THE MECHANICS OF BIRD FLIGHT.

A thesis presented for the degree of Doctor of Philosophy in Zoology in the University of Canterbury, Christchurch, New Zealand.

by

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1969
PLATE I

Wing bones of *Columba livia*

Wooden models, ten times full size
A  Radiale (radial carpal)
B  Extensor process (Metacarpal II)
C  Ulnare  (ulna carpal)
II  Digit II (pollex)
III Digit III
IV  Digit IV
Mc III  Metacarpal III
Mc IV  Metacarpal IV

Fig. 5
ACKNOWLEDGEMENTS.

The Author wishes to thank all those who have helped in the preparation of this thesis.

In particular, thanks are due to the late Professor Percival who inspired the original work, to Dr. Stonehouse for his help and encouragement as supervisor, and also to Professor Knox and all those members of academic staff, Department of Zoology, for their interest.

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## CONTENTS

<table>
<thead>
<tr>
<th>LIST OF PLATES</th>
<th>Page No.</th>
<th>(iv)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LIST OF FIGURES</td>
<td>Page No.</td>
<td>(v)</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>Page No.</td>
<td>(viii)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Chapter No.</th>
<th>Page No.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>1.1 General</td>
<td>1</td>
</tr>
<tr>
<td>1.2 Review of Literature</td>
<td>2</td>
</tr>
<tr>
<td>1.3 The Duties of the Wing during Flight</td>
<td>11</td>
</tr>
<tr>
<td>1.4 An Outline Specification for a Wing</td>
<td>11</td>
</tr>
<tr>
<td>1.5 Aerodynamic Terms and Symbols</td>
<td>14</td>
</tr>
<tr>
<td>1.6 A Note on Aerofoils</td>
<td>16</td>
</tr>
<tr>
<td>2. STRUCTURE</td>
<td>19</td>
</tr>
<tr>
<td>2.1 General</td>
<td>19</td>
</tr>
<tr>
<td>2.2 Arthrology</td>
<td>20</td>
</tr>
<tr>
<td>2.3 Proportions</td>
<td>29</td>
</tr>
<tr>
<td>3. MYOLOGY</td>
<td>31</td>
</tr>
<tr>
<td>3.1 Introduction</td>
<td>31</td>
</tr>
<tr>
<td>3.2 List of and Notes on Muscles</td>
<td>33</td>
</tr>
<tr>
<td>4. GEOMETRY AND FORCES</td>
<td>47</td>
</tr>
<tr>
<td>4.1 General</td>
<td>47</td>
</tr>
<tr>
<td>4.2 Geometry</td>
<td>48</td>
</tr>
<tr>
<td>4.3 Loading</td>
<td>49</td>
</tr>
<tr>
<td>4.4 Forces</td>
<td>52</td>
</tr>
<tr>
<td>4.5 Conclusion</td>
<td>57</td>
</tr>
<tr>
<td>Chapter No.</td>
<td>Page No.</td>
</tr>
<tr>
<td>------------</td>
<td>----------</td>
</tr>
<tr>
<td>5. FLIGHT -</td>
<td>58</td>
</tr>
<tr>
<td>5.1 Introduction</td>
<td>58</td>
</tr>
<tr>
<td>5.2 Gliding</td>
<td>59</td>
</tr>
<tr>
<td>5.3 Flapping Flight</td>
<td>68</td>
</tr>
<tr>
<td>5.4 Hovering</td>
<td>79</td>
</tr>
<tr>
<td>5.5 Take-off</td>
<td>82</td>
</tr>
<tr>
<td>5.6 Landing</td>
<td>87</td>
</tr>
<tr>
<td>5.7 Conclusion</td>
<td>91</td>
</tr>
<tr>
<td>6. CONTROL -</td>
<td>93</td>
</tr>
<tr>
<td>6.1 General</td>
<td>93</td>
</tr>
<tr>
<td>6.2 Yaw</td>
<td>93</td>
</tr>
<tr>
<td>6.3 Pitch</td>
<td>94</td>
</tr>
<tr>
<td>6.4 Roll</td>
<td>95</td>
</tr>
<tr>
<td>6.5 Turning</td>
<td>96</td>
</tr>
<tr>
<td>6.6 Conclusion</td>
<td>97</td>
</tr>
<tr>
<td>7. CONCLUSION -</td>
<td>98</td>
</tr>
</tbody>
</table>

