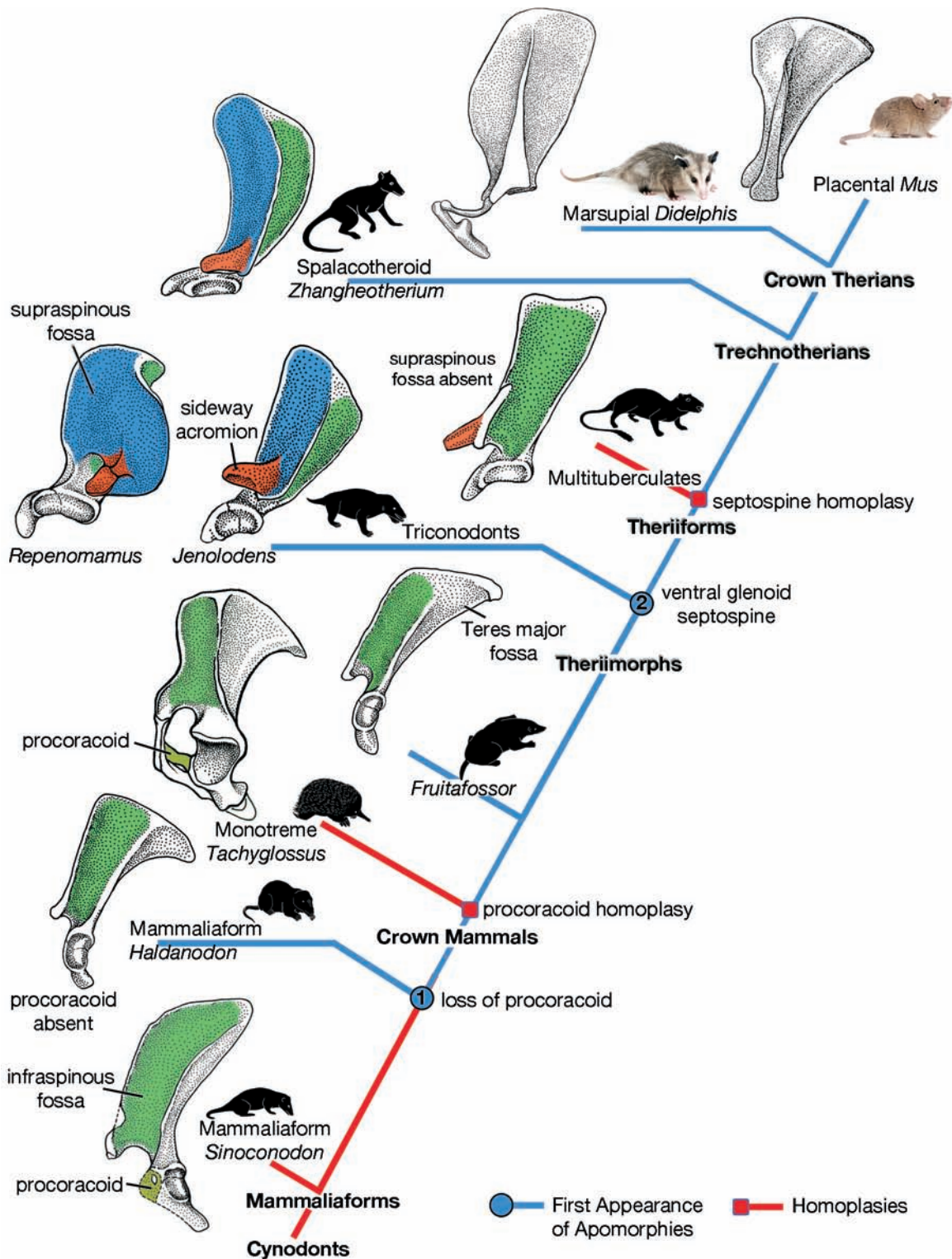


FIG. 10.3 Evolutionary patterns of scapulocoracoids through the cynodont-mammal transition. Two major evolutionary apomorphies: (1) loss of the procoracoid in derived mammaliaforms starting with *Haldanodon* (although homoplastic in monotremes and unknown in *Pseudotribos*), and (2) reorientation of scapular glenoid, and appearance of the supraspinous fossa with triconodonts and spalacotheroids, although lost in multituberculates by homoplasy. A general evolutionary trend: the size of the sternal elements, especially the interclavicle, is greatly reduced in theriimorph mammals. The schematic illustrations standardized to the length of the clavicle, not on the same scale. Sources: *Haldanodon* redrawn from Martin (2005), *Tachyglossus* redrawn from Jenkins and Parrington (1976), *Fruitafossor* modified from Luo and Wible (2005), *Repenomamus* redrawn from Hu (2006) with personal observation of other specimens, multituberculate a composite restoration from *Kryptobaatar* (Sereno 2006), *Catopsbaatar* from Hurum and Kielan-Jaworowska (2008) and personal observation of several multituberculates, *Zhangheotherium* based on Chen and Luo (2013) and observation of other specimens.

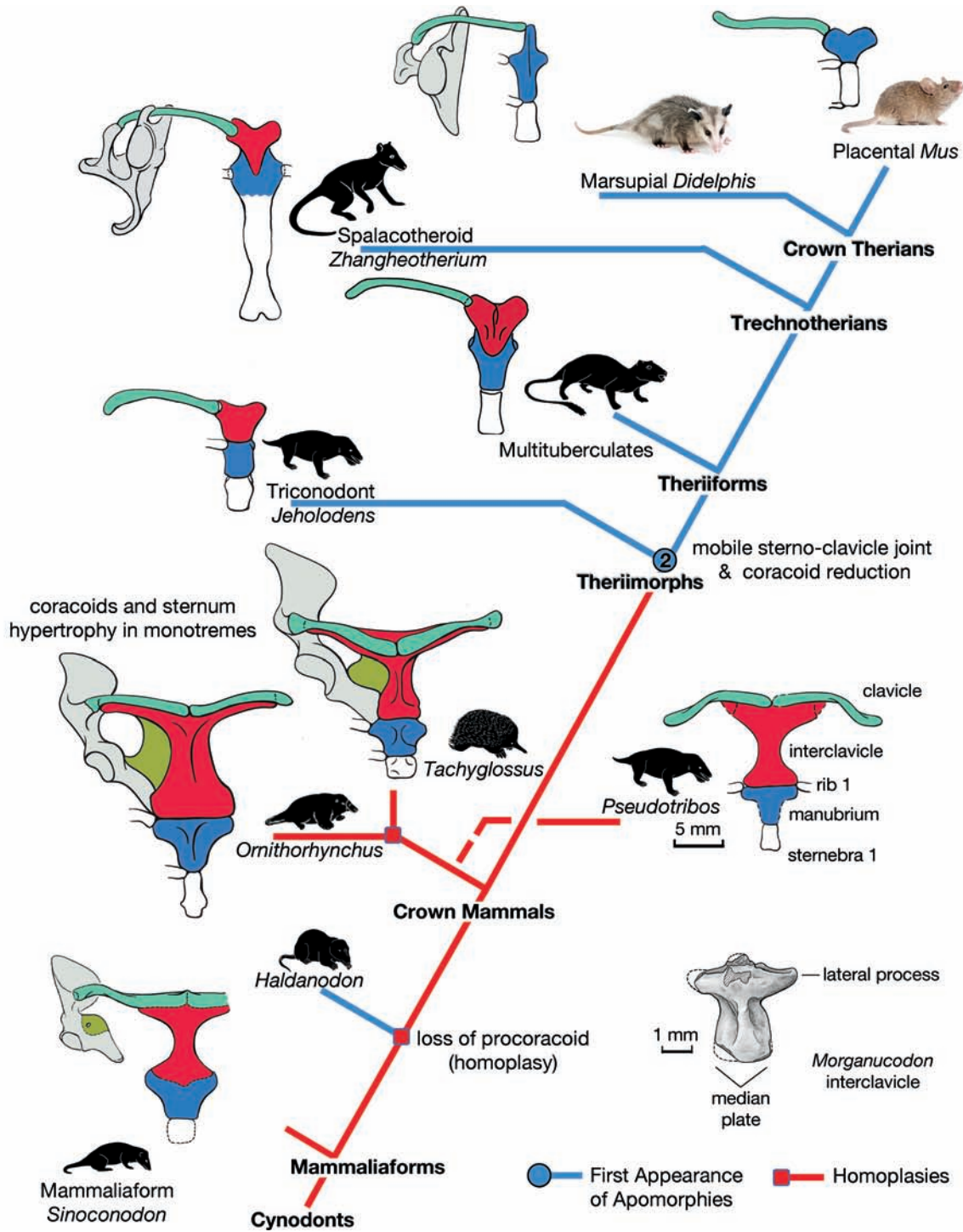
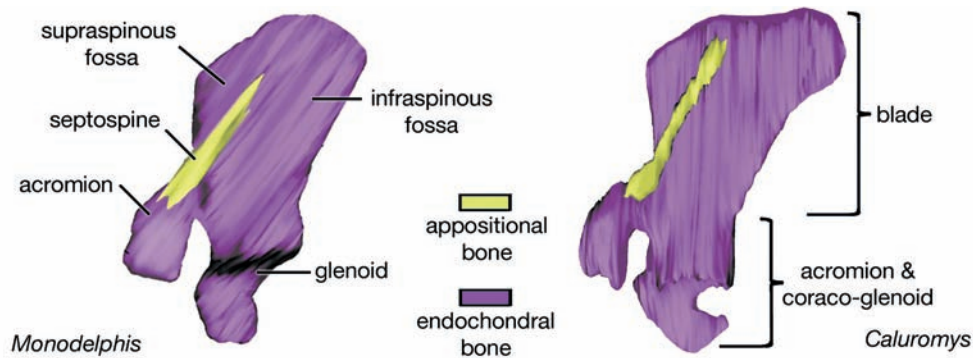


