INTRODUCTION

Ever since the dawn of civilisation man has watched jealously and zealously the flight of birds, which has kindled in him a desire to conquer the air. His early interest in the study of birds was (naturally) to understand the mechanism of flight so that he could adopt suitable devices to keep himself afloat and travel in the air. The emergence of the aeroplane was the ultimate result of his endeavours. However, his interest in the flight of birds continued with special emphasis on the patterns of body and wing architecture and their implications on the aerodynamics of flight, in the (vain) ? hope of being able to build, in the light of the new knowledge thus made available, better machines. To-day engineers hardly expect to get ideas from the study of the flight of birds (for in building better machines ? order to better their machines. On the contrary the experience of the engineer in the field of aeronautics could be of considerable help in understanding the mechanism of bird flight. At best, birds have been an encouragement by demonstrating the practicality of heavier-than-air flying machines. This is understandable because the bird is not designed as an aeroplane but (on the other hand it) is a product of evolution governed by natural selection, a product in which structure and function are complementary and where survival is determined (on the by the touchstone of) adaptation.

Birds differ considerably in their mode of flight. Although birds exhibit three chief modes of flight, namely, flapping, gliding? shooting and soaring, each type is modified in different ways in different birds. In fact, each type of bird has its own distinct way of flying and no two types (resemble are affect they each alike other absolutely,) in the execution of the different phases of flight. Associated with these differences are great variations in the architecture of the wing. Flight (has been is ? conceived as) a morphological problem and (considerable much amount of) valuable work has been done on the morphology of the musculoskeletal system of the wing, ~~which~~ this has greatly enhanced our knowledge about of the homology of the different muscles and skeletal elements of the wing. However, comparatively (very) little attention has been paid to the functional aspects of this important system.

Our knowledge regarding the origin and evolution of birds is far from satisfactory. Palaeontological studies, which have contributed so much towards our understanding of the evolution of the other vertebrate groups, have (done contributed less comparatively little to our knowledge of with regard to) birds, possibly because the major strides in their evolution have been physiological. (Fewer fossils Interrelationships ~~of~~ between the different orders of birds therefore remain vaguely defined and striking structural differences are not discernible. ~~to separate them with the~~ as a result ~~that~~ ? we are left with a classification of birds based on comparativly minor morphological differences, unlike that of other vertebrate groups.

Since Flight be~~ing~~ is the most characteristic activity of birds, the problem of energetics of flight is of considerable importance and interest to the avian biologists. What is the source of energy for migrating birds for their long intercontinental flights or for a bird like the kite to be able to remain afloat high in the air for hours? why the Ratitae never took to flight while some birds like the domestic fowl and domestic duck are unable to indulge in sustained flight, are some salient questions which deserve more satisfactory answers than hitherto given. It is most likely that answers to these and such other similar questions have to be sought for on the broad frontiers of comparative physiology where other scientific disciplines meet and coalesce.

The flying equipment of a bird contributes a major part to the (major bulk of the) body, since the flight muscles alone, in most birds, constitute over one sixth of the total weight of the body. This is primarily because the bird uses the resistance of the air column as a fulcrum for its movements and when compared to a terrestrial or an aquatic habitat, the medium in which a bird moves is far more yielding, to develop sufficient resistance that is required for propulsion. The bird should therefore possess strong and (fast moving) muscles. Among the flight muscles again, the enormous pectoralis major which has no parallel with respect to morphological and physiological complexity in any other group of vertebrates with perhaps the sole exception of the bat (among the mammals), is undoubtedly the most important. It is the realisation of this fact during the course of investigations on the flight muscles in general that compelled me to suspend for the present the investigations on other muscles and to concentrate on this muscle alone. not needed ? as I visualised in so doing, sufficient promise of fruitful results. Preliminary reports on some of the results obtained have been published in joint authorship with Dr. J. C. George, my guiding teacher (George and Naik, 1957a, b; 1958a, b, c).

The present work is by no means an attempt to provide complete answers to the problems I have outlined above; but rather I have tried to wade through the hazardous mire seeking here and there a suitable prop to hold on in order to reach the journey's end.