BIBLIOGRAPHY - - - - - - - - - 104

APPENDICES -

I Wing Loading 114
II A Note on the Alula 120
III Wing Beat Frequency 122
IV Extension of Manus 124
<table>
<thead>
<tr>
<th>Plate</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Bone Models</td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>Wing Skeletons</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Frontispiece</td>
<td></td>
</tr>
</tbody>
</table>
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure No.</th>
<th>Description</th>
<th>Page No.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Aerofoils</td>
<td>13</td>
</tr>
<tr>
<td>2.</td>
<td>Axes of Reference</td>
<td>16</td>
</tr>
<tr>
<td>3.</td>
<td>Air flow over aerofoils</td>
<td></td>
</tr>
<tr>
<td>4.</td>
<td>Cascade and slot</td>
<td></td>
</tr>
<tr>
<td>5.</td>
<td>Wing skeleton</td>
<td>19</td>
</tr>
<tr>
<td>6.</td>
<td>Second phalangeal joint a) <em>Columba livia</em> b) <em>Geography of joint</em></td>
<td>20</td>
</tr>
<tr>
<td>7.</td>
<td><em>Larus novaehollandiae</em></td>
<td></td>
</tr>
<tr>
<td>8.</td>
<td><em>Anas</em></td>
<td></td>
</tr>
<tr>
<td>9.</td>
<td>Comparison, <em>Cygnus</em> and <em>Anas</em> phalangeal joint</td>
<td>22</td>
</tr>
<tr>
<td>10.</td>
<td>First phalangeal joint - <em>Columba</em></td>
<td>23</td>
</tr>
<tr>
<td>11.</td>
<td><em>Columba</em> First phalangeal joint</td>
<td>24</td>
</tr>
<tr>
<td>12.</td>
<td><em>Hemiphaga</em> First phalangeal joint</td>
<td></td>
</tr>
<tr>
<td>13.</td>
<td><em>Anas</em> First phalangeal joint</td>
<td>25</td>
</tr>
<tr>
<td>14.</td>
<td><em>Cygnus</em> First phalangeal joint</td>
<td></td>
</tr>
<tr>
<td>15.</td>
<td><em>Larus novaehollandiae</em> First phalangeal joint</td>
<td>26</td>
</tr>
<tr>
<td>16.</td>
<td><em>Larus dominicanus</em> First phalangeal joint</td>
<td></td>
</tr>
<tr>
<td>17.</td>
<td><em>Columba</em> - wrist joint</td>
<td></td>
</tr>
<tr>
<td>18.</td>
<td>Wrist joint - <em>Columba</em></td>
<td>27</td>
</tr>
<tr>
<td>19.</td>
<td>Elbow joint - <em>Columba</em></td>
<td>28</td>
</tr>
<tr>
<td>20.</td>
<td>Muscle runs</td>
<td>33</td>
</tr>
<tr>
<td>21.</td>
<td><em>Columba livia</em></td>
<td></td>
</tr>
<tr>
<td>22.</td>
<td><em>Hemiphaga</em></td>
<td></td>
</tr>
<tr>
<td>23.</td>
<td><em>Anas</em> Manus and muscles</td>
<td>34</td>
</tr>
<tr>
<td>24.</td>
<td><em>Cygnus</em></td>
<td></td>
</tr>
<tr>
<td>25.</td>
<td><em>Larus novaehollandiae</em></td>
<td></td>
</tr>
<tr>
<td>26.</td>
<td>Tendons at wrist</td>
<td></td>
</tr>
<tr>
<td>27.</td>
<td><em>Columba livia</em> Wing and axes</td>
<td>48</td>
</tr>
<tr>
<td>28.</td>
<td><em>Larus dominicanus</em> Wing and axes</td>
<td></td>
</tr>
<tr>
<td>29.</td>
<td>Loading diagrams</td>
<td>49</td>
</tr>
<tr>
<td>30.</td>
<td>Hinge joint</td>
<td></td>
</tr>
<tr>
<td>31.</td>
<td>Forces on elbow joint a) <em>Columba</em> b) <em>Larus</em></td>
<td>53</td>
</tr>
<tr>
<td>32.</td>
<td>Forces on wrist joint a) <em>Columba</em> b) <em>Larus</em></td>
<td></td>
</tr>
<tr>
<td>Figure No.</td>
<td>Page No.</td>
<td></td>
</tr>
<tr>
<td>-----------</td>
<td>----------</td>
<td></td>
</tr>
<tr>
<td>33.</td>
<td>Ventral ligament of elbow</td>
<td>54</td>
</tr>
<tr>
<td>34.</td>
<td>Medial ligaments of wrist</td>
<td></td>
</tr>
<tr>
<td>35.</td>
<td>Effect of droop of manus</td>
<td></td>
</tr>
<tr>
<td>36.</td>
<td>Ulnare and tendons</td>
<td></td>
</tr>
<tr>
<td>37.</td>
<td>Attitudes in flight</td>
<td>61</td>
</tr>
<tr>
<td>38.</td>
<td>Washout</td>
<td></td>
</tr>
<tr>
<td>39.</td>
<td>Larus novaehollandiae</td>
<td>63</td>
</tr>
<tr>
<td>40.</td>
<td>Larus novaehollandiae</td>
<td>64</td>
</tr>
<tr>
<td>41.</td>
<td>Larus novaehollandiae</td>
<td>Gliding</td>
</tr>
<tr>
<td>42.</td>
<td>Larus novaehollandiae</td>
<td>66</td>
</tr>
<tr>
<td>43.</td>
<td>Larus novaehollandiae - flapping flight</td>
<td>67</td>
</tr>
<tr>
<td>44.</td>
<td>Larus novaehollandiae - strong flapping flight</td>
<td>74</td>
</tr>
<tr>
<td>45.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>46.</td>
<td>Wing attitudes</td>
<td>75</td>
</tr>
<tr>
<td>47.</td>
<td>Position of manus during stroke</td>
<td></td>
</tr>
<tr>
<td>48.</td>
<td>Flapping flight - Larus dominicanus</td>
<td>77</td>
</tr>
<tr>
<td>49.</td>
<td>Flapping flight - Larus novaehollandiae</td>
<td>79</td>
</tr>
<tr>
<td>50.</td>
<td>Hovering - Larus novaehollandiae</td>
<td>80</td>
</tr>
<tr>
<td>51.</td>
<td>Hovering - Larus novaehollandiae</td>
<td>81</td>
</tr>
<tr>
<td>52.</td>
<td>Columba livia</td>
<td>83</td>
</tr>
<tr>
<td>53.</td>
<td>Larus novaehollandiae</td>
<td>Normal take-off</td>
</tr>
<tr>
<td>54.</td>
<td>Jump take-off - Larus novaehollandiae</td>
<td>84</td>
</tr>
<tr>
<td>55.</td>
<td>Take-off - Passer domesticus</td>
<td>85</td>
</tr>
<tr>
<td>56.</td>
<td>Take-off - Phalaenoptilus varius</td>
<td>86</td>
</tr>
<tr>
<td>57.</td>
<td>Normal landing - Columba livia</td>
<td>87</td>
</tr>
<tr>
<td>58.</td>
<td>Landing on water - Larus novaehollandiae</td>
<td>88</td>
</tr>
<tr>
<td>59.</td>
<td>Normal landing on ground - Larus novaehollandiae</td>
<td>90</td>
</tr>
<tr>
<td>60.</td>
<td>Landing on a post - Larus dominicanus</td>
<td>91</td>
</tr>
<tr>
<td>61.</td>
<td>Various wing configurations</td>
<td>92</td>
</tr>
<tr>
<td>62.</td>
<td>Definitions of control axes</td>
<td>94</td>
</tr>
<tr>
<td>63.</td>
<td>Stability</td>
<td></td>
</tr>
<tr>
<td>64.</td>
<td>Use of tail as a rudder</td>
<td></td>
</tr>
<tr>
<td>65.</td>
<td>Effect of roll on lift</td>
<td>96</td>
</tr>
<tr>
<td>66.</td>
<td>Forces involved during turn</td>
<td></td>
</tr>
<tr>
<td>67.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>68.</td>
<td>Geometry of the wing and loading distribution</td>
<td>115</td>
</tr>
<tr>
<td></td>
<td>Columba livia</td>
<td></td>
</tr>
<tr>
<td>Figure No.</td>
<td>Description</td>
<td>Page No.</td>
</tr>
<tr>
<td>-----------</td>
<td>-----------------------------------------------------------------------------</td>
<td>----------</td>
</tr>
<tr>
<td>69.</td>
<td>Geometry of the wing and loading distribution - <em>Larus dominicanus</em></td>
<td>117</td>
</tr>
<tr>
<td>70.</td>
<td>Estimated positions of insertion points</td>
<td>118</td>
</tr>
<tr>
<td>71.</td>
<td>Effect of extending the manus</td>
<td>118</td>
</tr>
<tr>
<td>72.</td>
<td>Effect of the alula</td>
<td>119</td>
</tr>
<tr>
<td>73.</td>
<td>Wing as a simple system</td>
<td>123</td>
</tr>
<tr>
<td>74.</td>
<td>Wing as a compound system</td>
<td>123</td>
</tr>
<tr>
<td>75.</td>
<td>Aerodynamic extension of manus</td>
<td>124</td>
</tr>
</tbody>
</table>
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table No.</th>
<th>Description</th>
<th>Page No.</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>Comparative dimension of six species</td>
<td>30</td>
</tr>
<tr>
<td>II</td>
<td>Moments on the wing - overall</td>
<td>51</td>
</tr>
<tr>
<td>III</td>
<td>Moments on the wing - elbow</td>
<td>53</td>
</tr>
<tr>
<td>IV</td>
<td>Moments on the wing - wrist</td>
<td>54</td>
</tr>
<tr>
<td>V</td>
<td>Moments on the wing - [first phalangeal joint; second phalangeal joint]</td>
<td>56</td>
</tr>
<tr>
<td>VI</td>
<td></td>
<td></td>
</tr>
<tr>
<td>VII</td>
<td>Details of loads etc - <em>Columbia livia</em></td>
<td>116</td>
</tr>
<tr>
<td>VIII</td>
<td>Details of loads etc - <em>Larus dominicanus</em></td>
<td>117</td>
</tr>
</tbody>
</table>
Chapter I

Introduction
CHAPTER ONE

1. INTRODUCTION.

1.1 General:

The wing movements of a bird, appearing to the cursory eye fairly simple, are in fact highly complicated and necessarily so if the flight requirements are to be satisfied. Whilst the anatomy of the wing has been extensively studied and there has been a large body of work done on bird flight, the latter has been unco-ordinated and little attempt made to correlate it with the former.

The object of the present work is to analyse the wing actions from observation and slow motion photography and to relate this to the structure and operating mechanisms. This required a detailed study of the form and arthrology of the structure and the myology of the mechanism.

Much of the information contained herein has been obtained from a study of the following species:-
Colomba livia

Hemiphaea novaeseelandiae

Anas superciliosa/platyrhynchus

Cygnus atratus

Larus novaehollandiae

Larus dominicanus

1.2 Review of the Literature

From the earliest times man has shown considerable interest in flight but the first known scientific investigation into its nature is believed to be that of Leonardo da Vinci (1452 - 1519). Considering his lack of what is considered today to be the most basic aerodynamic knowledge, his observations were remarkably acute. His sketches of the wings and suggested operating mechanisms for man-powered flight reveal that he had a good knowledge of the anatomy and movements of the wing. He was the first to note the figure eight movement of the wing tip, subsequently confirmed by Marey and others. White (1710 - 1793) in his book on the Natural History of Selbourne notes some of his observations of the different types of flight of various birds which, though shrewd, lack any aerodynamic insight.

In the middle of the 19th century investigations
and observations of a more rigorous nature began to appear. Hutton (1872) reports on observations of the flight of the Black-backed gull (*Larus dominicanus*) and compares the conclusions of Marey (1869) and the Duke of Argyll (1867) amongst others, with his own deductions. With an inherent appreciation of aerodynamics probably derived from experience in sail, he has analysed the motions very effectively. In particular he shows that turning is achieved by banking rather than by the complicated manoeuvres suggested by some of his contemporaries. Hutton (1869) also discussed the flight the the Albatross (presumably *Diomedia exulans*) and attempts to deduce the drag of the bird. Webb (1869) makes some comments on Hutton's paper but neither of them has appreciated the significance of the wind velocity gradient over the sea. This velocity gradient of the wind over the surface of the earth is noted by Headley (1895) and he discusses the dynamic soaring of a gull.

Much of this early work was an attempt to deduce from observation of birds the principles of aerodynamics. This was, of course, logical but presented very great difficulty. With the lack of high speed photographic apparatus it is extremely difficult to determine the configuration and attitude of the wing during flight,
and it is greatly to the credit of these workers that their deductions were reasonably correct in many cases.

Eiffel (1913) proceeded to investigate the behaviour of a number of aerofoil shapes in the wind tunnel and from these it was possible to deduce the aerodynamic principles involved. It is worthy of note that one of the shapes tested was designated "Bird's wing". A number of other investigations were made during this period, notably R. & M. Nos. 72, 110, 152.

From 1920 onwards the relationship between the knowledge gained of aerodynamics and the flight of birds began to be examined. Fullerton (1925) endeavoured to deduce the power expended by a bird in flight and a discussion followed with Gnosspeilus (1925). In the same year Walker tackled the problem of flapping flight of the Rook (Corvus frugilegus) on a mathematical basis and made the important point that the inner wing supplies lift during both the up and down strokes.