FIG. 10.4 Evolutionary patterns of the clavicular and sternal structures through the cynodont-mammal transition. A major evolutionary apomorphy is the mobile claviculo-interclavicular joint through reduction of the interclavicle and loss of the procoracoid, which first occurred in mammal evolution with *Fruitafossor* and theriimorphs, although loss of the procoracoid likely occurred independently in *Haldanodon*. Sources: *Morganucodon* based on a specimen courtesy of Prof. Susan Evans.



Independent Embryonic Components of Scapula in Opossums

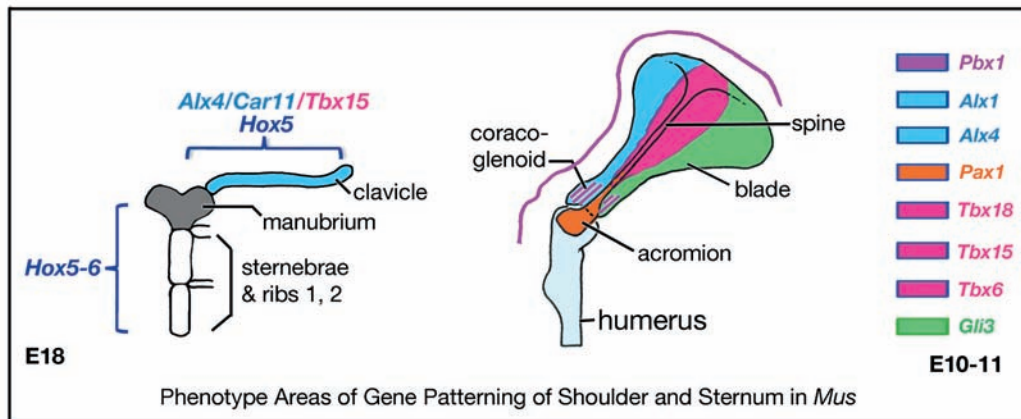


FIG. 10.5 Phenotype areas of gene patterning of the shoulder girdle and sternal structures and modular development of embryonic components of scapula. Top, Modular development of the scapular spine in didelphid marsupials; adapted with permission from Sánchez-Villagra and Maier (2003). Bottom (Box), Functional phenotype areas of major genes in morphogenesis of the mouse shoulder girdle and sternal structure: scapular patterns about embryonic days 10–11 adapted with modification from Capellini et al. (2010) with additional information from Wehn and Chapman (2010), and Hübler et al (2013); sternal patterns of mouse about embryonic day 18 after McIntyre et al. (2007). The gene expression areas may overlap, and are based on stylistic outline, not on the same scale.

coraco-gleno-acromial region is also manifest in the gross morphological features during the ontogenetic growth, and in morphometric patterns of variation (Sears et al. 2013). In marsupials, the coracoid process in the coraco-gleno-acromial region shows a distinctly slower developmental rate, and has a different growth trajectory from the rest of the scapula, likely by different gene patterning in marsupials (Hübler et al. 2010, 2013).

The glenoid of the scapula in therians is a shallow, uniformly concave fossa and has a nearly oval outline in ventral view (fig. 10.1D, E). The concave glenoid and the hemispherical head of the humerus form a spheroidal (ball-in-socket) or an ovoidal joint (Williams et al. 1989; Hildebrand and Goslow 2001). The glenohumeral joint of therians is capable of movement of the humeral head to the scapula in any direction with three degrees of freedom in flexion-extension, adduction-abduction, and circumduction and mediolateral rotation around the

humeral long-axis, or any combination of these (Williams et al. 1989). The concave glenoid with oval outline is the most common, presumably a general condition of therians (Lessertisseur and Saban 1967a; Evans 1993). However, the shape of the glenoid can vary with different habits or locomotor specializations among closely related species of marsupials and placentals (Taylor 1974; Argot 2001; Sargis 2002).

The glenoid of therians is oriented nearly perpendicularly to the scapular blade; its functional synovial surface is faced ventrally in life. The scapular blade is dorsal to the glenohumeral joint and the humerus shaft. This perpendicular orientation of a ventrally facing glenoid, or nearly so, is important for the parasagittal or nearly parasagittal posture of the forelimb in therians (Jenkins 1971a; Sereno 2006), in contrast to the more sprawling forelimb posture of the majority of the non-therian amniotes including monotremes (Gambaryan

and Kielan-Jaworowska 1997). The glenoid is shallow, partly incongruent with, and smaller than the much larger humeral head. This kind of joint enables a great freedom of movement, but it is also weak due to the lack of restraining. The highly mobile but simultaneously weak glenohumeral joint is stabilized compensatorily by the tension of ligamentous capsule of the glenohumeral joint and reinforced by the large supraspinous muscle, an evolutionary apomorphy of therians (Jenkins and Goslow 1983; Williams et al. 1989; Evans 1993; Fischer 2001).

The coracoid process (= “metacoracoid”) is a small projection anterior to the margin of the glenoid (fig. 10.2B, C). It shows different relationships to the scapular glenoid and blade among therians, monotremes, and stem mammaliaforms. Also within different therian groups, the coracoid can vary in size, curvature, and shape, related to functional differences of the biceps and coracobrachialis muscles among species of different habits within families or genera (Taylor 1974; Argot 2001; Sargis 2002). The coracoid process is known for its different growth rates in different phases of ontogeny in marsupials (Hübner et al. 2013).