CHAPTER 1

CHARACTERISATION OF THE PECTORALIS MAJOR MUSCLE OF BIRDS

While considerable (amount of) work has been done on the morphology, histology and physiology of the mammalian skeletal muscles, comparatively little is known of these aspects of ~~the~~ avian muscles. Among the flight muscles, though the pectoralis major of the pigeon has been extensively used for studying some aspects of biochemistry and physiology, but very few observations have been made on the structure of this muscle. Denny-Brown (1929) in his work on vertebrate muscles made some observations on the structure of the pectoralis of the pigeon and described the 'dark' and 'light' fibres in this muscle. Tiegs (1954) noted the heavy sarcoplasmic inclusions in the muscle fibres of the flight muscles of birds as compared to the striated muscles of other animals. George and Jyoti (1955a), who studied the histological structure of the teased out fibres of the pectoralis major muscle of some birds and a bat, observed that in the pigeon this muscle is made up of two types of fibres: one which is narrow, containing in its sarcoplasm dense lipoid granules and numerous fat globules which render the characteristic striations hardly visible and ~~that~~ in which these fat droplets become fewer when the muscle is subjected to sustained exercise; ~~In the~~ and an other type which is broad and devoid of dense lipoid inclusions in its clear sarcoplasm and in which the striations are clearly visible. The broad variety (type?) of fibres was found to be predominating in the kite, whereas in the fowl

Sc. names?

only this the broad ? variety was found to be present and only the narrow variety in the bat. In subsequent papers they (1955b, 1957) discussed the role of fat as the chief fuel in flying birds for sustained muscular activity. Recently George and Scaria (1956) showed the presence of high lipase activity in the breast muscle of the pigeon and discussed its possible role in the utilisation of fat as energy fuel in sustained muscular activity. High lipase values were obtained also for the bat breast muscle (George, Sushila and Scaria, 1958), for flight muscles of insects (George, Vallyathan and Scaria, 1958) and for ~~the~~ vertebrate heart muscle (George and Scaria, 1957). Lawrie (1952) stressed the importance of myoglobin in the breast muscle of birds, as an oxygen carrying system.

The recent studies cited above have shown that the breast muscle of birds is a complex morphologico-physiological system and a clearer and more comprehensive understanding of it from the structural and functional points of view should be of considerable value. It was therefore thought desirable to conduct an investigation on these aspects of the *pectoralis major* muscle of some birds exhibiting different modes of flight.

Materials and Methods

Structure of muscle: 3 not needed

The *pectoralis major* of the following birds was were studied:

1. The domestic fowl (<u>Gallus domesticus</u>)
2. The pariah kite (<u>Milvus migrans</u>)
3. The blue rock pigeon (<u>Columba livia</u>)
4. The green parakeet (<u>Psittacula kramari</u>)
5. The green bee-eater (<u>Merops orientalis</u>)

The above birds were selected as representing different structural types of the <u>pectoralis major</u> muscle and consequently different modes of flight; the fowl for a non-flying bird, the kite for a soarer, the parakeet and pigeon for a flapping type of flier and the bee-eater for a gliding shooting type.

The birds were shot and within half an hour of killing small pieces of the <u>pectoralis major</u> were cut out and some were fixed in 10% neutral formalin, some in Zenker's fluid (Guyer, 1939), while the rest frozen fresh for sectioning. Microtome sections of the pieces fixed in Zenker's fluid were cut at 8µ and stained with Mallory's Phosphotungstic Haematoxylin (Mallory, 1900) and observed under the microscope. Since there was a considerable amount of shrinkage, it was found more desirable to take the measurements of the fibres from the transverse sections of the fresh frozen material. Camera lucida sketches of the sections magnified to a thousand times were made and the diameter of the fibres was calculated from the measurements made from the sketches. In measuring the diameter of the fibres only the circular ones or the ones more or less circular were measured. The figures obtained are the average of several hundreds of fibres measured from the muscle of three individual birds.

Quantitative estimation of fat:

All the birds obtained for this work were shot with an air-rifle and within fifteen minutes of the death of the animal the portion of the pectoralis major was cut into small pieces, dehydrated in an electric oven at 80 ° C, ground into powder and transferred into a fat extraction thimble. The fat was extracted with 1:1 ethanol-ether mixture in a Soxhalet apparatus.