In 1929 Boel approached the problem from first principles and included in his work extensive feather trimming experiments. Large portions of the secondary feathers of the pigeon (Columba livia) may be removed without preventing flight, thus showing the paramount importance of the primaries. This seems to show that, although in the natural state, the inner wing supplies lift during both strokes, the manus can replace this
if necessary. He noted the separation of the primaries but in his discussion appears not to have appreciated that they form a cascade of aerofoils. This is not surprising as at that time little work had been done in the cascade wind tunnel. In considering the separated primaries it must be remembered that a properly designed cascade gives less turbulence, and, therefore, drag, than does a solid aerofoil for the same lift except possibly for low values of the latter. Again, the cascade may be made to produce a greater deflexion (and therefore greater lift) than the single. Excellent examples of cascades may be seen in wind tunnels where they are used to turn the air flow through a right angle with very little loss. Handley-Page (1921) experimented with multi-slotted wings but found their performance disappointing. Arguments concerning wing-tip vortices must be treated with caution since, for a finite wing, these are a necessary accompaniment of lift production.

It must be remembered that the primary feathers flex considerably under pressure and this is particularly well marked when there are large gaps between them. This means that the resultant force, while it may still be inclined forward, is no longer perpendicular to the Z axis of the wing. Thus considerable thrust may be supplied without producing undue lift. By this means the effort put into moving the manus contributes thrust without an unwanted amount of lift, most of the lift required being
supplied by the portions of the wing nearer the body.

Graham (1932) made some interesting comments on what he termed "Safety Devices in the Wings of Birds" and showed that air pressure alone could cause the feathers of the manus to open. He gives some very good sketches of wing shapes and their adaptation to different modes of flying. He notes the stalling of the inner wing of a Montago's Harrier (Circus pygargus) which apparently caused some confusion when the photograph first appeared. Lachman (1932) in his reply to Graham takes issue over the use of the alula. He maintains, correctly, that it is too short to act as a slot-forming aerofoil in the same way as that of Handley-Page and concludes that it is probably a useless vestigial appendage. In this latter it is believed he was wrong.

Aymar (1938) collected a large number of action photographs which show various flight attitudes in great detail and there is some information on flight and the origin of birds. Guidi (1938) produced a series of photographs of a pigeon in flight, the views being taken from the side, behind and above, and although they are not exactly synchronised, they are sufficiently close for reasonable correlation. Mangan (1938) also took high speed photographs and endeavoured to analyse the air movements by injecting tobacco smoke. Holst and Kuchemann (1942) discussed various aspects of aerial flight and deduced the Reynolds numbers for representative
birds and insects. They noted the important fact that the outer wing can give thrust on the upstroke as well as on the down, and that the negative lift due to this is balanced by increasing the inner wing lift.

Schufeldt (1890) and Gadow and Selenka (1891) are probably the best known pioneers of avian myology but were more concerned with anatomy than flight. Chamberlain (1943) produced a very good atlas of avian myology but Fisher (1946) considered not only the wing myology in detail but also described their actions. This was a valuable step forward, since a knowledge of the muscle actions is essential when analysing the wing movements. Berger and George (1966) have produced a good modern work on avian myology and have defined the nomenclature more systematically.

From 1948 onwards there has been an increasing volume of work on this subject being published. Storer produced a useful little book on the subject in this year and Brown published his first paper on the flight of birds. Saville (1950) successfully corrected the misconception concerning alternate flapping of the wings of the Swift (Chaetura pelagica). He also noted the shape required for a high speed wing and the specialised wrist joint of the Ruby-throated Humming Bird (Archilochus colubris). Maynard-Smith (1952) propounded that a bird in flight is inherently unstable. The case for this is well argued and convincing and does not appear to have been considered previously.
Berger (1954), Nair (1954) and Swinebroad (1954) all studied in detail the wing myology of certain birds. Berger was concerned with comparing the myology of three species of American cuckoos (*Geococcyx californianus*, *Crotophaga sulcirostris* and *Coccyzus erythrophthalmus*) a poor, intermediate and good flier respectively. Nair, dealing with *Psittacula kramori* and *Milvus migrans*, suggests that the duplication of Mm. extensor metacarpi radialis, flexor carpi ulnaris and extensor metacarpi ulnaris in the Milvus allows the parts to rest alternately thus easing fatigue during long flights. Swinebroad, comparing certain passerines (*Passer domesticus*, *Richmondena cardinalis*, *Zonotrichia albicollis* and *Melespiza melodia*) is concerned to note the innervation of the muscles and the relationship of this to the mode of flight.

Fisher (1957) discusses the mechanism of the radio-ulnar complex in connection with the extension of the manus and reported the effect on flight of various surgical modifications. These results confirm that aerodynamic forces play a large part in fixing the position of the manus. The alterations to the tendons and bones are of interest but it must be remembered that animal mechanisms are extremely adaptable and are able to compensate, to a large extent, for malformations.

Shostokova (1956) produced an interesting analysis of flight in *Laridae*. Some of the statements and deductions
are difficult to follow but this may be due to the translation rather than to fault on the part of the author. The statement that the wings move downwards and forward at an angle to the Y axis is not clear. From general observation it appears that the humerus moves very nearly in a plane with respect to the body and that the forward movement of the wing is confined to that part distal to the elbow.

Steinbacher (1960) compares the sterni of various types of birds and discusses dynamic soaring and flapping flight (including that of Humming Birds) on the basis of known aerodynamics. Newman (1958) and Pennycuick (1960) were both interested in the gliding and soaring flight, the former with Black Vultures (Coragyps atratus atratus) and the latter with Fulmar Petrels (Fulmarus glacialis). Raspet (1960) has some further remarks to add to his former paper (1950) on performance measurements of soaring birds using a glider in which to follow them. Berger and Göhde (1965) have shown, theoretically, that the albatross cannot make use of dynamic soaring at wind speeds below 40 m.p.h. unless it also extracts energy from the upward flowing air current at the face of the wave.

Pennycuick and Parker (1966) produced some information on the structural limitations of Pigeons' flight muscles and a symposium edited by Evans (1966) gives some figures for the strength of bone and tendinous
materials. Pennycuick (1967) measured the strength of fresh bones from a Pigeon's wing.

Meinertzhagen (1955) and Terres (1968), amongst others, have commented on the speed and altitude at which birds fly. Although average speeds quoted in the literature agree reasonably well, maximum speeds are by no means so certain.

From the foregoing brief outline two significant points emerge.

First, considerable work has been done on the anatomy of the wing and on various modes of flight. Little or no attempt has been made, so far as the author is aware, to consider the whole wing as a mechanical device. Observation of a wing movement may be misleading but if the joint structure, say, is studied in detail the question of whether a particular movement is physically possible may be determined. The effect of one muscle acting with another may produce quite a different movement from that caused by each separately.

The second point concerns the aerodynamic properties of a flexible feathered wing. Of these far too little is now known, probably because of the extreme difficulty of measurement.
1.3 **The Duties of the Wing During Flight.**

Besides acting as a simple supporting surface in the air the wing must be capable of providing thrust, stability and control, braking, and possibly act as a kind of parachute on occasions.

To reduce the energy required to a minimum, the efficiency, particularly when fulfilling the first three functions enumerated above, must be as high as possible. Precise data on the aerodynamic characteristics of the bird's wing is lacking but from observation and deduced load distribution (Pennycuick 1966, chapter 4 of the present work) it appears that a much greater efficiency and lift coefficient may be achieved by nature than by any aircraft or glider. This is a field in which very little investigation has been done but which, despite the technical difficulties, must be explored before the picture can be completed.

1.4 **An Outline Specification Covering the Duties.**

The following specification is presented in the form which would be used in engineering.

1.4.1 **Strength:**

The structure shall be capable of performing all duties with a sufficient margin of safety to survive all normal misadventures.
1.4.2. Flexibility:

The wing shall be provided with joints giving freedom of flexion and rotation to cover all configurations required in the simplest possible manner. Provision shall be made for varying the area and also for altering the aerofoil section of the wing.

1.4.3. Rigidity:

In certain positions, notably when fully extended, the structure shall maintain its shape with the minimum of muscular strain. The joints shall be provided with positive stops and locks sufficient to satisfy these requirements.

1.4.4. Shape:

The shape shall be such as to suit the habitat of the creature. Birds required to fly in confined spaces shall have short wide wings. Birds with a predominantly gliding or soaring habit shall have, in general, a longer wing. The aspect ratio shall be determined by the habitat, feeding pattern and type of soaring.

1.4.5. Weight and weight distribution:

The bone structure shall be as light as is compatible with adequate strength. The covering shall be smooth, light and renewable. The muscles shall be
concentrated, as far as possible, close to the body in order to keep down heat loss and to reduce the moment of inertia of the wing about the shoulder joint.