The clavicle is present in the most extant therians although some have lost this bone. The aclavicate mammals, by losing the clavicle, can achieve a wider range of movement of the scapula relative to the axial skeleton, such as seen in therians of cursorial (running) adaptation. In clavicate therians, the medial end of the clavicle articulates with the manubrium by a mobile joint (fig. 10.1). The clavicle serves as a spoke to guide the arcuate movement of the glenohumeral joint, and also as a strut to support the shoulder joint (Jenkins 1974). The dual function of strut and spoke of clavicle is crucial for a wide range of locomotor functions, especially among placentals (Jenkins 1974; Hildebrand and Goslow 2001; Polly 2007).

**Monotremes (figs. 10.3 and 10.4)**—Extant monotremes differ significantly from therians in having an interclavicle. The large interclavicle has a broad median plate and long lateral processes, developed, respectively, from the unpaired chondral element and the paired desmal elements in embryogenesis (Klima 1973, 1985). The lateral process forms a tongue-in-groove contact with the clavicle along the entire length of the latter. Bounded by ligament, the clavicle is immobile relative to the in-

terclavicle. The lateral process of interclavicle and the clavicle both reach the acromio-clavicle joint, which is mobile (Klima 1973; Jenkins and Parrington 1976; Augee et al. 2006). The interclavicle may have highly variable distal epiphyses at the joint with the manubrium (Cave 1970). The interclavicle and the manubrium are not mobile, but their junction has a synovial joint for the coracoid process of the scapulocoracoid (Cave 1970; Sereno 2006).

Monotremes have a hypertrophied coracoid process, and it is homologous to the metacoracoid of non-mammalian amniotes (reviewed by Vickaryous and Hall [2006]). The coracoid is so massive that it reaches the sternal series and articulates with the manubrium-interclavicle joint. Monotremes differ further from therians and are unique among amniotes in having a large, plate-like procoracoid (Lessertisseur and Saban 1967a; Vickaryous and Hall 2006), which is developed in ontogeny from the medial part of the embryonic coraco-scapular plate (Klima 1973). Posteriorly, the procoracoid abuts tightly the coracoid process (metacoracoid) of the scapulocoracoid. Anteriorly and medially it can either overlap, or attach loosely to the interclavicle (fig. 10.3). Besides a variable relationship to the interclavicle, the procoracoid can be variable in shape and often asymmetric between two sides (Cave 1970).

With mobile joints of the acromion and clavicle and between the coracoid process and the interclavicle-manubrium, the scapulocoracoid is capable of limited dorso-ventral movement to the sternum. The clavicle and the hypertrophied coracoid process cannot function as a spoke in a therian fashion. Instead, these collectively serve as a strong strut for the glenohumeral joint, for powerful forelimb movement for burrowing of monotremes (Jenkins 1970b; Augee et al. 2006), and secondarily for rowing in swimming by the platypus of semiaquatic habits.

The glenoid of scapulocoracoid in monotremes has a half-saddle shape, also known as hemi-sellar joint (*sensu* Jenkins 1993) (fig. 10.3). By comparison to the shallow ovoidal glenoid of therians capable of movement in any direction, the hemi-sellar joint is more restrictive for elevation and depression of the humerus to the glenohumeral joint, although not for protraction and retraction (Jenkins 1993). The half-saddle joint permits translational movement along the short axis of the glenoid surface, and long-axis rotation of the humerus that



is held more or less perpendicular to the sagittal plane (Jenkins 1970b).

The glenoid of monotremes is oriented obliquely to the main plane of the scapular blade. With the scapula oriented anterodorsally in life, the glenoid is facing laterally, in contrast to the ventrally facing glenoid of therians (Lessertisseur and Saban 1967a; Jenkins 1971b; Sues and Jenkins 2006). The glenoid is more similar to those of stem mammaliaforms than therians, and plesiomorphic in its characteristics. The coracoid and the scapula contribute equally to the synovial surface of the glenoid joint in monotremes, different from the therian condition of the glenoid formed mostly by the scapula, almost to the exclusion of the coracoid. The glenoid surface of monotremes is relatively larger for the humeral head than in therians. The scapula-coracoid junction is reinforced by the greater bone thickness, likely for bracing the forelimb for burrowing.

The scapulas of monotremes have an extensive fossa for the infraspinous muscle (*sensu* Diogo and Abdala 2010), also known as subscapularis fossa (Jouffroy and Lessertisseur 1971). This is an ancestral feature of pre-mammalian cynodonts and stem mammaliaforms (Jenkins 1971b; Jenkins and Parrington 1976; Sun and Li 1985; Sues and Jenkins 2006). The scapula lacks a fully developed supraspinous fossa as seen in therians. A small muscle, recognized either as a small supraspinous muscle by some (Coues 1871; Walter 1988; Diogo and Abdala 2010) or as the “pars suprascapularis” of the supracoracoideus by others (Jouffroy and Lessertisseur 1971; Jenkins 1971b) is attached to the base of the acromion (Jouffroy and Lessertisseur 1971; Walter 1988). These alternative terms of this muscle are both consistent because the supraspinous muscle of therians is partly homologous to the supracoracoideus of non-mammalian amniotes by ontogeny (Cheng 1955; Romer 1956; Diogo and Abdala 2010). However, in monotremes, the supraspinous muscle on the scapula is miniscule (Walter 1988), and much smaller than those of therians. It coexists with the much larger supracoracoideus muscle that originates from the plate-like procoracoid bone and inserts on the great tubercle of the humerus, to pull the humerus forward and simultaneously rotate it along its long axis (Jouffroy and Lessertisseur 1971, figures 627, 631; Jenkins 1971a; Walter 1988).

The scapula has a well-developed dorso-posterior angle and a prominent teres major muscle fossa marked

by a distinctive crest from the infraspinous fossa, for a hypertrophied teres major muscle for the burrowing movement of the forelimb. A similar, large teres major fossa is present in some specialized fossorial therians (Hildebrand 1985; Hildebrand and Goslow 2001), although this is not the case for the majority of therians with generalized forelimb function.

A major difference in musculature and muscle function between monotremes and therians is related to how the glenohumeral joint is stabilized. The supraspinous muscle is an evolutionary apomorphy of therians, and it is a major muscle in stabilizing the glenohumeral joint that has a considerable laxity due to a shallow glenoid smaller than the large humeral head (Fischer 2001; Sánchez-Villagra and Maier 2002). The supraspinous fossa and the infraspinous fossa are both well developed on the scapular blade; the supraspinous and the infraspinous muscles insert on the greater tubercle of the humerus, with equitable muscle fiber contributions to stabilizing the glenohumeral joint during movement (Jenkins and Goslow 1983; Evans 1993; Fischer 2001).

By contrast, the supraspinous muscle (or equivalent to the therian supraspinous) is miniscule in monotremes (Howell 1937; Jouffroy and Lessertisseur 1971; Walter 1988). The glenohumeral joint is stabilized by the infraspinous muscle and by the large supracoracoideus muscle originating from the procoracoid to insert on the greater tubercle of the humerus (Jouffroy and Lessertisseur 1971; Walter 1988), analogous to the supracoracoideus function to stabilize the glenohumeral joint, as seen in lizards (Jenkins and Goslow 1983). In contrast to the lax joint of therians that maximizes mobility at the expense of stability, the monotreme glenohumeral joint is more massive and strongly reinforced, suggesting the stabilization by a miniscule supraspinous muscle, if needed at all, is not as critical for monotremes as for therians.

