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Flight capability and the pectoral girdle of *Archaeopteryx*

AS the earliest birds known, the late Jurassic specimens of *Archaeopteryx* have been the object of great speculative interest. Ostrom[1-3] has argued that *Archaeopteryx* was a terrestrial, cursorial predator that represents a preflight stage in the origin of birds in which the forelimbs were used as nets to trap insects. So far, this has been challenged mainly on the grounds that such activity would have caused excessive feather wear[4]. The principal evidence for regarding *Archaeopteryx* as flightless, or at best an inept non-flapping glider, has come from interpretations of the structure of the pectoral girdle. The absence of an ossified sternum for attachment of flight muscles has long been cited. More recently, it has been argued that the structure of the coracoid of *Archaeopteryx* would not have permitted the supracoracoideus muscle to function as a wing elevator[2,5]. Because the asymmetrical remiges of *Archaeopteryx* prove that the wing had an aerodynamic function[6], we now hope to show that neither of the preceding points precludes a capacity for powered flight in *Archaeopteryx*.

There are several generally held misconceptions concerning the pectoral girdle of modern birds. The most prevalent of these is that the carina of the sternum is the principal site of origin of the massive pectoralis muscle, which provides the power stroke of the wing. This is not so. In most birds, m. pectoralis originates to a greater extent from the furcula and the coraco-clavicular membrane (Fig. 1). As it passes posteriorly its fibres originate on the sternum only from those areas not pre-empted by the underlying m. supracoracoideus. Typically, these areas consist of a narrow band on the ventral margin of the carina and the most lateral and posterior portions of the sternal plate (Fig. 2). In such birds as the Dendrocolaptidae, in which the carina is reduced to facilitate tree-trunk foraging[7], the pectoralis muscle becomes thin and broad, spreading out laterally and dorsally well past the sternum and on to the rib cage. Once anchored to the furcular area, it would seem that m. pectoralis could expand posteriorly and attach to any underlying structure that happened to be present.

Apart from feathers, the character of *Archaeopteryx* most often cited as being bird-like is the well developed furcula. Relative to modern birds of the same size, the furcula of *Archaeopteryx* is actually hypertrophied. There has been no satisfactory explanation of this structure which has received mostly perfunctory treatment. Ostrom merely asks: "Did it function as a transverse spacer between the shoulder sockets?"[2] Why such a structure would be needed in *Archaeopteryx* and not in any of its suggested ancestors is never dealt with. We consider that the extremely robust furcula of *Archaeopteryx* is best interpreted as having been the site of origin of a well developed pectoralis muscle.

When it is observed that m. pectoralis arises to a large extent from the furcular area, it can then be seen that the main function of the ossified sternum and carina in modern birds is to provide attachment for the supracoracoideus muscle (Fig. 2). Although the belly of m. supracoracoideus is situated ventrally, it serves to raise the wing because its tendon passes above the glenoid facet and over the acrocoracoid process of the coracoid to insert on the dorsal aspect of the humerus (Fig. 2). In modern birds it is the largest of the muscles that effect the recovery stroke of the wing. For this reason, Ostrom[2] has emphasised the absence of an acrocoracoid process in *Archaeopteryx*, suggesting that if m. supracoracoideus had been present it could not have functioned to raise the wing. Ostrom interprets this as evidence for *Archaeopteryx* having been flightless, the implication being that m. supracoracoideus is essential for flight. That this is not the case has been conclusively proven by Sy[8], who cut the supracoracoideus tendons in living examples of crows (*Corvus*) and pigeons (*Columba*) and found that the birds were still capable of normal, sustained flight. It is of considerable interest

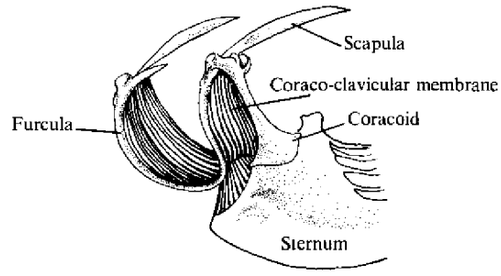

Fig. 1 Left side of pectoral girdle of the duck *Bucephala clangula* showing the furcula and extensive coraco-clavicular membrane from which m. pectoralis has its main origin (redrawn from Sy[8]).

that the only capacity lost was the ability of the pigeon to take off from level ground.

It has thus been proved that in modern birds the dorsal elevators (principally m. deltoideus major[8]) are completely capable of effecting the recovery stroke of the wing. These muscles originate mainly from the scapula, which in *Archaeopteryx* forms an acute angle with the coracoid, as is true in adults of modern flying birds. The acute angle shortens the distance through which the dorsal elevators must act, thus giving greater power. In most flightless birds, on the other hand, the acute angle is lost and the scapula is more nearly vertical[9].

The dorsal musculature is present and is used to raise the forelimb in virtually all vertebrates; furthermore, it is the dorsal musculature that elevates the wing in such volant forms as bats. Therefore, it is logical to assume that in the evolution of avian flight the recovery stroke of the wing would first have been carried out by the dorsal elevators. The enlarged, ventrally situated m. supracoracoideus, the acrocoracoid process, and the ossified sternum with a keel, constitute a single functional complex that is not a requisite of flight but merely a refinement that was superimposed in later birds on an apparatus probably already capable of full flight. The enlarged m. supracoracoideus probably evolved to counter the action of an increasingly enlarged m. pectoralis and, as evidenced by Sy's experimental pigeons, may have been necessary for birds to adopt purely terrestrial habits.

In conclusion, the robust furcula of *Archaeopteryx* would have provided a suitable point of origin for a well developed pectoralis muscle. Furthermore, the supracoracoideus muscle, and hence an ossified sternum, is not necessary to effect the recovery stroke of the wing. Thus the main evidence for *Archaeopteryx* having been a terrestrial, cursorial predator is invalidated. There is nothing in the structure of the pectoral

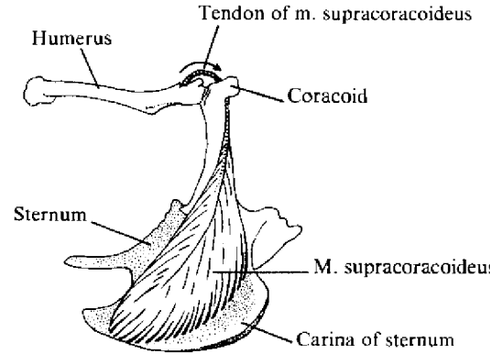

Fig. 2 Right side of pectoral girdle of the pigeon *Columba livia* to show the action of m. supracoracoideus and the extensive area of the sternum that this muscle occupies. M. pectoralis attaches to the sternum only on those areas shown in stipple. (Modified from Ostrom[2], after George and Berger[10].)

girdle of *Archaeopteryx* that would preclude its having been a powered flier.

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