THE MORPHOLOGY OF THE PECTORALIS IN THE LIZARD, BIRD AND BAT AND ITS RELATION WITH OTHER FORELMB MUSCLES
Bats and birds are both flying animals, the remote ancestors of which could be traced to the reptiles. In the evolution of the flying habit the basic morphological and physiological constitution of the reptilian ancestors of birds and bats has been modified in two diverse directions in order to build up the flying equipment of these two groups. The common factor in both the groups is sustained flight and the common base has been reptiles. This chapter gives the morphological modifications of the pectoralis and the adjoining muscles of the forelimb as a prelude to explain the structural changes involved in flight. The animals studied are a ground lizard, *Uromastix hardwickii*, an arboreal lizard *Calotes versicolor*, the bird *Columba livia* and the bat *Rousettus lechinsaulti*. The task is made rather difficult on account of the confusion in nomenclature. The terminology adopted is that of Fisher and Romer.
Dorsal Muscles:

The latissimus dorsi (Fig. 1) which is a powerful retractor of the shoulder is in the mammals the largest muscle on the dorsal side of the trunk. In Uromastix (George, 1948) and Calotes also it is well-developed and it arises from the dorsal fascia and is inserted on the medial surface of the upper end of the humerus. In the pigeon the muscle is very poorly developed and consists of only a narrow strip arising from the dorsal fascia at the level of the neck of the humerus and inserted on the humerus slightly posterior to that of the deltoideus. In the bat, however, the primitive latissimus dorsi is divided as in mammals in general, into latissimus dorsi and the teres major. The two muscles run close together and get inserted on the ventral surface of the neck of the humerus. The latissimus dorsi in the bat is thus clearly mammalian in character.

The subscapularis (Fig. 2) in Uromastix and Calotes corresponds to the primitive subcoraco–scapularis and scapulohumeralis posterior. The former arises from the
lateral border of the scapula on its ventral aspect and is inserted on the medial side of the head of the humerus. The latter arises from the medial side of the suprascapula on its dorsal side and is inserted along with the former. In the pigeon the subcoraco-scapularis and the scapulo-humeralis posterior muscles are reduced owing to the reduction of the scapula into a rod-like structure. The two muscles cannot be clearly demarcated and appear more or less as a single mass arising from the dorsal as well as the ventral aspects of the scapula on its anterior half and inserted on the lesser tuberosity of the proximal end of the humerus. The former and the latter together correspond to the subscapularis muscle of mammals. In the bat also they are represented by a large subscapularis muscle. It arises from the ventral surface of the scapula and is inserted on the medial side of the head of the humerus.

The deltoideus (Fig.3) which is a powerful protractor and abductor of the arm is a large muscle in the lizards consisting of two parts at its origin. The anterior part, deltoideus clavicularis arises from the medial half of the clavicle, and the posterior one deltoideus scapularis from the anterior and medial borders of the outer surface of the suprascapula. The
two join together and finally get inserted on the deltoid ridge of the humerus. In the pigeon the deltoideus consists of three parts. (1) The tensor patagii (deltoideus clavicularis) consisting of the anterior t.p.longus and the posterior t.p.breviss parts, arises from the coraco-clavicular junction and is inserted on the patagial tendon and also on the fascia over the radio-ulna. A few fibres form the accessory tensor patagii towards the insertion of the muscle, which join the patagial tendon. (2) The deltoideus minor (deltoideus scapularis) which lies below the former arises from the same place of origin as that of the former and gets inserted on the deltoid ridge. (3) The deltoideus major (deltoideus scapularis) arises from the dorsal side of the proximal end of the scapula and is inserted on the mid-dorsal part of the shaft of the humerus. In the bat as in other mammals and in the pigeon the deltoideus consists of three parts. (1) The deltoideus clavicularis arises from the lateral half of the anterior border of the clavicle and proceeding laterally forwards, some of its fibres get attached to the deltoid ridge of the humerus and then it gets merged with the patagium as in the pigeon. (2) The acromio-deltoides (deltoideus scapularis) originates from the acromion process of the scapula and gets inserted on the proximal two-thirds of the humerus. (3) The spino-deltoides (deltoideus scapularis) originates from the spine of the scapula and
gets inserted just distal to the deltoid ridge. The deltoideus clavicularis of the bat is modified as in the pigeon in having an attachment to the patagium as an adaptation for flight.

