

## INTRODUCTION

Flight is the most characteristic feature of birds and the ability to fly has made them the most successful group of vertebrates other than mammals. The adaptive changes that have taken place in the evolution of the avian body to meet the demands of an aerial life have left imprints almost on all the systems, of which the skeletal and muscular are the most prominent. The gross morphology of the musculature has been a subject of inquiry since long and several authors have made substantial contributions to our understanding of this aspect (reviewed by George and Berger, 1966). These observations paved the way to further explorations of the biochemical organization of the skeletal muscles particularly the flight muscles at the cellular and subcellular levels (reviewed by George and Berger, 1966). Considerable work has accumulated in the recent years in this field. These studies have clearly shown that the flight muscles are structurally and metabolically adapted to specialized activity. In the cellular organization of the muscle, morphological patterns are only the gross exposition of the heterogeneity that exists at the molecular level. Thus the presence of two distinct types of fibres - the narrow red (R) and the broad white (W) ones in the pigeon pectoralis muscle presents a classical example of morphological diversity at the molecular and biochemical levels (Chapter 1).

This fundamental specialization of the two distinct types

of fibres (red and white) has been shown to have some bearing on the mode of muscle action and consequently on the mode of flight. It was therefore thought rewarding to study the cellular organization in the flight muscles of a number of different species of birds, indulging in different modes of flight. These studies have revealed the wide variety of muscle types encountered in the flight muscles of birds.

The occurrence of an intermediate type of fibre (I) as intermediate in the various characteristics between the R and W types<sup>was</sup> encountered in the pectoralis muscle of some birds. The presence of all the three types of fibres the W type predominating was found in the pectoralis of the Domestic Fowl which<sup>is</sup> practically a non-flying bird. In sharp contrast to this pattern some passerine birds such as the Sparrow, Munia etc. possess only the R type of fibre in their pectoralis muscle whereas in some soarers such as the Vulture the fibres are all of the I type. It should be mentioned that none of the birds studied showed the presence of entirely W type of fibres in their pectoralis. In a survey of the cellular organization of the pectoralis muscles of various birds it was found that muscles could be grouped into six different groups. The possible relationship between the fibre architecture of the muscle and the mode of flight is suggested (Chapter 2).

The supracoracoideus muscle, which is the principal elevator of the wing was also studied in the various birds. It was found that this muscle is less developed than the pectoralis with the sole exception of that of the Rubythroated Hummingbird (Archilochus

colubris) where both the flight muscles (pectoralis and supra-coracoideus) are more or less equally well developed (Chapter 3).

It is now well established that fat is the chief fuel for the sustained muscular activity (George and Berger, 1966) and it was found to be of interest to study the component fibres of the two flight muscles in the various birds. It was found that the maximum load of fat occurred in the red fibres, the minimum in the white fibres and medium in the intermediate fibres. However, a few exceptions to this general pattern <sup>were</sup> also noted. (Chapter 4).

Bats also being good fliers like birds it was considered to be of interest to study the cellular organization of their flight muscles. In the present study the pectoralis major and the pectoralis minor of a few representative bats were studied and the results compared with those obtained on birds. With the absence of the great variety in the modes of flight seen in birds, the patterns of organization met with in bats were found to be fewer (Chapter 5).

The Rosy Pastor (Sturnus roseus) is a migratory starling visiting Baroda every year in large numbers. From their breeding grounds (probably U.S.S.R.) they come in flocks in the Winter (October) and spend about six months in Baroda. At the onset of Summer (April) they fly back to their breeding grounds. Recent investigations by George and his associates have shed much light on the various aspects of their physiological adaptations. They observed that there is a great increase of fat and glycogen in the flight muscles of these birds from the post- to premigratory

period. However, we have no information on the diurnal variations in the glycogen and fat levels of the pectoralis of these birds during the pre- and the postmigratory periods. Data along these lines were obtained from an investigation described in chapter 6.

Since it was noted that there is an increase in the glycogen content of the muscle in the Rosy Pastor towards migration, and that the glycogen is considerably depleted during night, a study on the effect of cold stress on pigeons was undertaken with a view to find out if glycogen is utilized for thermogenesis (Chapter 7).

A study of the diurnal variations in the glycogen and fat levels of the flight muscles (pectoralis major and pectoralis minor) of bats (Hipposideros speoris) was also undertaken since bats which are active at night and rest in the day time offer a striking contrast to the birds studied which are active during day and rest during night (Chapter 8).

Phosphorylase activity is known to be high in the broad fibres and low in the narrow fibres of the pigeon pectoralis. A histochemical survey of the distribution of this enzyme in the various fibres in the flight muscles of a few representative flying and non-flying birds was carried out, the results of which are presented in chapter 9.

That the distribution pattern of the various fibre types is related to the nature and extent of activity of the muscle is evident from the studies of the flight muscles of birds and bats reported herein. Since apart from the wings, the legs of birds also

called upon to perform various kinds of activity, it was thought interesting to study the fibre composition of the leg muscles of a few selected birds exhibiting diverse adaptations of the leg. The gastrocnemius muscle being the largest and the most powerful in the movements of the leg, a study of this muscle with respect to the localization and distribution pattern of succinic dehydrogenase activity and fat was also undertaken (Chapter 10).