Observations and Results

Structure of the muscle:

On examining all the three preparations, *viz*., the teased out fibres, the cross section of the frozen tissue, microtome sections of the fixed tissue (fixed in Zenker's fluid), it was observed that the pigeon pectoralis consists of the two types of fibres — a broad type and a narrow one.

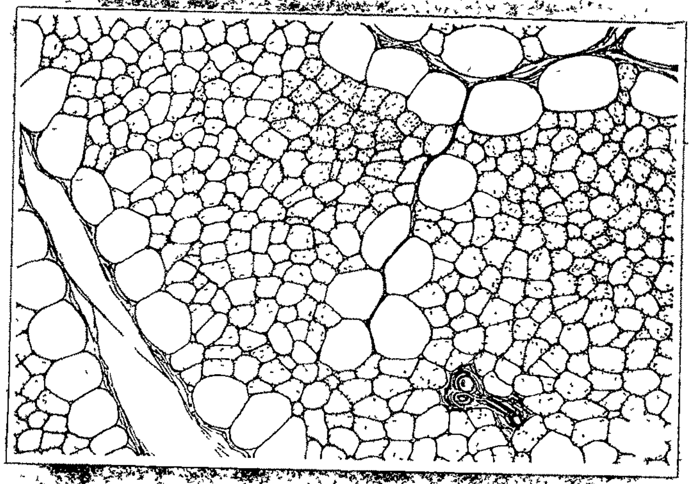

Fig. 1.1 Camera lucida sketch — t.s. of untreated pigeon pectoralis x 100

X-sect.

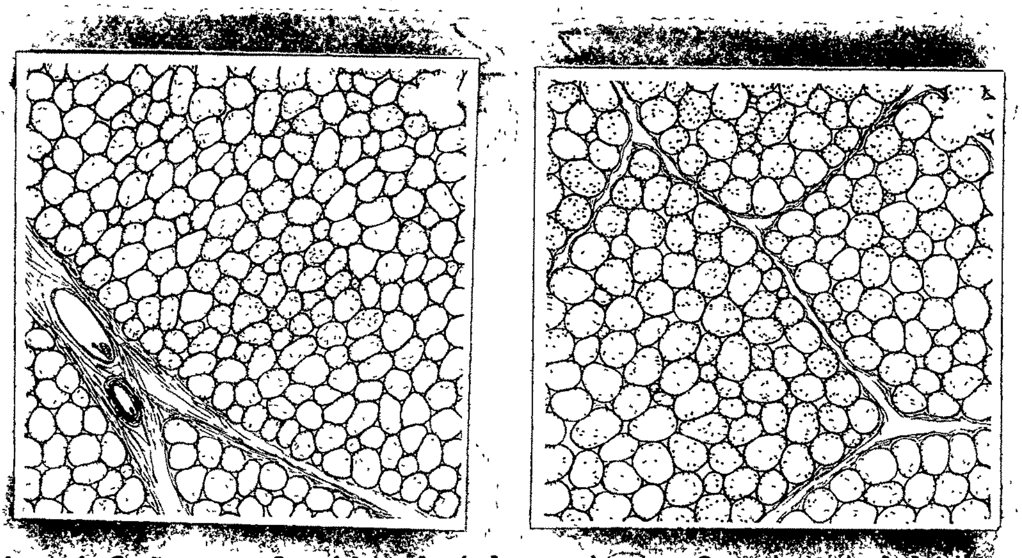

Fig. 1.2 Camera lucida sketch — t.s. of untreated kite pectoralis
1.3 Camera lucida sketch — (t.s.(of untreated bee-eater pectoralis
×100 ?