1.4.6 Actuating mechanism:

The muscles shall be so arranged that, whilst there is freedom for the several parts to move independently, there is sufficient interconnection for some movements to be semi-automatic. For example, contraction of M. triceps shall straighten the elbow and tend to extend the manus at the same time without, however, being directly connected to the latter.

1.4.7 General:

The whole wing shall be capable of folding close to the body when not in use and extension shall automatically smooth and align the covering.
Figure 1: Aerofoils definition and typical lift-drag curves.

\[ \alpha = \text{angle of attack} \]
\[ i = \text{angle of incidence} \]
\[ \psi = \text{camber angle} \]
\[ D = \text{drag force} \]
\[ L = \text{lift force} \]
\[ R = \text{resultant force} \]
a Camber line

b Pitching moment = R \times a

c Fig. 1

- Angle of attack

### List of Aerodynamic Terms

<table>
<thead>
<tr>
<th>Term</th>
<th>Description</th>
<th>Figure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aerofoil</td>
<td>An aerodynamic shape</td>
<td>Fig:1</td>
</tr>
<tr>
<td>Angle of attack</td>
<td>The angle between the air stream and the chord line</td>
<td>$\alpha$, Fig:1</td>
</tr>
<tr>
<td>Angle of incidence</td>
<td>The angle between the air stream and the tangent to the camber line at the leading edge</td>
<td>$\iota$, Fig:1</td>
</tr>
<tr>
<td>Aspect ratio</td>
<td>The ratio of wing length to mean chord ($\text{Span}^2/\text{area}$)</td>
<td></td>
</tr>
<tr>
<td>Axes</td>
<td>The reference axes are shown and the x-z plane is horizontal</td>
<td>Fig:2</td>
</tr>
<tr>
<td>Camber</td>
<td>The curvature of the aerofoil datum line</td>
<td></td>
</tr>
<tr>
<td>Camber angle</td>
<td>The angle between the tangents to the camber line at the leading and trailing edges</td>
<td>$\psi$, Fig:1</td>
</tr>
<tr>
<td>Camber line</td>
<td>The aerofoil datum line</td>
<td>Fig:1</td>
</tr>
<tr>
<td>Cascade</td>
<td>An arrangement of aerofoils in a manner shown in the diagram</td>
<td>Fig:4(a)</td>
</tr>
<tr>
<td>Chord</td>
<td>The length of the chord line</td>
<td>$C$, Fig:1</td>
</tr>
</tbody>
</table>
Chord line  
A line passing through the extreme points of the leading and trailing edges

Density (air)  
\( \rho \)

Dihedral  
The angle between the wings in the y-z plane

Drag  
The force on the aerofoil parallel to the direction of the undisturbed air flow  
\( = C_D \frac{1}{2} \rho V^2 S \)  
\( D, \) Fig:1

Drag coefficient  
\( C_D \)

Lift  
The force on the aerofoil normal to the direction of undisturbed air flow  
\( = C_L \frac{1}{2} \rho V^2 S \)  
\( L, \) Fig:1

Lift coefficient  
\( C_L \)

Pitching moment  
The moment of the resultant aerodynamic force about the quarter point

Fig:1

Quarter point  
A point on the chord line 25% of the chord from the leading edge

Fig:1

Reynolds number  
\( = \frac{\rho V C}{\mu} \)  
\( R, \)
Figure 2: Axes of reference

Figure 3: Air flow over aerofoils
a) showing streamlines
b) showing breakdown of flow over upper surface
c) highly cambered aerofoil at positive angle of attack and negative incidence
d) section of wing close to shoulder (*Columba livia*)

Figure 4: a) Cascade of aerofoils
b) Slot showing streamlines
Slot
The space between a small auxiliary aerofoil and the main aerofoil (e.g. the bastard wing and the main wing Fig:4(b)

Stall
The separation of the streamline flow from the upper surface of the aerofoil Fig:3(b)

Thrust
The force produced in a forward direction Fig:2

Velocity (ft./sec.) \( V \),
Viscosity \( \mu \),
Wing area \( S \),
Wing span (shoulder to tip) \( b \),

Note: The terms abduction and adduction will be used in the sense indicated in Fig:2.

1.6 A Note on Aerofoils.

For a cambered aerofoil as shown in Fig:1 the angle of attack becomes several degrees negative before the lift fails to zero and the angle of incidence is less than the angle of attack. With profiles such as (b) or (c), which are reflex aerofoils, there is little change in the pitching moment as the angle of attack changes, the maximum lift occurs at approximately \( 15^\circ \) and the minimum drag at approximately \( -1^\circ \).
As the angle of attack is increased the point of separation, that is the point at which the flow ceases to follow the surface closely, moves forward over the upper surface and the drag increases. The reflex curvature tends to keep this separation point nearer to the trailing edge.

The lift and drag curves in Fig:1 are based on those obtained by Eiffel (1913) for a nominal bird's wing and it is important that the maximum lift/drag ratio should be high in order to minimise power requirements. This maximum usually occurs at about 40° angle of attack. However, as is discussed below, the minimum power requirement is achieved when $C_{L}^{3/2}/C_D$ is a maximum.

There is one matter concerning aerofoils noted by Curry (1928) and Aymar (1936) which requires some comment. Aymar quotes Lilienthal's experiments with streamers on the underside of a cambered aerofoil during which it was noted that, contrary to expectation, those towards the leading edge were blown forward. The author has, unfortunately, been unable to check this particular reference but the details of the aerofoil and the angle of attack need to be stated before meaning can be attached to this phenomena.

For a cambered aerofoil the flow is, in general, that shown in Fig:3(a), provided that the angle of attack is not too great. If, however, the camber is very pronounced, towards the leading edge, as in Fig:3(c) or there is an
eminence on the underside Fig:3(d), reverse flow may occur in certain circumstances. Fig:3(c) shows a highly cambered aerofoil at a small angle of attack and, because of this large camber, the angle of incidence has a considerable negative value. In these circumstances the flow cannot follow the under surface and forms an eddy as shown which, in turn, gives a reverse flow near the surface and is accompanied by increased drag.

In Fig:3(d) an eddy is shown behind the ventral eminence and this shape corresponds to that of the pigeon's wing near the shoulder, Fig:27 section A.
CHAPTER II.

STRUCTURE.
Plate II

Wing skeletons

a) *Columba livia*

b) *Hemiphaga novaeseelandiae*

c) *Larus novaehollandiae*

d) *Larus dominicanus*

e) *Anus superciliosa/platyrhynchus*

f) *Cygnus atratus*
2. **STRUCTURE.**

2.1 **General:**

The structure of the bones and the general anatomy of the wing have been studied by many research workers and sufficient is known, therefore, to cover some of the requirements set out in the specification.

Pennycuick (1966) has shown that there is a large factor of safety in the strength of the bones and the muscle insertions and from recent work (Evans, 1966) it has been shown that tendon material (human) has a strength of about 6 kgf./mm$^2$ (8500 lbf./in$^2$).

The bones correspond to the spar or spars in an aircraft wing and the aerofoil shape is completed by the muscles, skin and feathers.

Because of this the whole structure is extremely flexible and both the camber and plan form may be readily altered to meet the requirements of the moment.

Since there are two schools of thought regarding the numbering of the digits a choice had to be made. The system used will be II, III and IV thus assuming that I has been incorporated in the extensor process of the carpometacarpus, (Fig:5).
Figure 6  a) Details of second phalangeal joint (*Columba*) Antero-Ventral view

Scale:  $\times 10$

b) Geometry of joint
Fig. 6
2.2 Arthrology:

While the arrangement of the bones has been well studied and the general form of the joints discussed, details of the articular surfaces appear to be lacking. Since the range of possible movements is prescribed by these articular surfaces it is necessary to consider them in detail not only as regards the general pattern but also the variations with flight habit.

In some cases the joints have been incorrectly described, notably the phalangeal joints. Chamberlain (1943) designates these as hinges but, as will be shown below, they have more the properties of ball and socket joints.

In order the better to appreciate the details of the joints, models of the bones of a pigeon's wing, ten times full size, were made. These were carved from wood and the study of the dimensions and shape necessary to do this proved of great value. The fronticepiece is a photograph of these models.

2.2.1 Phalanges:

The articular surfaces of the first and second phalanges of digit III are shown in Fig:6(a) which is an antero-ventral view of the phalanges of Columba. Posteriorly there is a partly toroidal condyle on phalanx 1, (A), over which fits the socket (B) in the proximal face of phalanx 2. The face (C) is conical in form, the axis of the cone lying in a
plane at right angles to the axis of the first phalanx. The geometry of the condyle is illustrated in Fig:6(b) and it consists essentially of part of a tore or anchor ring. This form of joint allows the second phalanx to rotate to some extent since the socket slides round the tore and, at the same time it is slightly raised or lowered due to the fact that the plane of the tore is inclined to the axis of the joint. The conical face not only guides this movement but prevents the phalanx from flexing forward. There is, however, sufficient flexibility in the anterior ligaments to allow posterior movement when subjected to an exterior force. The flexing produced by muscular action (chiefly by M interosseus palmaris) is slight and the flexing produced by external forces is a safety feature to prevent mechanical damage. From the above analysis it will be seen that the joint is not primarily a hinge. The socket B is more spherical than the condyle A and the difference is bridged by the joint cartilage.