## Shoulder Girdles of Mammaliaforms

Mammaliaforms are defined by the common ancestor of *Sinoconodon*, *Morganucodon*, and living mammals, and can be diagnosed by the key skull features (Rowe 1988, as modified by Luo 2007). Stem mammaliaforms are Mesozoic relatives to living mammals. Many of their features are intermediate for the cynodont-mammal

transition, more derived than cynodonts, but primitive for crown Mammalia.

*Morganucodon* is an insectivorous mammaliaform from the Late Triassic to Early Jurassic. Its shoulder girdle provides important information on the ancestral condition from which the girdles of mammals have likely evolved (Jenkins and Parrington 1976; Jenkins and Weijs 1979; Sues and Jenkins 2006). The scapulocoracoid of the Late Jurassic docodont *Haldanodon* is also represented by extensive fossils and has been reconstructed (Martin 2005). However, the clavicle and interclavicle are unknown for these mammaliaforms (Evans 1981; Martin 2005).

*Sinoconodon* from the Early Jurassic (fig. 10.1C) has relatively well-preserved interclavicle and clavicle, which made it possible to reconstruct their relationship to the rest of the shoulder girdle (Luo, Ji, and Yuan 2007). The interclavicle has a dumbbell shape. Its median plate has a constricted middle portion, a widened posterior part abutting the manubrium, and two short lateral processes in the anterior part overlapping with clavicles. The interclavicle of *Sinoconodon* has nearly the same shape as an isolated interclavicle of *Morganucodon* (specimen courtesy of Prof. Susan Evans). The broad interclavicle with a constricted waist and an expanded posterior end is monotreme-like, more derived features than the ancestral cynodont condition of a narrow interclavicle with a tapering posterior end, as seen in several cynodonts (Jenkins 1970a, 1971b; Sun and Li 1985; Sues and Jenkins 2006). Most cynodonts lack the lateral processes (Jenkins 1970a, 1971b; Romer and Lewis 1973), although these are present in tritylodontids (Sun and Li 1985; Sues and Jenkins 2006).

The interclavicle, manubrium, and procoracoid of *Sinoconodon* provide an expanded area for muscles, presumably for the pectoralis and supracoracoideus muscles as in monotremes (Jouffroy and Lessertisseur 1971; Walter 1988). The clavicle is curved in boomerang shape, as those of tritylodontids (Sues and Jenkins 2006) with its lateral end articulating with the acromion process of the scapula. The acromio-clavicle joint appears to be mobile.

The procoracoid is integrated into the scapulocoracoid. It is interpreted here to have a coracoid foramen, and is excluded from the glenoid (fig. 10.1C). The coracoid process (= metacoracoid) has a pointed apex, directed posteromedially toward, but is short of

contacting the sternum. The short coracoid process without sternal contact is obviously different from the monotreme condition of a long and massive coracoid process in synovial articulation to the sternum. The hemi-sellar glenoid is oriented to face ventrolaterally (fig. 10.1C). The infraspinous fossa is a deep, trough-like structure, and occupies the entire lateral aspect of the scapular blade (figs. 10.1C and 10.2G). The acromion is a short protuberance on the scapular spine at the anterior (cranial) margin of the scapula. If the supraspinous muscle is present, it would be attached to a small surface on the anterodorsal aspect of the spine, and its muscle fibers would pass below the clavicle and acromio-clavicle joint to insert on the humerus, as previously interpreted for *Morganucodon* (Jenkins and Weijs 1979). The posterior (or posteroventral) margin of the infraspinous fossa is curved.

There is not an expanded fossa for the teres major muscle although this muscle could be attached to the posterodorsal angle of the scapula. It would be small if present (fig. 10.2G). The large teres major muscle fossa is present in some pre-mammalian cynodonts and mammaliaforms, inferred to have fossorial habits by limb features for digging (Martin 2005; Luo and Wible 2005; Sues and Jenkins 2006), although the fossorial adaptation is not a uniform condition of mammaliaforms, as evident from *Sinoconodon*.

The scapulocoracoid of the mammaliaform *Haldanodon* is well represented by extensive fossils (Martin 2005), and is similar to *Morganucodon* and *Sinoconodon* in many features (fig. 10.4). However, it differs from and is more derived than *Morganucodon* and *Sinoconodon* in that the scapulocoracoid lacks a distinctive procoracoid that typically bears a coracoid foramen (Martin 2005). The coracoid process has a blunt apex. It is smaller and shorter than the glenoid, in contrast to *Sinoconodon* and *Morganucodon*, both of which have a longer coracoid process than the length of the glenoid. Because the coracoid process is so short it is unlikely to have contacted the sternal series as in monotremes. This needs to be verified by sternal elements to be discovered for *Haldanodon*. A prominent fossa is present on the posterodorsal part of the scapula (= postscapular fossa of Martin 2005) for the teres major muscle. Its large size indicates a massive muscle, for powerful flexion and retraction of the humerus to the scapula, related to *Haldanodon*'s fossorial and semiaquatic habits,

as can be inferred from other skeletal features (Martin 2005). The difference of *Haldanodon* from other mammaliaforms suggests that basal mammaliaforms already have developed different locomotor functions, related to different niches (Martin 2005; Ji et al. 2006).

### Shoulder Girdles of Mesozoic Mammalia

Mesozoic lineages of the Mammalia have diverse forelimb features, indicating locomotor functions for swimming, gliding, and fossorial adaptations (Luo and Wible 2005; Ji et al. 2006; Meng et al. 2006; Luo 2007). Their shoulder girdles show a wide range of the primitive to derived characteristics. The partially preserved shoulder girdle of the Middle Jurassic mammal *Pseudotribos* has a monotreme-like interclavicle. It has an expanded anterior end with lateral processes, and a broader posterior end of the interclavicle in juxtaposition with a broad manubrium, also present in *Sinoconodon* (fig. 10.4). The shoulder features of *Pseudotribos* are likely related to extensive pectoral muscles and the sternocleidomastoid muscle for fossorial adaptation (Luo, Ji, and Yuan 2007).

*Fruitafossor* is a Late Jurassic mammal with convergent dental features to extant armadillos and aardvarks specialized for tongue feeding (Luo and Wible 2005). It appears to be fossorial, from the distinctive forelimb features otherwise known only in the burrowing mammals (Hildebrand 1985), and convergently in *Haldanodon* and in the tritylodontid *Kayentatherium* of fossorial adaptation (Martin 2005; Sues and Jenkins 2006). Its scapula has a prominent teres major fossa in addition to the infraspinous fossa, and a hemi-sellar glenoid that is oriented obliquely to the scapular blade with a laterally facing surface (fig. 10.3). However, there is no procoracoid bone, and the coracoid process is much smaller than those of monotremes and mammaliaforms, and evolutionarily more derived than monotremes.

**Theriimorph mammals**—Triconodonts, multituberculates, and spalacotheroids (also known as “symmetrodonts”) are three mammal clades with an extensive fossil record in the Mesozoic (Kielan-Jaworowska et al. 2004). They are closer to extant therians than to monotremes, and belong to the theriimorph clade defined by the common ancestor of triconodonts through living therians (Rowe 1988).

Triconodonts, such as *Jeholodens* and gobiconodontids (fig. 10.3), are characterized by an ovoid to spheroidal glenoid, oriented perpendicularly (or nearly so) to the scapular blade (Jenkins and Schaff 1988; Ji et al. 1999; Hu 2006; Luo, Chen, et al. 2007). The coracoid process is pointed anteroventrally. The scapular blade has a fully developed supraspinous fossa separated by the spine from the infraspinous fossa. The supraspinous fossa and the perpendicular glenoid suggest that triconodonts have acquired a therian-like glenohumeral joint, stabilized and reinforced by the supraspinous muscle, in addition to the infraspinous. Theriimorph mammals including triconodonts differ from crown therians in a prominent feature—the acromion is projected from the side of the scapular spine and has complex morphology (Hu 2006; Chen and Luo 2013), not from the apex of the spine as seen in extant therians (figs. 10.2 and 10.3). Among triconodonts known so far, there are significant variations in shape of the spine, the acromion, and the size of the supraspinous fossa (Jenkins and Schaff 1988; Ji et al. 1999; Hu 2006; Luo, Chen, et al. 2007), suggesting size difference in muscles attached to these bony features, and likely also functional differences for shoulder girdle.