The pectoralis of the fowl and of the kite was found to consist of ~~only~~ broad fibres only, (so also of the kite,) while that of the parakeet Red only narrow ones ~~only~~. In the bee-eater pectoralis, however, the fibres were broader than those of the kite. In the sections of fresh frozen muscle of the pigeon the narrow fibres were red in colour and while the broad ones were white, the latter being more than twice the (~~broader in~~) diameter of ~~than~~ the former. The broad white fibres, circular in cross section, were confined to the periphery of the muscle and also to ? of the fasciculus within the muscle. On the other hand, the red, narrow ones, which were much more numerous, were closely packed in the interior of the fasciculus. Often a few white fibres ~~too~~ were also found in the interior of the fasciculus more or less in the middle (Fig. 1.1). It appears from the above observations that the formation of a new fasciculus by the splitting of the parent one takes place in between two inner broad fibres so that when the daughter fasciculi are formed they too will be lined by the broad ones on the periphery. All the fibres of the muscle in the kite and bee-eater, were red, circular in cross section, and loosely packed within the fasciculus (fig.1.2,1.3). Those of the parakeet pectoralis ? too were also red but, unlike those of the kite and bee-eater, very much narrower in diameter and closely packed within the fasciculus (fig.1.4). All the fibres of the fowl pectoralis on the other hand were white, much broader, and most of them polygonal in cross section, ~~and~~ though few were more or less circular (fig. 1.5).

Diameter and certain general features of the fibres in the *pectoralis major* muscle of different birds studied are given in table 1.

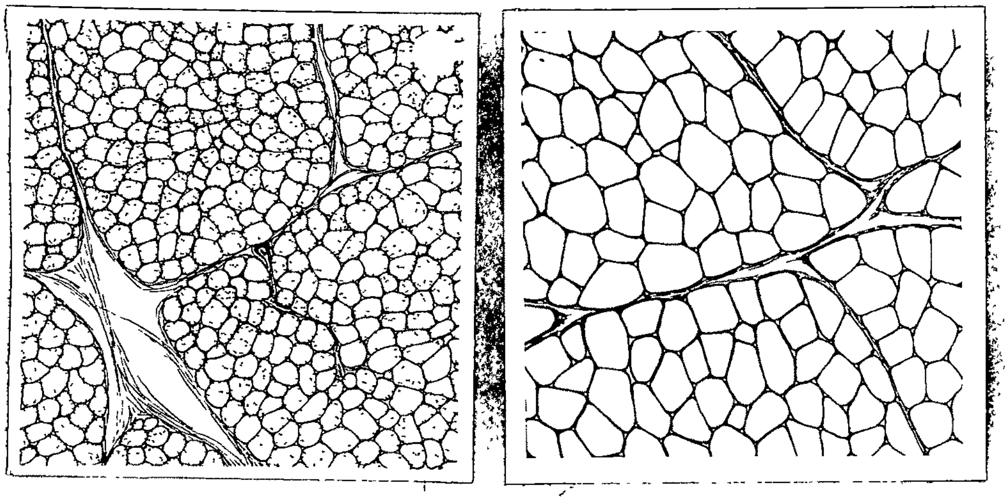

Fig. 1.4 Camera lucida sketch — t.s. of untreated parakeet pectoralis
1.5 Camera lucida sketch — t.s. of untreated fowl pectoralis

x100

— needs title

Table 1

Diameter and Nature of Pectoralis major fibres

— (double line)

No.	Bird		Nature of the fibres	Average diameter μ	
1	Fowl		White Polygonal in c.s.	64.0	S
2	Kite		Red Circular in c.s., loosely packed	46.6	S
3	Pigeon	i	Red Closely packed in the interior of the fasciculi	30.1	S
		ii	White Bordering the fasciculi	69.0	S
4	Merops		Red Circular in c.s., loosely packed	39.0	S
5	Parakeet		Red Closely packed	36.6	- ok

lines not needed

Quantitative estimation of fat:

Table 2 gives the fat content of the pectoralis major of some birds.

Table 2 - Title ?