Comparative Data:
Figure: 7  Second phalangeal joint (Larus novaehollandiae)
Antero-Ventral view

Figure: 8  Second phalangeal joint (Anas)

Figure: 9  Comparison between distal ends of first phalanges of (Cygnus) and (Anas). Dorsal view
    Scale x 10
Fig. 7

Gull (red bill)

Fig. 8

Duck

dorsal view

Swan

Duck

Fig. 9
Columba livia - The condyle (A, Fig:6(a)) is quite prominent and has a small radius in the plane of the bone. This latter enables considerable flexing to take place without greatly straining the anterior ligament. The angular movement possible is of the order of 10° - 15° although the exact amount is difficult to determine.

Hemiphaga novaeseelandiae - There is little difference, except in size, between this and Columba.

Anas superciliosa/platyrhynchos (Fig:8) - The condyle G is as prominent as in the pigeon but the posterior extension (Fig:9(b)) is considerably shorter.

Cygnus atratus - Similar to Anas but extension G is slightly longer (Fig:9(a)). The antero-ventral process E (Fig:6(a)) is more pronounced and the latter, in conjunction with the process F on phalanx 2, serves to limit the clockwise rotation at this joint. F and E lock in a far more positive manner than they do in the case of the pigeon.
Figure: 10  First phalangeal joint - *Columba*

Antero-Ventral view

A  insertion point of *M.abductor indicis*

B  Process with groove for tendon of *M.extensor indicis longus*

C  Antero-ventral prominence

D  Condyle for digit IV

Scale:  x 10
**Larus novaehollandiae** (Fig:7) - The condyle is much less pronounced and the face D is no longer conical. There is a slight depression mid-way between the dorsal and ventral edges on this face and rotary motion is severly restricted. As in *Columba* the posterior extension G is pronounced.

**Larus dominicanus** - This is almost the same as that of *Larus novaehollandiae*, the only difference of any note being that the antero-ventral process E is much more prominent.

2.2.2 **Carpometacarpus-phalangeal joint:**

Fig:10 is an antero-ventral view of the carpometacarpus and first phalanx of digit III of *Columba*, the phalanx being on the left. In Figs:11 - 16 inclusive (a) is the proximal face of phalanx 1,

(b) is the distal face of the carpometacarpus and (c) is the joint viewed in the direction of the arrow, phalanx to the left. The condyle and anterior surfaces for phalanx 1, digit III, are similar in form to the joint described above but there is the additional condyle, D Fig:10, for the phalanx of digit IV. The latter acts as a support for digit III since it is closely attached to it by a ligament.

Phalanx 1, digit III, is able to rotate slightly and
Figure: 11  First phalangeal joint - *Columba*

Figure: 12  First phalangeal joint - *Hemiphaga*

In both figures:-

(a) Proximal face of first phalanx  
(b) Distal face of carpometacarpus  
(c) Joint viewed in direction of arrow  

Scale: x 10
at the same time it moves up and down in a like manner to phalanx 2. Because of the close attachment of the first phalanges of digits III and IV flexing of the former can only be slight but its rotation is not appreciably restricted. Thus the phalanx of digit IV serves as a brace against flexing of digit III and it also helps to support the bases of some of the primaries.

Comparative Data:

*Columba livia* - The general form is illustrated in Fig:10, 11 and the condyle for digit IV is shown at D. The process A is for the insertion of *M.* abductor indicis while the tendon of *M.* extensor indicis longus runs in the groove at B.

*Hemiphaga novaeseelandiae* (Fig:12) - The form is very like that of *Columba livia* but the upper surface of the phalanx is flatter in the *Hemiphaga*. Also in the anterior view (c) the process A is not so pronounced.

*Anas superciliosa/platyrhynchos* (Fig:13) - The processes B and C are prominent and considerable rotation, accompanied by downward flexing is possible. The greater depth of the first phalanx compared with the distal end of the carpometacarpus is worthy of note, since this
Figure: 13  First phalangeal joint  -  Anas

Figure: 14  First phalangeal joint  -  Cygnus

Scale:  x 10
gives greater leverage to the ligaments and tendons and, therefore, greater control.

*Cygnus atratus* (Fig:14) - The process A is not as prominent as in *Anas* but is more square. Also the curvature of the distal end of the carpometacarpus is less pronounced (*J, Fig:14*) and so, while appreciable rotation is possible, it is not accompanied by so great a downward flexion as in *Anas*.

*Larus novaehollandiae* (Fig:15) - The general shape differs markedly from the four types mentioned above. Process A is increased in size and prominence with two distinct lobes, the more dorsad serving as the insertion point for *M.extensor digitorum communis*. It also projects considerably below the joint thus giving greater leverage to *M.abductor indicis*. B is prominent but the groove for the tendon of *M.interosseus dorsalis* is not clearly marked. C is extended considerably in the antero-ventral sense and locks with A at the limit of rotation in the supinating sense.

*Larus dominicanus* (Fig:16) - Similar to *Larus novaehollandiae* in many respects but A does not lock with C and the face of the carpometacarpus is narrower.
Figure: 15  First phalangeal joint - *Larus novaehollandiae*

Figure: 16  First phalangeal joint - *Larus dominicanus*

Scale:  x 10
Figure: 17 Wrist joint - *Columba*

A, B Attachment points of intercarpal cartilage

C, D Bearing faces for carpometacarpus

E Bearing face of carpometacarpus

F, G Attachment points for ulnare carpometacarpal ligament

H Groove for tendon of M. extensor metacarpi ulnaris

J Groove for tendons of M.M. extensor indicis longus and extensor digitorum communis

K Extensor process of carpometacarpus

Scale: x 10
Fig. 17

Os radale

Os ulnare
2.2.3 Wrist:
The components of the wrist joint *Columba* are shown in Fig:17, the upper figure being a view from above and in front and the lower viewed from below and behind. The assembled joint is shown in Fig:18. As will be appreciated, there are two sets of articular surfaces, namely, that between the radius and ulna and the linked carpals, and that between the carpals and the carpometacarpus. The two carpals, the os radiale and os ulnare, are joined between A and B (Fig:17) by cartilage so that they move as a unit over the distal face of the ulna. This movement is not great and is brought about by the slight adjustment of the radius which takes place as the elbow is flexed or extended. There is no locking of the manus in the fully flexed position by the projection of the radius, as is sometimes stated.

In the extended position the root of the extensor process, K, of the metacarpus tends to lock down on the antero-distal edge of the os radiale, aided by *M.obliquus*, so that the joint attains some degree of rigidity.

The metacarpal face, E, rides on the curved face C of the os radiale and the process D of the os ulnare as well as on the articular cartilage joining them. As the manus is flexed the metacarpal face slides along the os radiale in the dorsal
Figure: 18  Wrist joint -  

Scale:  x 4

Insets - Left, extended wing
Right, folded wing
(From X-ray photographs)

K  ligament
L  tendon of M.flexor carpi ulnaris

Scale:  f.s.
Fig. 18

Dorsal

Posterior

K

L
direction thus tending to bring the outer wing clear of the ulna during folding, the latter being a movement of approximately $135^\circ$ in the plane of the wing. When slightly flexed the joint is free to allow a wide range of movement to the manus. It may be rotated about its axis and also flexed downwards so that, at the end of the down stroke in fully flapping flight, it may reach a position such that the plane of the outer wing is vertical and parallel to the $x$-$y$ plane. Flexing and rotation at the elbow joint aids in attaining this latter position.

Between the os ulnare at $F$ and the process $G$ of the carpometacarpus there is a ligament ($K$, Fig:18) which allows some relative lateral movement of the two parts as well as the rotation required during flexing.

The os ulnare acts as a powerful reinforcement against upward flexing of the manus. The tendon of $M.$ flexor carpi ulnaris ($L$, Fig:18) braces the ulnare and this force is transferred to the manus through the ligament $K$. In addition this linkage, in conjunction with other muscles, may be used to lower, flex and supinate the manus.

Comparatively, there are no very marked differences, other than in size, between the six species under investigation in this work. There are
Figure: 19  Elbow joint - Columba

Scale: x 5

Insets - Left, extended wing
Right, folded wing
(From X-ray photographs)

Scale: f.s.
minor differences in shape and proportions, the most notable being the groove in, and the projection of the process G (Fig:17). Part of the latter acts as a pulley for the tendon of M. flexor digitorum profundus while the tendon of M. flexor sublimus runs posteriorly round the os ulnare. The insets at the top of Fig:18 show, on the left, the position with the wing extended and, on the right, with the wing folded. These drawings are taken from X-ray photographs.