Triconodonts have retained the interclavicle (Ji et al. 1999; Hu 2006; Luo, Chen, et al. 2007). In extant monotremes, the interclavicle is distinguished from the sternal manubrium by embryogenesis: the former is primarily a membranous bone while the latter is primarily an endochondral bone consisting of a pair of ossifications (Lessertisseur and Saban 1967b; Cave 1970; Klima 1973). Also the interclavicle can be distinguished from the manubrium by contacting relationship with the first thoracic rib (Lessertisseur and Saban 1967b; Hu et al. 1997). For extinct mammals that cannot be examined for embryogenesis, the distinction of the interclavicle and the manubrium can be established only on their topographic relationship to the first costal ribs (fig. 10.1D). In general, the manubrium is the anterior-most sternal element with direct contact with the first costal rib while the interclavicle has no exclusive contact with this rib. In the case of the manubrium preserved as paired elements, as has been recognized in tritylodontids, it can be distinguished from the single interclavicle (Sun and Li 1985; Sues and Jenkins 2006). These topographical characters for distinguishing the interclavicle from the manubrium in fossils are consistent with the

embryological observation that manubrium is developed from the paired sternbral bands connected to anlagen of the first costal ribs, while the median chondral element (the “pars chondralis interclaviculae”) of the presumptive interclavicle has no such connection (Klima 1973, 1985).

The interclavicle of triconodonts lacks the lateral process (Ji et al. 1999; Hu 2006; Luo, Chen, et al. 2007). It has a point contact to the clavicle. The clavicle is a fully mobile spoke to the interclavicle for the arcuate swing of the shoulder girdle. Triconodonts are the basal-most group among Mesozoic mammals to show a mobile shoulder girdle (Ji et al. 1999; Hu 2006; Sereno 2006) and have acquired the therian-like function of the shoulder and forelimb, as seen in living therians (Jenkins 1971a, 1974).

Multituberculates are omnivorous to herbivorous mammals with a diverse range of feeding adaptations (Wilson et al. 2012). They are the most abundant group in the mammal faunas from the Late Jurassic to Cretaceous (Kielan-Jaworowska et al. 2004) and can have diverse habits: some inferred to be terrestrial (Kielan-Jaworowska and Gambaryan 1994; Sereno and McKenna 1995; Hu and Wang 2002), fossorial (Kielan-Jaworowska and Qi 1990), or arboreal (Jenkins and Krause 1983; Krause and Jenkins 1983). There are also alternative interpretations of the forelimb posture of multituberculates (Kielan-Jaworowska and Gambaryan 1994; Sereno and McKenna 1995; Gambaryan and Kielan-Jaworowska 1997; Sereno 2006; Kielan-Jaworowska and Hurum 2006). But the scapular morphology is relatively uniform across a range of multituberculates, and so is the rest of the shoulder girdle (Jenkins and Weijs 1979; Sereno 2006; Hurum and Kielan-Jaworowska 2008).

The multituberculates’ shoulder girdle has a mobile clavicle-interclavicle joint, and is fully capable of the arcuate shoulder movement of modern therians (Sereno and McKenna 1995; Sereno 2006). The scapular glenoid is oriented perpendicularly to the scapular blade, and facing ventrally. In these features, multituberculates are unquestionably therian-like and derived (Krause and Jenkins 1983; Kielan-Jaworowska and Gambaryan 1994; Sereno 2006; Kielan-Jaworowska and Hurum 2006). Besides a well-developed acromion, the scapular spine also has a prominent metacromion (Sereno 2006), a derived feature of some therians (Lessertisseur and Saban 1967a; Großmann et al. 2002), not present in monotremes and

mammaliaforms. Among the primitive features, the scapular spine is truncated dorsal to the metacromion (Jenkins and Weijs 1979; Sereno 2006). The short multituberculate spine appears to be equivalent to the acromial (ventral-most) part of the therian spine, but lacks the septal part of the therian spine (Sánchez-Villagra and Maier 2003). The position of the spine along the anterior scapular margin and the absence of a supraspinous fossa are primitive conditions of monotremes and stem mammaliaforms.

Spalacotheroids are characterized by molars with a symmetrical triangle of cusps (thus known as the “symmetrodonts”) for insectivory. The scapulas of spalacotheroids and more derived therian relatives, such as *Henkelotherium* and *Vincelestes*, already have the derived condition of living therians, such as the full supraspinous fossa, and the perpendicular glenoid (Krebs 1991; Rougier 1993; Hu et al. 1997; Rougier et al. 2003; Li and Luo 2006; Chen and Luo 2013).

In *Zhangheotherium* and *Akidolestes*, the acromion process and its topographical relationship to the spine are quite different from those of living therians (Chen and Luo 2013). In *Didelphis*, the acromion is directly arising from the spine, and is apical with the spine in the majority of living therians (fig. 10.2). By contrast, the acromion of spalacotheroids arises from the anterior side of the spine, and the base of the acromion is offset from the apex of the spine (fig. 10.2D–F). This “side-way” attachment of the acromion is well documented in extensive fossils of the gobiconodontid *Repenomamus* (Hu 2006, figure 3-19; Luo, personal observation) and other triconodonts (Ji et al. 1999; Luo, Chen, et al. 2007; Chen and Luo 2013). Multituberculates have a similar condition of the acromion, although lacking the full supraspinous fossa of triconodonts (Sereno 2006; Hurum and Kielan-Jaworowska 2008). The offset acromion is not present in basal eutherians and metatherians (Argot 2001; Horovitz 2003; Wible et al. 2009). In *Vincelestes*, a Cretaceous mammal closer to crown therians than spalacotheroids (Rougier 1993), the acromion is apical to the crest of the spine as in crown therians. Another prominent, but primitive feature is the trough-like infraspinous fossa with its posterior margin curled and elevated (fig. 10.2), now documented in many stem mammaliaforms, triconodonts, and multituberculates (Martin 2005; Hu 2006; Sereno 2006; Hurum and Kielan-Jaworowska 2008; Chen and Luo 2013).

**Mesozoic crown theria and kin**—The scapula of the Early Cretaceous eutherian *Eomaia* (Ji et al. 2002) appears to have a plate-like scapular blade, and its infraspinous fossa is flat. The Late Cretaceous eutherians *Maelestes* and *Ukhaatherium*, however, differ from *Eomaia* in that the crest of the scapular spine is curved and overhangs the infraspinous fossa. The infraspinous fossa is trough-like (Horovitz 2003; Wible et al. 2009). A similar configuration is also present in *Vincelestes* (Rougier 1993, figs. 81 and 82), indicating that this may be phylogenetically primitive for eutherians (Wible et al. 2009). The trough-like infraspinous fossa suggests that some stem eutherians are either terrestrial as indicated by their generalized forelimbs as in the case of *Ukhaatherium* (Horovitz 2003), or could be fossorial, as indicated by the deep trough-like infraspinous fossa best developed in fossorial marsupial mole *Notoryctes* and the placental golden mole *Chrysochloris* (Lessertisseur and Saban 1967a; Asher et al. 2007; Wible et al. 2009) (fig. 10.2C). In this trough-like infraspinous fossa, *Ukhaatherium* and *Maelestes* differ from the shallow and flat infraspinous fossa of several other stem eutherians and metatherians interpreted to be scansorial or even arboreal (Szalay 1994; Argot 2001; Ji et al. 2002; Luo et al. 2003). Given the diversity of scapular features, likely the Cretaceous eutherians had already evolved differences in locomotor functions and habits (Goswami et al. 2011; Luo et al. 2011).