	%age gms. of fat		
	Mean	±S.D.	Maximum
Pied-crested Cuckoo (*Clamator jacobinus*)	6.3540 (1)		
King Crow (*Dicrurus macrocercus*)	5.6422(4)	±0.24	4.1380
Rosy Pastor (*Pastor roseus*)	4.7802(4)	±0.34	5.2740
Hawk Cuckoo (*Hierococcyx varius*)	4.6075(2)		4.8310
House Crow (*Corvus splendens*)	4.1665(5)	±0.63	5.2610
Blue-tailed Bee-eater (*Merops sinensis*)	3.9850(2)		4.2570
Cattle Egret (*Bubulcus ibis*)	3.8985(4)	±0.24	4.1380
White-breasted Kingfisher (*Halcyon smyrnensis*)	3.5537(4)	±0.83	4.5080
Barn Owl (*Tyto alba*)	3.6900(1)		
Jungle Crow (*Corvus coronoides*)	3.6130(1)		
Brahamini Myna (*Temenuchus pagodarum*)	3.4375(2)		4.2620
Golden Oriole (*Oriolus oriolus*)	2.8920(2)		3.0110
Hoopoe (*Up$\overset{u}{o}$pa epops*)	2.7520(1)		
Mahratta Woodpecker (*Liopicus mahrattensis*)	2.6520(2)		2.8800
House Sparrow (*Passer domesticus*)	2.6302(4)	±0.11	2.7660
Common Myna (*Aeridotheris tristis*)	2.5330(2)		
Koel (*Eudynamis scolopaceus*)	2.4307(4)	±0.42	3.0020
Red-vented Bulbul (*Molpastes cafer*)	2.1796(3)		2.2450
*Blue Rock Pigeon (*Columba livia*)	4.46		
*Pariah Kite (*Milvus migrans*)	4.80		
*Fowl (*Gallus* $\overset{gallus}{domesticus}$)?	0.98		
** Batrachus (fish) Body muscle	1.21		
** Rana (frog) Leg muscle	0.90		
** Uromastix (lizard) Leg muscle	1.40		
** Cavia (Guinea pig) Leg muscle	1.86		

* Jyoti (1955) ** George (1952)

For the sake of comparis~~i~~on, data on the fat content of some muscles of other vertebrates ~~is~~ are included in table 2. All the actively flying birds studied have a higher percentage of fat in their pectoralis than in that of the poor fliers or non-flying ones and than in the muscles of other vertebrates. tr.

Discussion

Muscular tissue in general exhibits a wide range of morphological and biochemical variations. That the homologous muscles of animals belonging to the same group may show great variations in microscopical structure is seen in the flight muscles of insects (Tiegs, 1954). The muscles of vertebrates are by no means an exception to this. It is well known to physiologists that different muscles react differently to the same chemical. Such differential behaviour in many cases ~~could~~ can be attributed to the difference in structure and function of the muscle. That such differences in the microscopical structure of the same muscle in different animals do occur is well indicated in the present study.

George and Jyoti (1955a) showed that the bat breast muscle consists of narrow fibres with dense lipoid inclusions, unlike those of the leg which are broad, ~~and~~ with clear sarcoplasm and hardly only a ? few small fat droplets. Kenney and Glenn Richards, in a recent publication (1955), noted the presence of narrow fibres (75 μ in diameter) in the flight muscle and broad ones (350-400 μ in diameter) in the leg muscle of the giant water bug, *Lethoceros americanus*. The occurrence of narrow types of fibres in the flight muscles of flying animals, like the breast muscles of the bird and bat, and the wing muscles of the insect, is therefore an interesting case of convergence. It also suggests a physiological correlation with the morphological differences seen in the flight and the leg muscles of one species as well as in the flight muscles (themselves) of different flying animals.