2.2.4 Elbow:
The elbow is, in general, a hinge joint but there is some degree of freedom of rotation under certain circumstances. The inferior condyle (A, Fig:19) of the humerus forms a ball and socket joint with the ulna (B) and the olecranon process, C, serves as a stop to limit the extensor movement.

The superior condyle, D, has an elongated form and on this the proximal end of the radius, E, rides. This elongated form causes the forearm to drop below the humerus when the wing is folded.

This joint must withstand considerable bending and twisting loads and, consequently, is deep and wide with strong ligaments.

In the species discussed there is little variation except in size. The insets at the bottom of
Fig:19 are the elbow positions corresponding with the wrist positions of Fig:18.

2.3 Proportions:

Apart from difference in relative lengths of the bones and in the joint details the most notable variation is in the ulna-radius relationship. (Plate II).

In the cases of the pigeons and duck both the radius and ulna are stout bones and there is considerable curvature of the latter. The opening between them is approximately 8% of the length of the ulna whereas in the case of Larus novaehollandiae it is less than 5%.

The chief muscles operating the manus, apart from M.extensor metacarpi radialis, are accommodated in this space and the wide opening developed in the strongly flapping species allows for the heavy muscles required.

Table I below shows the comparative lengths of the main wing bones on the basis of the humerus being unity. Dimension a is the maximum distance between the radius and ulna and b is the maximum width of the opening in the carpometacarpus.
## TABLE I.

<table>
<thead>
<tr>
<th>SPECIES.</th>
<th>ULNA</th>
<th>CARPUS</th>
<th>PH.1</th>
<th>PH.2</th>
<th>PH.3</th>
<th>a</th>
<th>b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Columba livia (6)</td>
<td>1.15</td>
<td>0.75</td>
<td>0.37</td>
<td>0.43</td>
<td>-</td>
<td>0.088</td>
<td>0.066</td>
</tr>
<tr>
<td>Hemiphaga novaeseelandiae</td>
<td>1.11</td>
<td>0.62</td>
<td>0.302</td>
<td>0.26</td>
<td>-</td>
<td>0.11</td>
<td>0.057</td>
</tr>
<tr>
<td>Anas superciliosa (3)</td>
<td>0.84</td>
<td>0.6</td>
<td>0.23</td>
<td>0.19</td>
<td>0.04</td>
<td>0.062</td>
<td>0.023</td>
</tr>
<tr>
<td>Cygnus atratus (3)</td>
<td>0.95</td>
<td>0.46</td>
<td>0.19</td>
<td>0.14</td>
<td>0.04</td>
<td>0.033</td>
<td>0.01</td>
</tr>
<tr>
<td>Larus novaehollandiae (4)</td>
<td>1.12</td>
<td>0.609</td>
<td>0.311</td>
<td>0.275</td>
<td>-</td>
<td>0.053</td>
<td>0.028</td>
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<tr>
<td>Larus dominicanus (3)</td>
<td>1.12</td>
<td>0.56</td>
<td>0.27</td>
<td>0.023</td>
<td>-</td>
<td>0.057</td>
<td>0.026</td>
</tr>
</tbody>
</table>

**NOTE:** The above must not be regarded as a final and conclusive average as the number of samples (figures in brackets) is not large. They are quoted only to indicate tendencies.
CHAPTER III.

MYOLOGY.
3. MYOLOGY.

3.1 General:

 Whilst the main muscles appear in all flying species, the proportions vary considerably with both the wing size and mode of flight. A muscle may appear not to occur in certain species but at least in some cases, it may be present with a difference of origin or insertion which makes identification difficult. As an example, M. flexor digitorum sublimus is described by Berger (1954) in three genera of American cuckoos and has been identified by him, with a different insertion, in the pigeon. It has, however, been described elsewhere as the pars anterior of M. flexor carpi ulnaris and it cannot be identified with any of the muscles listed by Chamberlain. Again, M. flexor carpi ulnaris is a single muscle in the pigeon but in Cygnus atratus there is, in addition, a strong tendinous strap running between the same points and having a small pennate muscle at its distal end, this muscle arises on the distal end of the ulna.

 The muscles and tendons serve two purposes in that they position the parts of the wing as required and also may act as bracings to resist the aerodynamic forces developed during flight. For instance the tendon of M. tensor patagii longus forms the leading edge support for the inner wing and keeps this reasonably taut when the elbow is partly flexed.
The magnitude and type of loading imposed on the joints will be discussed in a later chapter. Suffice it to note here that the precise location of the points of origin and insertion and the path taken by the tendons are governed by the two requirements above mentioned and their relative importance.

In discussing the myology it is perhaps unfortunate, as stated in the introduction, that a standard nomenclature has not been adopted. From the point of view of this work a system based on function and origin would have been more applicable and the anomaly of a muscle being designated flexor when in fact it acts as an extensor would have been avoided.

Since there are a number of cases where muscles have several different names the system adopted here is based on that given by Berger and George (1966).

In the following list of muscles the points of origin and insertion are given for the sake of completeness although they are, of course, very well documented in the literature. During the dissections, particular care was taken to note as exactly as possible the route followed by the tendons and the points of insertion.
Figure: 20 Muscle runs

1 M. extensor indicis longus
2 M. interosseus palmaris
3 M. interosseus dorsalis
4 M. flexor digitorum profundus
5 M. extensor digitorum communis
6 M. flexor digiti IV
7 M. abductor indicis
8 M. flexor metacarpi posterior
9 M. extensor metacarpi ulnaris
10 M. adductor pollicis
11 M. abductor pollicis
12 M. flexor pollicis
13 M. extensor pollicis brevis
14 M. extensor pollicis longus
15 M. extensor metacarpi radialis
16 M. flexor obliquus
17 M. flexor carpi ulnaris
18 M. flexor digitorum sublimus
19 M. supinator brevis
20 M. pronator profundus
21 M. pronator superficialis
3.2 **List of muscles:**

The muscles are numbered approximately in their order of insertion beginning at the distal end of digit III. Since the movement of the wing in flight is being considered the origin, insertion and run, or path, followed by the tendon is more important than particulars of the muscle belly.

The list of muscles, with their numbers, is given below and the general arrangement shown in Fig: 20.

**DORSAL**

1. M.extensor indicis longus
3. M.interosseus dorsalis
5. M.extensor digitorum communis
6. M.flexor digiti IV
8. M.flexor metacarpi posterior
9. M.extensor metacarpi ulnaris
13. M.extensor pollicis brevis
14. M.extensor pollicis longus
15. M.extensor metacarpi radialis

**VENTRAL**

2. M.interosseus palmaris
4. M.flexor digitorum profundus
7. M.abductor indicis
10. M.adductor pollicis
11. M.abductor pollicis
12. M.flexor pollicis
Figure: 21 Manus and muscles - *Columba livia*

Figure: 22 Manus and muscles - *Hemiphaga*

1. M. extensor indicis longus
2. M. interosseus palmaris
3. M. interosseus dorsalis
4. M. flexor digitorum profundus
5. M. extensor digitorum communis
6. M. flexor digiti IV
7. M. abductor indicis
8. M. flexor metacarpi posterior
9. M. extensor metacarpi ulnaris
10. M. adductor pollicis
11. M. abductor pollicis
12. M. flexor pollicis
13. M. extensor pollicis brevis
14. M. extensor pollicis longus
15. M. extensor metacarpi radialis
16. M. flexor digitorum sublimus
Figure: 23  Manus and muscles - *Anas*

Figure: 24  Manus and muscles - *Hemiphaga*

1  M.extensor indicis longus
2  M.interosseus palmaris
3  M.interossous dorsalis
4  M.flexor digitorum profundus
5  M.extensor digitorum communis
18 M.flexor digitorum sublimus
Figure: 25 Manus and muscles - *Larus novaehollandiae*

1. M.extensor indicis longus
2. M.flexor digitorum profundus
3. M.extensor digitorum communis
4. M.flexor digitorum sublimus
Figure: 26  Tendons at wrist

1  M. extensor indicis longus
4  M. flexor digitorum profundus
5  M. extensor digitorum communis
9  M. extensor metacarpi ulnaris
14 M. extensor pollicis longus
15 M. extensor metacarpi radialis
16 M. flexor obliquis
17 M. flexor carpi ulnaris
18 M. flexor digitorum sublimus

T.p.l. M. tensor patagii longus
16. M. flexor obliquus
17. M. flexor carpi ulnaris
18. M. flexor digitorum sublimus
19. M. supinator brevis
20. M. pronator profundus
21. M. pronator superficialis

Figs: 21 - 25 represent dorsal, anterior and ventral views of the manus skeleton of five species in the order
Columba livia;
Hemiphaga novaeseelandiae;
Anas superciliosa;
Cygnus atratus;
Larus novaehollandiae.
Larus dominicanus being almost the same as Larus novaehollandiae, is not drawn separately. Fig:26 illustrates the runs of the tendons round the wrist.