## Major Features of Phylogeny

**Coracoids and sternal series**—In basal synapsids, the procoracoid is a large element of the scapulocoracoid complex and a major component of the glenoid (Romer 1956; Jenkins 1971b). The procoracoid appears to be a discrete bone in some subadults but can merge with the scapula in skeletally mature specimens of some stem synapsids (Vickaryous and Hall 2006). More derived cynodonts differ from stem synapsids in that the procoracoid is excluded from the glenoid (Sues and Jenkins 2006), although it remains integrated in the scapula-coracoid in cynodonts and some stem mammaliaforms (fig. 10.1C). The mammaliaform *Haldanodon* has no procoracoid (Martin 2005), and it is phylogenetically intermediate between other mammaliaforms with an integrated procoracoid and monotremes that have an unfused procoracoid (fig. 10.3). In monotremes, the

procoracoid is developed from the medial part of the pre-cartilaginous coracoid-scapular plate of the embryonic and fetal stages (Klima 1973; Vickaryous and Hall 2006) and becomes an independent bony element in adults, loosely attached to the rest of the scapulocoracoid, but not sutured or fused to the latter like in several mammaliaforms, except *Haldanodon*.

The homoplasy of the procoracoid in *Haldanodon* and monotremes can be interpreted, alternatively, either as an independent loss of the procoracoid in *Haldanodon* among mammaliaforms (fig. 10.3), or as a convergent acquisition of this bone by monotremes. It is not possible to discriminate between these alternative interpretations because the procoracoid is unknown in the successive sister taxa of the monotreme lineage. For example, it is not known in the Jurassic *Pseudotribos*, a putative relative of monotremes (Luo, Ji, and Yuan 2007) (fig. 10.4). If it can be ruled out that this is not an artifact of preservation, then it can augment the likelihood that the procoracoid is a separate acquisition of monotremes. The loss of the procoracoid enhances the mobility of the shoulder girdle, accompanied by concomitant transformation of the glenohumeral joint.

**Glenohumeral joint**—The half-saddle or semi-sellar joint, an ancestral mammaliaform condition, is retained in monotremes and in *Fruitafossor*, the most derived Mesozoic mammal known to have this feature (Luo and Wible 2005) (fig. 10.3). Through the rise of crown therians and their theriomorph kin, the glenoid underwent changes from the half-saddle shape to the ovoidal or spheroidal shape, and from oblique orientation and laterally facing to the perpendicular orientation and more ventrally facing. The changes have resulted in functional differences (Jenkins 1974, 1993): the half-saddle joint permits the protraction-retraction swing of the humerus relative to the scapulocoracoid but limits the ranges for elevation and depression, and for long-axis circumduction of the humerus. The more massive coracoid, as seen in monotremes, strengthens the glenohumeral joint for more forceful movement of the humerus yet is also more restrictive on some movement. Also the glenoid joint is stabilized by the supracoracoideus muscle known from other amniotes (Jenkins and Goslow 1983; Walter 1988), and by the infraspinous muscle—a plesiomorphy, as evidenced by the infraspinous fossae of cynodonts through mammaliaforms.

A supraspinous muscle of the therian proportion is absent in monotremes (Howell 1937; Jouffroy 1971; Walter 1988), and is inferred to be absent, or poorly developed in cynodonts and mammaliaforms (Jenkins 1971b; Jenkins and Weijs 1979; Sun and Li 1985; Martin 2005; Sues and Jenkins 2006). Theriiform mammals have a spheroidal glenoid capable of a greater mobility, which is simultaneously less stable and more vulnerable to dislocation, to be stabilized, compensatorily, by an apomorphic supraspinous muscle (Jenkins and Goslow 1983; Williams et al. 1989; Fischer 2001).

**Supraspinous fossa and scapular spine**—Stem mammaliaforms and monotremes have a single-muscle (infraspinous) stabilization of the glenohumeral joint from the scapula, while therians and Mesozoic theriiforms have a double-muscle (both infraspinous and supraspinous) stabilization with the diagnostic skeletal features of the supraspinous fossa and the spine (fig. 10.1). Historically, the therian spine was hypothesized to be homologous to the cranial margin of the scapula in non-mammalian amniotes and monotremes (Romer 1956; Jenkins 1971b; Jenkins and Weijs 1979). Presumably the large supraspinous muscle of extant therians was transformed from an ancestral condition in which an incipient supraspinous muscle was attached to a small area on the anterior surface of the medially flared acromion and spine (Walter 1988, although see the different opinion of Jouffroy and Lessertisseur 1971). In therian evolution, the incipient supraspinous muscle rotated and concomitantly expanded much larger on to the lateral surface of the scapula, an evolutionary process that was recapitulated in the ontogeny of therians, at least in part (Cheng 1955; Jouffroy 1971).

Recent studies demonstrated that the scapular spine of marsupials and placentals is a compound structure (Sánchez-Villagra and Maier 2002; Großmann et al. 2002). The septospine and the coraco-gleno-acromial region have distinctive embryonic development: the former is formed by appositional bone following the intermuscular septum dividing the common anlagen of the presumptive supraspinous and infraspinous muscles (Sánchez-Villagra and Maier 2003) while the latter is preformed in cartilage.

The anlage of the ventral part of the supraspinous muscle appears initially on the cranial margin of the

acromial region, and subsequently rotates to the lateral surface of the scapula in early embryogenesis (Cheng 1955; Sánchez-Villagra and Maier 2003). However, anlage of the main part of the supraspinous muscle is on the lateral surface of the preformed, cartilaginous scapular blade upon its earliest mesenchymal condensation; the adult supraspinous muscle mass is developed through a vicariant separation from the infraspinous counterpart by the neomorphic septospine, not by rotation (Sánchez-Villagra and Maier 2003).

This new embryological observation suggests that not all of the therian (acromial + septal) spine is homologous to the cranial scapular margin of monotremes and sauropsids as previously believed (Romer 1956). Rather, only the acromial part of the therian spine is homologous to the cranial margin of scapula. Also, this suggests that the septospine is an evolutionary apomorphy, but the lateral surface of the supraspinous fossa, by itself, is not (Großmann et al. 2002; Sánchez-Villagra and Maier 2002).

Evolution of a therian-like septospine is homoplastic among the Mesozoic mammals: present in triconodonts and spalacotheroids, but absent in multituberculates that are phylogenetically intermediate between triconodonts and spalacotheroids. Either the septospine evolved convergently in triconodonts, and in spalacotheroids through crown therians, or the septospine had evolved in theriiform ancestors but was secondarily lost in multituberculates (fig. 10.3). Either way it is clear that the septospine has a relatively independent evolutionary history from the acromion and scapular blade, consistent with its morphogenesis in living mammals.

## Development and Evolution

Overall, therians and their more inclusive theriiform clade have fewer shoulder girdle elements, which are also more gracile, than their mammaliaform homologues. The simpler scapulocoracoid of theriiforms evolved by incorporation of the reduced metacoracoid into the adult scapula, and the loss of adult procoracoid. Concomitantly, the sternal structure underwent an evolutionary reduction, diminishing the manubrium and losing the interclavicle. The simpler shoulder girdle is more mobile, and the forelimb movement more versatile. By comparison, evolution of the shoulder and

sternal structure in monotremes shows the opposite: the shoulder girdle and sternum, ancestrally strong in mammaliaforms, have become even more hypertrophied for highly specialized fossorial adaptations. These phylogenetic patterns, however, are not linear trends toward extant therians and monotremes, respectively. Rather, there are convergent acquisitions of derived features and prominent cases of parallel reduction of ancestral features.