The scapulo-humeralis anterior (Fig. 3) of reptiles which corresponds to the teres minor of mammals is a well-developed muscle in Calotes and Uromastix. In lizards it arises from the lateral edge of the scapula on its ventral side and is inserted on the medial side of the head of the humerus. It acts as a retractor and an elevator of the arm. In the pigeon and the bat, however, this muscle is absent.

The triceps (Fig. 3 and 6): In Uromastix and Calotes this muscle consists of three bellies of the primitive, massive muscle, the anconeus. One belly (1) arises from the deltoid ridge of the humerus, the second (2) from the medial side of the scapula near the glenoid cavity and the third (3) from the medial side of the head of the humerus. In the pigeon this muscle arises from the postaxial tuberocity of the head of the humerus. The distal end of the muscle is flattened into a tendon which is inserted on the olecranon process of the ulna. This muscle is a powerful extensor of the forearm. In the bat the
Triceps is a well-developed muscle, but the fourth part of the primitive anconeus is left as a very poor remnant. In this animal, the lateral and the medial parts of the triceps arise from the proximal end of the humerus and is inserted on the olecranon process of the ulna, while the third part arises from the border of the glenoid cavity, the posterior part of which is thickened into a tendon and is inserted on the olecranon process of the ulna.

Ventral Muscles:

The pectoralis (Fig. 4): In Uromastix and Calotes, it is a flat muscle with a broad origin. Anteriorly it arises from the inter-clavicular joint and also from the epi-sternum and sternum in the mid-ventral line and from the xiphoid horns. The fibres converge towards the upper arm and get inserted by a flat tendon on the deltoid ridge. It is the most powerful adductor of the arm. In the pigeon this muscle consists of two parts namely (1) the pectoralis major and (2) the pectoralis minor. The former originates from the whole length of the carina and the clavicle, from the lateral part of the body of the sternum and the ventral side of the coracoid. The fibres arising from all
these parts converge towards the proximal end of the humerus and gets inserted on the deltoid ridge from the ventral aspect. It is assumed that the original single structure of the reptile has bifurcated into two parts in the evolution of birds. Of the two divisions, the pectoralis minor shifted its original insertion from the ventral to the dorsal side of the humerus. Moreover the tendon of these two divisions sank inside the muscle so as to facilitate the attachment of the fibres in a pinnate fashion. The pectoralis major is concerned with the down stroke of the wing. The pectoralis minor brings about the elevation of the wing. In bat, the pectoralis is divided into three component parts as in some of the mammals. (1) The pectoralis major arises from the keel-like expansion of the body of the sternum and the fibres run laterally and forwards converging in a flat tendon which is inserted at the medial base of the deltoid ridge. (2) The pectoralis minor arises from the lateral border of the posterior end of the sternum as a thin membranous strip which becomes fleshy towards the region of the sternal remnant of the coracoid where it again becomes membranous and gets fused with the bone and continuing forwards becomes fleshy and gets inserted below the insertion of the pectoralis major on the humerus. (3) The pectoralis
posterior ("xiphihumeralis") arises from the posterior most ribs by a large fleshy belly. The fibres converge to a thin flat tendon which gets inserted near the insertion of the pectoralis major. The pectoralis of the bat is essentially mammalian in pattern even though it has the general avian orientation.

The supracoracoideus (Fig. 5) arises in two lobes in uromastix and Calotes. The medial portion arises from the coracoid and a portion of the scapula, while the lateral one is from the scapula. Both these parts converge and get inserted on the deltoid ridge. The supracoracoideus in the pigeon corresponds to the dorsalis scapulae of Fisher (1946). It arises from the dorsal part of the posterior two-thirds of the scapula and gets inserted on the bicipital at the proximal end of the humerus. The supracoracoideus of lizards and birds corresponds to the supraspinatus and the infraspinatus muscles of the bat and other mammals. The supraspinatus in the bat arises from the supraspinus fossa and is inserted on the outer tuberosity of the humerus. The infraspinatus originates from the infraspinus fossa of the scapula and like the supraspinatus is inserted on outer tuberosity of the humerus. The action is elevation and abduction of the arm.
The biceps brachii (Fig. 6): In Uromastix and Calotes consists of two heads, one originating from the coracoid lateral to the origin of the coracobrachialis and the other lateral to the origin of the above-mentioned first head and both these bellies having later fused together get inserted on the upper end of the radius. The corresponding muscle in the pigeon arises as a single muscle belly from the anterior end of the coracoid and gets inserted on the proximal end of the ulna. In the bat also this muscle consists of two heads. One arises from the clavicular part of the coracoid and the other from the same bone lateral to the origin of the first head mentioned above. The two bellies join together at the elbow joint forming a thick cylindrical tendon and get inserted on the proximal end of the radius.