M. extensor indicis longus (1)

The origin is on the posterior surface of the radius and the insertion on the extensor process of the second phalanx of digit III.

Run of tendon: After passing round the distal end of the ulna the tendon passes under that of M. extensor digitorum communis, along the dorsal surface of the carpometacarpus, tending anterior towards the distal end,
and crossing over the tendon of M.extensor digitorum communis. It then passes along the anterior face of phalanx 1 digit III to insert on the extensor process of phalanx 2. In Columba, Larus novaehollandiae and Larus dominicanus there is little difference except that in Columba there is a sesamoid bone at the first phalangeal joint. Hemiphaga has a variation in that a small branch splits off near the base of the pollex and inserts on phalanx 1, digit III close to the insertion of M.abductor indicis. In Anas and Cygnus, after insertion on phalanx 2 the tendon continues distad to insert of phalanx 3.

**Action:**

Besides bracing digit III forward the muscle tends to supinate phalanx 2 to a greater or lesser degree in all but Anas. This muscle will restrict flexing of the digit when the angle of attack is small or negative.

M.interosseus palmaris (2)

The origin is on the facing surfaces of the bones bounding the intermetacarpal space on the ventral
side and the insertion is on the post-ventral edge of phalanx 2 distal to the joint.

**Run of tendon:** Dorsad over the base of digit IV and along the posterior dorsal edge of phalanx 1, digit III. In *Anas* and *Cygnus* the tendon continues, after insertion on phalanx 2 to an insertion on phalanx 3.

**Action:** Draws phalanx 2 (and 3 in *Anas* and *Cygnus*) posteriorly. In conjunction with *M.flexor digitorum profundus*, when the latter is contracted, it causes a slight pronation of the distal phalanx or phalanges. It will help to brace the phalanx when there is a forward force produced during the up stroke of the wing or at high angles of attack.

*M.interosseus dorsalis* (3)

The origin is superficial to *M.interosseus palmaris* and inserts on post-dorsal corner of phalanx 2.

**Run of tendon:** In the groove in the posterior edge of the dorsal ridge of phalanx 1 and continues distad under the posterior lip of this ridge. There is little difference in the six species.

**Action:** Except in *Anas* and *Cygnus* the muscle
tends to supinate the distal phalanx, particularly in conjunction with M. flexor digitorum profundus. In Anas and Cygnus the tendency is to pronate in conjunction with M. extensor indicis longus. This muscle helps to brace the distal phalanx against down loads on the first primary.

*M. flexor digitorum profundus* (4)

This is the medialis extensor digiti muscle of Chamberlain and, in view of its action, extensor is a better name than flexor.

The origin is on the proximal ventral surface of the ulna and the insertion on the antero-ventral process of phalanx 2.

**Run of tendon:** The tendon runs round the ventral process of the carpometacarpus, medially along metacarpal III and ventral to the anterior ridge of phalanx 1, digit III in all six species. In Anas and Cygnus there is a continuation, after the insertion on phalanx 2, to the distal phalanx.

**Action:** Extends digit III and pronates phalanx 2. The pronation effect is small in Anas and Cygnus. In addition to the
combined action in conjunction with other muscles noted above this muscle acts with M. extensor indicis longus in bracing the digit against backward bending in the plane of the hand and against upward flexing due to loading on the primaries.

M. extensor digitorum communis (5)

This has its origin on the lateral epicondyle of the humerus and inserts (i) on the proximal dorsal edge of the pollex close to the joint and (ii) on the proximal end of phalanx 1, digit III. The point of insertion on phalanx 1 varies considerably with the species.

Run of tendon: Round the dorsal epicondylar eminence on the distal end of the ulna and distad along the dorsal face of the carpometacarpus and near the pollex a branch tendon runs off to insert on base of the post dorsal edge of the latter. Both tendons are superior to that of M. extensor indicis longus at this point. In Columba, at the distal end of metacarpal III the tendon turns posterior, underneath the tendon of M. extensor indicis longus, to insert
posteriorly on phalanx 1, digit III. In the other five species the tendon turns more anteriorly.

**Action:** Causes pronation of phalanx 1, digit III in *Columba* and, supination in the other cases. It also braces digit III against pronation during the up stroke of *Columba*. The branch to the pollex adducts the latter and may cause some supination.

*M. flexor digitorum IV* (6)

The origin is on the posterior face of metacarpal IV and the insertion on the posterior edge of digit IV. The action is to flex digit IV (or to brace it against forward forces) and with it phalanx 1, digit III, because of the close attachment of the distal end of the former to the latter. There is little variation between the species and they are therefore not listed separately.

*M. abductor indicis* (7)

Originates on the antero-ventral surface of metacarpal III and inserts on the anterior process of phalanx 1 digit III. The action is to extend and brace forward phalanx 1 digit III and to pronate slightly. Apart from the fact that this muscle is
very small in *Larus novaeseelandiae* there is little difference between species.

**M. flexor metacarpi posterior** (8)

The origin is on the dorsal side of the ulna towards the distal end and the main insertion on the posterior surface of metacarpal IV. There is also an insertion in the fascia at the base of the proximal primaries. Again, there is little difference between the species and the action is to flex or brace the manus. If flexing be prevented by the extensor muscles it will tend to open the primaries and may have a slight pronating effect.

**M. extensor metacarpi ulnaris** (9) (M. flexor metacarpi)

The origin is on the lateral epicondyle *radialis* of the humerus. In some cases there is an aponeurotic connection to the dorso-proximal end of the ulna. The tendon inserts on the posterior surface of metacarpal III.

There is considerable confusion in the naming of this muscle and the above is that adopted by Berger (1966).

**Run of tendon:** Round the dorsal epicondylar eminence on the distal end of the ulna posterior to the tendon of *M. extensor digitorum communis* and passes
dorso-ventrally to insert on the posterior surface of metacarpal III.

**Action:**
Causes pronation of the manus if the latter be held extended and braces it against downward loads. As a secondary effect it may cause flexion of the manus.

**M.adductor pollicis** (10)
Originates on the anterior surface of metacarpal III close to metacarpal II and inserts on the posterior surface of the pollex. It adducts the alula and closes the slot and is similar in all the species.

**M.abductor pollicis** (11)
The origin is on the tendon of insertion of M.extensor metacarpi radialis and inserts on the antero-ventral surface of the pollex. It abducts the alula and braces it anteriorly. The muscle varies somewhat in detail from species to species but the general arrangement is similar.

**M.flexor pollicis** (12)
The origin is at the base of the carpus and on the sheath surrounding M.flexor digitorum profundus and the insertion is on the postero-ventral corner of the pollex. This muscle tends to adduct the pollex and also acts as a brace against upward movement when the slot is open.
M. extensor pollicis brevis (13)

Arises on metacarpals II and III and inserts antero-dorsally on the base of the pollex. It abducts the pollex and, if M. flexor pollicis be relaxed, tends to raise it.

M. extensor pollicis longus (14)

The origin is two-fold, one being on the proximal ventral surface of the ulna and the other in a similar position on the radius. The insertion is on the extensor process of the carpometacarpus close to the tendon of M. extensor metacarpi radialis.

Run of tendon: Over the distal end of the radius in a shallow groove to a wide insertion on the extensor process of the carpometacarpus.

Action: Extends the manus when the elbow is flexed.

M. extensor metacarpi radialis (15)

The origin is on the lateral ectepicondylar process of the humerus and the insertion on the extensor process of the carpometacarpus.

Run of tendon: Adjacent to tendon of M. extensor pollicis longus over the distal end of the radius.
**Action:** A powerful extensor of the manus. Because the origin is on the humerus some distance from the hinge point of the elbow, straightening of the latter places the muscle in tension and automatically extends the manus.

**M. extensor obliquus** (16)

This muscle is variously known as M.ulnometacarpalis ventralis and M.flexor carpi ulnaris brevis.

The origin is on the ventral surface of the ulna towards the distal end and the insertion on the dorsal surface of the carpometacarpus close to the root of the extensor process. The tendon runs obliquely upwards over the face of the os radiale and the muscle exerts a strong pronating force on the manus. With the wing fully extended the wrist joint will be held in a comparatively rigid state by the pull of this tendon and it will resist supination when the load on the manus is downward.

**M.flexor carpi ulnaris** (17)

The origin is on the medial epicondyle of the humerus and the insertion on the proximal end of the os ulnare. The muscle and tendon lie on the ventral face of the ulna (see Fig:20,anterior) and therefore
tends to prevent upward bending at the elbow.

Contraction of the muscle flexes the manus through inward movement of the ulnare. If, however, the manus is braced by the extensor muscles there will be a supinating force when M.flexor carpi ulnaris is contracted.