The following preliminary papers were published with the joint authorship of my guiding teacher, Dr. J. C. George.

1. Studies on the Structure and Physiology of the flight muscles of birds. 10. Certain biochemical differences in the cellular organization of the Fowl pectoralis. Pavo, 2: 61 - 64, 1964.
2. Studies on the Structure and Physiology of the flight muscles of birds. 11. Cellular organization and distribution of fat and succinic dehydrogenase in the pectoralis of some passerines. J. Anim. Morphol. Physiol., 2: C. J. George Felicitation Number, 90 - 96, 1964.
3. Studies on the Structure and Physiology of the flight muscles of birds. 12. Observations on the structure of the pectoralis and supracoracoideus of the Rubythroated Hummingbird. Pavo, 2: 111 - 114, 1964.
4. Studies on the Structure and Physiology of the flight muscles of birds. 13. Characterization of the avian pectoralis. Pavo, 3: 14 - 22, 1965.
5. Studies on the Structure and Physiology of the flight muscles of birds. 14. Characterization of the avian supracoracoideus. Pavo, 3: 23 - 28, 1965.

CHAPTER 1  
CHARACTERIZATION OF THE RED AND WHITE FIBRE  
TYPES IN THE PIGEON PECTORALIS

It is now well established that the various cellular components of a muscle are not homogeneous in their structural and biochemical characteristics. In his pioneering observations on the structure of the striated muscle Kölliker (1857, 1888) described mitochondria as interstitial granules distinct from fat droplets. Later, Bullard (1912) in a study of the histological organization of the pigeon pectoralis not only confirmed the mitochondrial inclusions which are different from fat droplets, but also recognized the fact that these fat inclusions are not uniformly distributed in all the fibres of the same muscle, but they differ considerably in different muscles as well as in different fibres of the same muscle. The differences in the structural and cellular organization among the fibres present in the same muscle has been confirmed later by George and Jyoti (1955) by the demonstration of two distinct types of fibres in the pigeon pectoralis - a broad white fibre and a narrow red fibre. A reinvestigation of the pigeon pectoralis (George and Naik, 1959; George and Talesara, 1962) showed that among the two types of fibres, the broad white fibres are glycogen loaded and are adapted for anaerobic metabolism using chiefly glycogen as fuel for energy and that the red fibres which are fat loaded are adapted for aerobic metabolism using fat as fuel.

The above observations showed that the pigeon pectoralis is not a homogeneous muscle consisting of an uniform type of fibres. Even the relative distribution of the red and white fibres were found to be different in the different regions of the muscle (George and Naik, 1959a). It should also be mentioned that in transverse sections all the fibres of the same type do not show the same intensity of staining either for fat or for glycogen. Taking the intensity of staining as an index of the concentration of the substance it may be stated that some of the white fibres contained more glycogen than the other white fibres while some of the red fibres more fat than other red fibres.

Among these two distinct types of fibres mentioned above, the red fibres were found to contain more numerous and larger sized mitochondria (George and Naik, 1958a). The presence of a greater concentration of succinate dehydrogenase located in the red fibres was also showed histochemically (George and Talesara, 1961a). By virtue of the red fibres having a greater concentration of fat, lipase and oxidative enzymes and the white fibres containing a greater concentration of glycogen and glycolytic enzymes, these two types of fibres have been shown to be two distinct different systems showing diverse metabolic adaptations (George and Talesara, 1962). Thus the pigeon pectoralis exhibits in its cellular organization two distinct specializations structurally and functionally. The red fibres are adapted for sustained activity and the white ones for quick and short <sup>lasting</sup> contractions. The various characteristic features of the two types of fibres

that constitute the pigeon pectoralis, are summarized in the following Table taken <sup>from</sup> "Avian Myology" (George and Berger, 1966).

CHARACTERIZATION OF THE FIBRE  
TYPES

Properties	Type 1	Type 2
Colour	Red	White
Diameter	Small	Large
Blood supply	Copious	Little
Myoglobin	High	Low
Sarcoplasm	Granular	Clear
Mitochondria	Numerous	Sparse
Fat	High	Low
Glycogen	Low	High
Lipase	High	Low
Phosphorylase	Low	High
UDPG-glycogen transglucosylase	Low	High
Aldolase	Low	High
Lactic dehydrogenase		
(Cytoplasmic)	Low	High
(Mitochondrial)	High	Low
Other oxidative enzymes	High	Low
Alkaline phosphatase	Fairly high	Moderate
Acid phosphatase	Moderate	Fairly high
ATPase (acid)	Low	High
ATPase (neutral)	High	Low



Properties	Type 1	Type 2
Acetylcholinesterase	High	Low
Butyrylcholinesterase	Low	High
Activity	Sustained	Rapid
Contraction	Slow	Fast

Basing the structural organization and the relative distribution of the red (R) type and white (W) type of fibres of the pigeon pectoralis as the basic pattern the occurrence and distribution of these two types of fibres in the pectoralis muscles of other birds were investigated with a view to a better understanding of the relationship between structure and function.

In the study of the pectoralis of the domestic fowl, however, a third intermediate type of fibre (I) was revealed. It therefore became clear that the occurrence and distribution of this type as well in addition to the other two types, in the pectoralis muscles of the various birds under investigation, are to be considered. The results of such an investigation is reported in the next chapter.