THE EVOLUTION OF THE PTEROSAURIAN PECTORAL GIRDLE

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The pectoral girdle of basal pterosaurs (e.g., *Eudimorphodon*, *Peteinosaurus*) consisted of a long strap-like scapula that passed posteriorly over the ribcage, an elongate strut-like coracoid that articulated with the sternum, the scapula and coracoid fused at an acute angle and together forming a deep saddle-shaped glenoid fossa for articulation with the humerus, and a broad sternum formed of coossified paired clavicles, interclavicle, and paired sternal plates (Wild, 1978, 1993). The pectoral girdle is superficially similar to that of extant birds (e.g., *Aquila*, *Corvus*), and that similarity lead to it being interpreted as functionally like that of birds (Padian, 1983a, b). It was proposed that M. supracoracoideus, originating on the coracoid and sternum and having the direction of its pull reversed by a pulley-like acrocoracoid process, was the primary elevator of the wing in pterosaurs, and therefore the dorsal muscles of the pectoral girdle were relatively unimportant. This interpretation has been generally accepted, yet has not been examined critically.

The essential morphology of the pterosaurian pectoral girdle did not change as the pterodactyloids evolved and eventually replaced the rhamphorhynchoids. However, in the large pterodactyloids the pectoral girdle was modified from the condition in basal pterosaurs in that the posterior end of the scapula was rotated medially and articulated with the notarium formed of fused anterior dorsal vertebrae. Although this unusual condition was first described over 100 years ago (Marsh, 1876; Seeley, 1891), little has been done to understand its functional morphology and it is generally described as simply strengthening the pectoral girdle.

I reconstructed the pectoral musculature of representative pterosaurs in order to examine the functional morphology of the basal pterosaurian pectoral girdle and the structural and functional changes that took place during the evolution of the advanced pectoral girdle of large pterodactyloids. The reconstructions were based on comparisons of pterosaurian pectoral osteology and muscle and ligament attachment scars with the known osteology and myology of extant archosauromorphs.

The reconstruction of the pectoral musculature of a representative basal pterosaur (*Campylognathoides*) suggests that M. supracoracoideus was not an elevator of the wing, but instead depressed and flexed the humerus anteriorly as in extant non-avian archosauromorphs. Wing elevation apparently relied on M. deltoideus and other dorsal muscles of the pectoral girdle. Thus, the pterosaurian pectoral girdle was not functionally like that of extant birds.

The reconstruction of the pectoral musculature of a representative large pterosaur with an advanced pectoral girdle (*Anhanguera*) suggests that the rotation of the scapula straightened the pull of M. deltoideus, improving its function in wing elevation. Likewise, the reconstruction suggests that the scapulonotarial joint would have permitted the scapula to act as a strut to resist compressive forces of muscles originating on the vertebral column and inserting on the humerus. As such it would mirror the function of the coracoid in resisting compressive forces of sternal muscles inserting on the humerus. It is probable that without the scapula braced against the vertebral column the great forces produced by wing elevators originating on the vertebral column could have pulled the scapulocoracoid medially and produced undesirable deformations of the ribcage. I argue that selection for improved function of M. deltoideus in wing elevation lead to medial rotation of the scapula. Subsequently, the approximation of the scapula and notarium lead to fixation of the posterior end of the scapula to the third and fourth notarial vertebrae, and finally to the evolution of a synovial joint between the scapula and supraneural plate of the notarium.

The advanced pectoral girdle of large pterodactyloids has been viewed either as a synapomorphy of a single clade of large pterodactyloids or as a correlate of large body size that evolved in parallel in several separate lineages of pterosaurs. Cladistic analyses that included pectoral characters (Bennett, 1989; Kellner, 1996) support a single origin of the advanced pectoral girdle, whereas cladistic analyses that excluded pectoral characters based on the *a priori* assumption that the advanced pectoral girdle might have evolved in parallel (Unwin, 1995; Unwin and Lü, 1997) support multiple origins of the advanced pectoral girdle. At present, no other evidence suggests that the advanced pectoral girdle evolved independently in several lineages of pterosaurs, and the distribution of other postcranial characters (e.g., exapophysial articulations, notarium) supports the interpretation of the advanced pectoral girdle as a synapomorphy of a single clade of large pterodactyloids.

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