The fibres of the kite pectoralis, like those of the pigeon, parakeet and bee-eater which are all flying birds, are circular in cross section, whereas those of the fowl, which is a non-flier, are polygonal in cross section. The polygonal shape is intimately related to the nonflying habit of the fowl, because in inactivity ~~there is~~ a certain amount of stability ~~that~~ is established with the result that the fibres tend to acquire more connective tissue to become fixed and thickened at places now distinguished as the corners of the polygonum. This could not happen in the case of the constantly active moving ? fibres of other birds and they therefore retain their original circular pattern in cross section. The pectoralis of the parakeet contains primarily narrow red fibres, whereas that of the pigeon contains narrow red as well as broad white fibres. The fibres in the pectoralis of the kite and bee-eater, though red in colour, are comparatively broader in diameter than the red fibres of the parakeet or pigeon. The method of distinguishing the *pectoralis major* of one bird from that of another on the basis of its colour alone is unsatisfactory because this muscle in the pigeon is red, but on microscopical examination is found to contain~~s~~ white fibres too. Again, the colour distinction (on the basis of colour), namely pale, red and white, is not diagnostic enough to be used as a (sufficiently sharp so as to deserve the dignity of a scientific) ? method of demarcation. Nevertheless, the method of distinguishing the breast muscles of birds as red and white, when certain other factors are also taken into account, becomes extremely useful. The red fibres, in possessing the oxygen-carrying system, have a definite advantage over the white ones in sustained muscular activity. In this connection the surface area of the fibres is an important factor in effecting ~~the~~ a more efficient gaseous exchange. ~~more efficient~~. Since, in an unit area, greater the number of fibres, greater would be the surface area, naturally lesser would be the size of the fibres. So, the diameter of the fibres should be an index of the surface area. ? sentence Among red muscles therefore, the narrow fibres of the pigeon and parakeet should provide ~~be~~ a very efficient oxygen-carrying system. On the other hand, the broad white fibres of the pigeon breast muscle, as well as those of the fowl, would have to depend more on the glycogen store for energy, ~~and~~ but? such energy could be made available under anaerobic conditions.

Examining the data obtained in the present study it is possible to visualise (as follows,) the following possible lines of modifications in the evolution of the pectoralis major muscle of ~~carinaceous~~ carinate? birds and also account for the differences in the respective modes of flight.

1. Red fibers — Narrow e.g. Parakeet — flapping type of flier
 — Broad e.g. Kite — soaring type of flier
 Bee-eater — shooting type of flier
2. Mixed — Narrow & Broad e.g. Pigeon — flapping type of flier
3. White fibers — Broad e.g. Fowl — nonflying type

I am fully aware of the fact that it is not safe to generalise - or draw conclusions ? ? (venture generalisations of this nature basing conclusions) on observations made on a few types. Nevertheless, I feel it useful and desirable to put suggest forth these ideas as a hypothesis for the present studies, as well as for future workers in this new field (that's is now opened up), whose efforts may result in its future elucidation, expansion, modification or even rejection. It should, however, be mentioned here that a study of the breast muscle of such some birds as like the ostrich and penguin should also have been made. But unfortunately, all my efforts to obtain this material, or even information regarding it, (from abroad) have been unsuccessful.

Another important feature of the pectoralis of birds is its high fat content. George (1947 and 1952) studied some muscles of a few representative vertebrates belonging to different groups and noted the higher fat content in the <u>pectoralis major</u> muscle of the pigeon. George and Jyoti (1955b) confirmed the high fat content in the pectoralis of other two birds (kite and parakeet). Data collected by these workers, by and Nair (1952) though only for few birds, are sufficiently suggestive to warrant the conclusion that the pectoralis of flying birds normally contains a high amount of fat. The present work supports this contention and now it can be safely concluded generalised that the pectoralis major of flying birds is ~~can be~~ characterised by high fat content.

Fat deposition in muscle is governed not only by the enzymatic system of muscle fibres but also by certain hormones in the peripheral circulatory system and since both these factors appear to be equally important, direct correlation between the amount of muscle fat and the activity cannot be expected. Though utilisation of fat in the flight muscles of birds, bats and insects during long and sustained activity is now established, high percentage of fat does not mean that fat is utilised more in the muscle. But nevertheless it is a fact that the muscle fat (intracellular fat) serves the purpose of the reserve store of energy, which is mobilised when needed.

Since it is now known that fat is utilised in long and sustained flight and that the avian flight muscles contain a high percentage of fat in comparision to muscles of other vertebrates, it should be interesting to see whether (structurally) the avian flight muscles show any structural specialisation for this purpose, and how far such a specialisation, if any, is related to with the variation in the gross structural details (of the flight muscles,) which have been already mentioned. It is towards an understanding of this problem that the present work is dedicated ? attempted.

Summary

1. The structure of the *pectoralis major* of a few representative birds exhibiting different modes of flight was examined. The possibility of a relation between the structure of this muscle and the flight of birds is discussed.

2. On examining the fat content of the pectoralis of 18 birds belonging to different groups, it is observed that in the actively flying birds the *pectoralis major* contains a higher percentage of fat (as than in compared to that of) the poor fliers.

3. The scope of the present thesis is thus outlined.