Homoplasies of the shoulder girdle on a broad evolutionary scale are consistent with the labile development well documented by comparative embryology (Klima 1973, 1985, 1987) and the studies of cellular mechanism in skeletogenesis (Hall and Miyake 1992; Vickaryous and Hall 2006). A discrete element of a mature skeleton represents coalescence of clusters of embryonic progenitors, discernible by cell condensation. For example, adult interclavicle of monotremes is composed of embryonic components of the paired pars interclaviculae desmalis (presumptive lateral process) and the unpaired median pars chondralis interclaviculae (presumptive median plate) (Klima 1973). Adult manubrium of therians integrates components of the embryonic “procoracoid,” the pars chondralis interclaviculae, and the paired sternal bands (Klima 1987). Coalescences of these cell condensations can change by mitosis (cell proliferation), by identity (differentiation), by the size of aggregation, and by localized heterochrony (Vickaryous and Hall 2006). The gain, loss, or change in shape and size in evolution are attributable to these labile cellular processes in skeletogenesis (Vickaryous and Hall 2006).

Several components of the shoulder girdle can be recognized as evolutionary and developmental modules in which the transformation of fossil mammals can be hypothesized as consequence of variation in skeletogenesis for which the genetic controls are already known to some extent:

**Coracoids**—The procoracoid of monotremes is developed from the medial part of the embryonic coracoid-scapular plate of fetal stage (Klima 1973). The three-element primary girdle (of the procoracoid, the metacoracoid, and the scapula) is a basic feature of basal synapsids, reptiles, and birds (Vickaryous and Hall 2006). Birds are now known to have conserved the deep homology of gene patterning for these coracoid

elements (Huang et al. 2000, 2006). Absence of one of the adult coracoids in some amniote lineages can occur by differential coalescence of coracoids with the scapula into a single adult morphology (Vickaryous and Hall 2006). Thus the procoracoid and metacoracoid are ancestral features for mammaliaforms. Discrete adult procoracoid can be interpreted as a retention of an embryonic feature for monotremes, relative to the mammaliaform *Haldanodon*, and to *Fruitafossor* and theriomorphs, which have lost the procoracoid (fig. 10.3, node 1). Alternatively, the absence of the procoracoid and the greatly reduced coracoid process (metacoracoid) in *Haldanodon* (Martin 2005), and separately in *Fruitafossor* and theriomorphs, can result from an early coalescence of the procoracoid (*sensu* Vickaryous and Hall 2006) or as arrested growth of the coracoids, or both. Arrested growth of the coracoids in extant therians is documented by Hübner et al. (2010, 2013) who show that in the marsupial *Monodelphis*, growth rate of the coracoid has slowed down in late fetal development relative to the rest of scapula. Homoplasy of the procoracoid and the size change of the coracoid process in mammaliaform evolution can be hypothesized as manifestation of heterochrony of the embryonic coraco-scapular plate.

**Clavicle and sternum (fig. 10.5)**—Development of the clavicle-sternum connection is influenced by *Hox5* and *Hox6*. Mutant mice with *Hox5* triple knockout (*Hox5abc<sup>-/-</sup>*) are missing the sternal manubrium and the first rib associated with the manubrium (McIntyre et al. 2007). The clavicle is disconnected from the sternum, except by connective tissue. In mutant mice with *Hox6* triple knockout (*Hox6abc<sup>-/-</sup>*), the manubrium and the first sternebra are miniscule and poorly developed, and their associated first rib fails to develop. This suggests that normal function of these genes is required for morphogenesis of the sternum (McIntyre et al. 2007). Formation of the sternum and the clavicle also requires the complementary function of *Pax1* (paired box 1) gene and *Hoxa5* (Timmons et al. 1994; Dietrich and Gruss 1995; Aubin et al. 2002), illustrated by the fact that mutant mice with deficient *Pax1* have a defective sternum (Timmons et al. 1994).

So far, influence of *Hox* genes and *Pax1* on the clavicle and sternum is demonstrated only in the mouse, a

highly derived placental with a simple sternal manubrium. For marsupials, Keyte and Smith (2010) observed that widening of expression zones of *Hoxb5* and *Hoxc6* along the antero-posterior axis is related to the earlier and faster development of the shoulder girdle and forelimb in *Monodelphis*. However, monotremes have yet to be studied for the *Hox* patterning of the interclavicle. It is still unknown if the *Hox* and *Pax1* patterning in mouse, which has no interclavicle, can be extrapolated to monotremes with an interclavicle formed from composite embryonic progenitors, let alone to a wide diversity of Mesozoic nontherian clades that show great variation in the interclavicle.

**Acromion-glenoid of scapula**—With the exception of the septospine formed by appositional bone (Sánchez-Villagra and Maier 2003), the entire scapulocoracoid develops endochondrally. Within the endochondral part of the scapula, morphogenesis of the acromio-glenoid region is relatively independent from that of the blade and the septospine. The blade with its spine appears to be under different genetic control (fig. 10.5), from the fact that the scapular blade and septospine are missing in mutant mice with knockout *Emx2* and *Pax1* (*undulate* compound mutant), while the acromio-glenoid region can develop normally in the mutants (Timmons et al. 1994, fig. 5; Dietrich and Gruss 1995; Pellegrini et al. 2001).

The endochondral development of the entire scapula and the glenohumeral joint requires *Pbx1* (Selleri et al. 2001, fig. 8). It was further demonstrated that different combinations of the *Pbx* genes can influence the glenohumeral joint and different parts of the scapula (Capellini et al. 2011). *Pbx1* and *Emx2* cooperatively activate *Alx1* and *Alx4* and are parts of the gene network of the morphogenesis of these scapular features (Capellini et al. 2010; Hübler et al. 2013). Specific influence of *Pbx1* on the acromion and the glenoid is demonstrated by the hypoplasia of the acromion and the fusion of the glenohumeral joint in the *Pbx1* null mutant (*Pbx1*<sup>-/-</sup>). Moreover, formation of the acromion and the acromion-clavicle joint requires normal function of *Pax1* and *Hox5*, demonstrated by the hypoplasia or total absence of acromion in the mutant mouse of *Pax1*<sup>-/-</sup> and *Hox5abc*<sup>-/-</sup> (Timmons et al. 1994; Dietrich and Gruss 1995; Aubin et al. 1998, 2002; Selleri et al. 2001; Kuijper et al. 2005; McIntyre et al. 2007; Capellini et al. 2010). The devel-

opment of the acromion, the coracoid process, and the glenohumeral joint is only modestly influenced by the genetic pathway that patterns the limb (Selleri et al. 2001; Capellini et al. 2010; Hübler et al. 2013), and not influenced by the genetic pathway for the scapula blade and the septospine.

**Supraspinous fossa and septospine**—The septospine defines the supraspinous fossa, and these two features have great functional significance, and also prominent homoplasy, in theriomorph evolution (fig. 10.3). Sánchez-Villagra and coworkers demonstrated that in most marsupials and some placentals, the septospine is formed by appositional bone in embryonic septum in the supraspinous and infraspinous muscle anlagen, whereas the acromial spine is developed endochondrally (Sánchez-Villagra and Maier 2002, 2003; Großmann et al. 2002). This distinction in embryogenesis is consistent with differences in gene patterning of development.