The brachialis (Fig. 6): In Uromastix and Calotes it arises from the deltoid ridge of the humerus and lying very close to the shaft of the humerus gets inserted along with the tendon of the biceps. This muscle is an auxiliary flexor of the forearm. In the pigeon it arises from the ventral distal end of the humerus and gets inserted on the inner surface of the anterior one-fourth of the ulna. In the bat it originates from the ventral and the lateral surfaces of the
distal end of the humerus and gets inserted along with the tendon of the \textit{biceps}.

The \textit{coraco-brachialis} (Fig. 6); The origin of this muscle in Uromastix and Calotes is on the ventral side of the coracoid. It proceeds forwards along the medial side of the arm and is inserted on the antero-medial surface of the lower end of the humerus. In the pigeon the corresponding muscle comprises of two muscles, the \textit{coraco-brachialis brevis} and the \textit{coraco-brachialis longus}. The former arises as two bellies from two different places of origin. The posterior part is from the \textit{spina sterna} of the sternum and lies dorsal to the doracoid. The other belly arises from the junction between the coracoid and the clavicle. Both these parts unite and give off a common tendon which is inserted on the head of the humerus. The \textit{coraco-brachialis longus} arises from the outer border of the coracoid and from the costal process of the sternum. Its fibres are attached to a central tendon which is inserted on the head of the humerus. This muscle in the pigeon brings about slight depresson of the humerus. In the bat, this is a single muscle. It arises from the clavicular part of the coracoid and is inserted on the proximal end of the humerus. It is the flexor of the humerus. This muscle is of reptilian type.
The subclavius (sternocoracoideus) (Fig. 6) which is absent in the reptiles is a very insignificant muscle in the higher mammals as in man, but in the pigeon and the bat it is a fairly powerful muscle. In the pigeon this muscle arises from the first two true ribs and is inserted on the dorso-lateral corner of the coracoid. Its main function is to keep the coracoid in place. In the bat it arises from the manubrium sternum and gets inserted on the lateral three-fourths of the clavicle and the head of the humerus. This muscle in the bat has to keep the clavicle in its place, as its corresponding muscle in the bird does to keep the coracoid in its place. This is a case of convergence in the two flying animals. In man the subclavius is a poorly developed, arising from the junction of the first rib and its costal cartilage in front of the costoclavicular ligament and inserted on the under surface of the intermediate third of the clavicle.

In conclusion it may be mentioned that since the bird and the bat are both flying animals and have arisen from reptilian ancestors, several of their flight muscles show similar orientation; though the majority of them in the bat show typical mammalian characteristics, while many of the muscles of the bird are essentially reptilian with some so modified as to give
an avian touch. The deltoideus clavicularis having the patagial attachments as in the bird, the presence of a well-developed subclavarius very similar in position and action to the sternocoracoideus of birds and the well-developed pectoralis muscles, are all adaptations for flight. But in the bat the presence of a well-developed latissimus dorsi with teres major, a single subscapularis and separate supraspinatus and infraspinatus muscles, a poorly developed anconeus and the attachments of others are distinctly mammalian features. In the pigeon, however, the fusion of the biceps and the presence of two coracobrachialis muscles and the sternocoracoideus and the unparalleled development of the pectoralis set of muscles are clearly special features in the birds.

The general conclusion that can be drawn is that each type of the flying animals has evolved along its own lines and the modifications of the muscles betray two such divergent lines of evolution. It must also be added that the morphological features of the shoulder muscles there is hardly any difference between Uromastix, the ground lizard and Calotes the arboreal form.