Pellegrini et al. (2001) showed that the scapular blade and the septospine are influenced by *Emx2*, a gene in the pathway for cell condensation and chondrogenesis and provides a positional signal for cell fates (Kuijper et al. 2005; Capellini et al. 2011), relatively independent of the acromio-glenoid region of the scapula. The scapular blade and the septospine fail to develop in the homozygous mutants of *Emx2* (*Emx2*<sup>-/-</sup>). Subsequent studies of mutants of deficient *Tbx15*, *Gli3*, *Alx4*, and related genes demonstrated that the anterior (“supraspinous”) part corresponds to the functional area of *Alx1-4*. The septospine and middle part of the blade corresponds to the functional area of T-box transcription factors (*Tbx6*, *Tbx15*, and *Tbx18*) (Kuijper et al. 2005; Wehn and Chapman 2010), and *Pax3* (Farin et al. 2008). The posterior (“infraspinous”) part is the functional area of *Gli3* (fig. 10.5) (Kuijper et al. 2005; Farin et al. 2008; Capellini et al. 2010). Mutant genotypes of these genes can result in hypoplasia of the scapular blade. In compound mutants of *Tbx* genes, an abnormal gap occurs where the septospine is expected in the scapular blade (Kuijper et al. 2005; Capellini et al. 2010).

The labile morphogenesis of the scapular blade and septospine under relatively independent genetic influence is consistent with the evolutionary homoplasy of the septospine among triconodonts, multituberculates, and spalacotheroids. For the evolution of the mammalian shoulder girdle, this is perhaps the best evolution-



ary and development module where fossil patterns can be well informed by developmental mechanisms.

## Paleo Evo Devo

There is much new insight to be gained by integrating embryogenesis and developmental genetics into hypotheses for the phylogenetic evolution of fossils. The development of living mammals can provide mechanistic hypotheses for prominent homoplasies in early mammals. Reciprocally, the deep-time fossil record can help to demonstrate that phenotypes that are teratological, and demonstrable only by knockout genetic experiments on extant mammals, can actually occur in evolution. Morphological disparity of the sternum and shoulder girdle is especially prominent in Mesozoic mammal clades that have no living descendants (Kielan-Jaworowska et al. 2004; Luo 2007). The scope of this disparity has far exceeded what is possible for extant mammals (figs. 10.3–10.4). For example, the offset acromion (fig. 10.2D and fig. 10.3) common in Mesozoic theriomorphs is unknown for extant mammals. The unique scapular character combination of multituberculates of a perpendicular glenoid (derived) and the absence of the supraspinous fossa (primitive) can neither fit the scapular morphotype of living therians nor that of monotremes. The greater lineage diversity of Mesozoic mammals is a greater arena for repeated evolutionary experimentation of characters that are singular and unique among extant mammals. Fossils are milestones on what evolutionary transition was impacted by development at what time in geological history.

**Caveats**—There are limits on extrapolating development into fossils to account for macroevolutionary patterns. Interpretation of homoplasies in mammal phylogeny as repetitive developmental experimentations is ultimately dependent on a well-resolved phylogeny. But phylogenetic topology can differ by alternative analyses (e.g., Rowe et al. 2008 vs. Phillips et al. 2009). The phylogenetic framework in which to interpret shoulder girdle evolution can change with new discoveries of fossils and new characteristics assimilated into analyses (e.g., see Luo et al. 2002; Luo and Wible 2005; Luo, Ji, and Yuan 2007; Wible et al. 2009; Rougier et al. 2011). Thus the development hypothesis for homoplasies in macroevolution has inherent uncertainty.

It is important to note that the genetic control of shoulder girdle development has not been studied in monotremes. Without genetic underpinning of their embryological observations (Klima 1973), it will be difficult to account for the evolutionary pattern of Mesozoic mammals that are intermediate between therians and monotremes. Despite much progress, the current understanding of genetic control of phenotype features is still rudimentary for the shoulder girdle of mouse, as widely acknowledged by many studies (e.g., Capellini et al. 2011), although gene patterning of some shoulder girdle features in marsupials are just beginning to be deciphered (Hübner et al. 2013). Many genes and pathways that can influence the development of the sternum and shoulder girdle can also have pleiotropic effects elsewhere. Phenotype areas of gene expression often overlap; thus a genotype may lack sufficiently specific correlation to a discrete feature seen in fossils. Perhaps more importantly the network of the genes influencing the same structure is not completely known. All are hurdles to overcome for using the gene patterning of morphogenesis of living mammals to account for evolutionary patterns.

Evolutionary development is not the only approach toward mechanistic understanding of phylogenetic evolution. Developmental interpretation of the homoplasies of the shoulder and sternal features is not mutually exclusive with the understanding of their functional evolution. Functional adaptation is also fundamental to convergent evolution. In the case of the supraspinous muscle of the scapula, functional adaptation to strengthen the glenohumeral joint of theriomorph mammals by the double muscle stabilization (Jenkins and Goslow 1983; Fischer 2001) can be a driving mechanism for convergent evolution, as is the known mechanism of labile morphogenesis of the related scapular features (fig. 10.5).

## Summary

1. Transformation of the shoulder girdle from pre-mammalian cynodonts through mammaliaforms to extant therians is characterized by the evolutionary reduction of the girdle elements, both by number and in size, ultimately simplifying the shoulder girdle in therians and their theriomorph relatives. But monotremes have retained the ancestral mammaliaform shoulder and

sternal structures and further developed these for fossorial adaptation.

2. Major transformation in theriomorph mammals includes the evolution of the mobile clavicle as a spoke for the arcuate movement of the shoulder girdle, and a reorientation of the glenohumeral joint stabilized by the derived supraspinous muscle, for greater mobility of the shoulder and forelimb.

3. Evolution of the shoulder girdle and sternal structure shows some prominent homoplasies, especially in

the coracoid bones related to the pectoral and coracoid muscles in mammaliaforms and monotremes, and in the supraspinous fossa and septospine for muscle function to stabilize the glenohumeral joint in theriomorph mammals.

4. Genetic studies of the mammalian shoulder girdle can now attribute some phenotype features in increasingly specific ways to gene patterning of morphogenesis. The relatively independent and labile development of some features of the shoulder girdle can provide new insight on the mechanism of their evolution.

\* \* \*

## Acknowledgments

Professor Farish A. Jenkins Jr. is the inspiration for this review of the shoulder girdle evolution of mammals. His seminal studies on the evolution and function of the mammalian appendicular skeleton laid a foundation for our understanding of early mammal evolution. I want to thank Drs. Qiang Ji and Chongxi Yuan (Chinese Academy of Geological Sciences, Beijing), Peiji Chen and Gang Li (Nanjing Institute of Geology and Palaeontology), Qingjin Meng (Beijing Museum of Natural History), Ailin Sun and the late Yaoming Hu (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) for the opportunities to study the original fossils of Mesozoic mammals from China. During the course of this study, I benefited from many discussions with my colleagues K. Christopher Beard, Meng Chen, Thomas Martin, Guillermo Rougier, Timothy B. Rowe, Marcello Sánchez-Villagra, Karen Sears, Paul Sereno, Hans-Dieter Sues, Matthew Vickaryous, and John Wible. Paul Sereno and John Wible shared with me many observations from their own studies of the mammalian shoulder girdles. Susan Evans generously provided the specimen of the interclavicle of *Morganucodon*. Mary Dawson, Hans Sues, John Wible, and the editors of the volume helped to improve the manuscript. Lastly, I would like to thank Lauren Conroy and April Isch for assistance with illustrations. Research was supported by National Science Foundation (US), the Humboldt Foundation of Germany, and the University of Chicago.

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