**M.flexor digitorum sublimus** (18)

Also known as M.flexor digitorum superficialis.

As noted in paragraph 3.1 above, there is considerable variation in this muscle, more particularly in the insertion. The origin is on the medial epicondyle of the humerus.

**Run of tendon:** In *Columba* and *Hemiphaga* the tendon divides into a number of small branches. One passes round the base of the os ulnare into the manus where it fuses into the fascia on the base of some of the primaries. Another branch leads into the fascia surrounding the base of the pollex.

In *Hemiphaga* one branch continues parallel to the tendon of M.flexor digitorum profundus and fuses with it near the first phalangeal joint.

In the other four species a single tendon runs round the base of the os ulnare and then follows that of
M. flexor digitorum profundus to insert on phalanx 2, digit III adjacent to the insertion of the latter. In Anas there is a small insertion on the fascia surrounding the first phalangeal joint.

**M. supinator brevis** (19)

The origin is on the humerus adjacent to the origin of M. extensor digitorum communis and the insertion is on the anterior surface of the radius. This muscle is able to apply a considerable twisting moment to the radius thereby supinating the wrist. It is also of extreme importance during the down stroke as it resists the pronating moment of the aerodynamic forces on the wing distal to the elbow.

**M. pronator profundus (longus)** (20)

The origin is on the medial epicondyle of the humerus adjacent to the origin of M. flexor digitorum sublimus and the insertion on the post-ventral surface of the radius. Pronates the fore-arm and resists the supinating moment due to aerodynamic forces during the up stroke.

**M. pronator superficialis (brevis)** (21)

Arises on the epicondylar eminence proximal to the origin of M. pronator profundus and inserts on the
antero-ventral surface of the radius. Pronates the fore-arm.

The relative positions of insertion of the two pronator muscles vary somewhat in different species but their actions are the same. It will be noted from a study of Fig:20 that these muscles brace the fore-arm against upward bending in addition to the function mentioned above.
CHAPTER IV.

GEOMETRY and FORCES.
CHAPTER FOUR.

4. GEOMETRY AND FORCES.

4.1 General.

Since the wing shape varies so much with the species it is not easy to make general statements about the geometry. However there are some approximations which may be applied to particular groups.

In strongly flapping birds the manus is considerably longer than the inner wing and the distance from the wrist to the end of the distal phalanx of digit III is considerably less than half the length of the manus. In Columba livia and Hemiphaga novaeseelandiae the proportions are similar and in the former one sample gives:

- manus/inner wing 3.5
- manus/hand bones 3.2

For Larus dominicanus the ratio of manus to inner wing is considerably less while the ratio of the manus to the hand bones is not very different:

- manus/inner wing 1.75
- manus/hand bones 3.0

A general comparison of the skeletons of the six species is shown in Plate II. It must be borne in mind, however, that these are photographs of dry bones reconstructed and are not, therefore, exactly as they would be in nature.
Figure: 27  Wing and Axes  -  *Columba livia*

Wing sections

Resultant centre of pressure  thus  ©
Figure: 28  Wing and Axes - *Larus dominicanus*

Resultant centre of pressure thus ©
A particular point is that in the natural state, the angle between the humerus and the fore-arm is more acute in the strongly flapping species.

4.2 **Geometry.**

Fig:27 shows the extended wing of *Columba livia* 5/8ths full size and Fig:28 the extended wing of *Larus dominicanus* 1/3rd full size. Both figures were constructed from tracings of the outline and X-ray photographs.

Fig:27 also shows the approximate cross section of the wing at various points. These were obtained by investing a deep-frozen wing in plaster-of-paris and sawing it into strips when thoroughly set. From the time of the initial set of the plaster until cutting took place the block was kept frozen.

The main axis of reference, Z, is chosen to pass through the centre of the condyle on the head of the humerus, point 0, and the extreme tip of the wing. The X axis is at right angles to Z through 0 and the section planes are parallel to XOX. Z1 passes through 0 and the centre of the elbow joint, Z2, through the centres of the elbow and wrist joints and Z3 through the centre of the wrist joint and the tip of the distal phalanx of digit III.

The subsidiary axes Z1, Z2 and Z3 are chosen in order to evaluate the moments at the wrist and elbow. Since the
Figure: 29  Loading diagrams
Fig. 29

(a) Columba livia

(b) Larus novaeseelandiae
wing is assumed to be fixed these moments will give a
measure of the forces required to maintain position and
shape.

4.3 Loading.

There is no known method at present for measuring
the forces on a bird's wing during flight. All that is
definite is the total weight and the wing area and even
the latter can only be obtained by assuming a particular
extension. For this reason a hypothetical span-wise loading
has been constructed (Fig:29) based on the meagre information
available. From this the moments and joint loading may be
calculated and these are probably a reasonable approximation
to the actual values.

The conditions chosen are those for the bird gliding
in still air at a constant speed of 30 m.p.h. with the wings
rigid and parallel to the Z axis of Fig:2. The curves
chosen are shown in Fig:29 and, apart from some minor
adjustments made in order to smooth them, and adjust the
position of the centre of pressure, are as originally
sketched by eye. It has been assumed that each wing
supports half the weight of the bird, which it is believed,
results in a higher loading than will occur in practice.
The reason for the latter statement being that some lift
may be expected from the body and tail, even when this
latter is closed.
The three considerations governing the shape of the curve are:

i) The centre of lift (CP) will be as close to the body as possible in order to reduce the load on the pectoral muscles, which must carry the body weight.

ii) The primaries show no signs of bending which indicates that the load on them is small.

iii) The lift coefficient, $C_L$, calculated from the loading, must not be unrealistically large at any point.

The first point is obvious and is consistent with the general provisions of nature whereby any normal action is performed with the minimum of effort.

The second point follows from the first and confirmed by photographs and observation.

The third point constitutes a check. While it seems probable that the lift coefficients of birds' wings are considerably higher than those of normal man-made aerofoils they could not be expected to have a maximum much over 3, (Pennycuick 1966) if indeed this figure could be reached.

The deduced angles of attack vary from $-2.5^\circ$ at the tip to $10.5^\circ$ half way between the wrist and elbow in the case
of *Columba* and from $-2.5^\circ$ to $3.9^\circ$ near the elbow in the case of *Larus dominicanus*.

Appendix I gives the details of the calculations, suffice it here to tabulate the main results. In Table II the moments $M(Z)$, $M(Z_1)$, $M(Z_2)$, and $M(Z_3)$ are considered to be positive if they tend to pronate the wing.

The following table gives the principal moments in units of grams force x centimetres, (gf.cm.) since this is consistent with engineering practice. It may be noted that, by measurement, the supinators of the human arm are able to apply a moment of about 100,000 of gf.cm.

**TABLE II.**

<table>
<thead>
<tr>
<th></th>
<th>COLUMBA</th>
<th>LARUS DOMINICANUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of wing cm.</td>
<td>30</td>
<td>62.5</td>
</tr>
<tr>
<td>Area of wing cm.</td>
<td>262</td>
<td>757</td>
</tr>
<tr>
<td>Total load g.</td>
<td>150</td>
<td>371</td>
</tr>
<tr>
<td>$x$ cm.</td>
<td>6.5</td>
<td>14.5</td>
</tr>
<tr>
<td>$z$ cm.</td>
<td>0.57</td>
<td>0.85</td>
</tr>
<tr>
<td>$C_L$ (average)</td>
<td>1.16</td>
<td>0.99</td>
</tr>
<tr>
<td>$M(X)$ gf.cm.</td>
<td>968</td>
<td>5358</td>
</tr>
<tr>
<td>$M(X_1)$ gf.cm.</td>
<td>420 (0.43)</td>
<td>1735 (0.32)</td>
</tr>
<tr>
<td>$M(Z)$ gf.cm.</td>
<td>-35.7 (0.04)</td>
<td>-318 (0.06)</td>
</tr>
<tr>
<td>$M(Z_1)$ gf.cm.</td>
<td>-282 (0.29)</td>
<td></td>
</tr>
<tr>
<td>$M(Z_2)$ gf.cm.</td>
<td>294 (0.30)</td>
<td>400 (0.07)</td>
</tr>
<tr>
<td>$M(Z_3)$ gf.cm.</td>
<td>114 (0.12)</td>
<td>161 (0.03)</td>
</tr>
</tbody>
</table>
In the above table, $M(X)$ is the total moment at the shoulder about $XX$ and $M(X_1)$ the moment at the elbow about an axis parallel to $XX$. The values of $x$ and $z$ are the distances of the resultant centre of pressure, $CP$, from the $X$ and $Z$ axes respectively. In *Larus dominicanus* the $OZ$ and $OZ_1$ axes coincide, hence the single value for $M(Z)$ and $M(Z_1)$. The figures in brackets express the moments as a fraction of $M(X)$.

The wing is divided into strips for calculating the moments and the load is assumed to be applied at the quarter point which, as pointed out above, is reasonable for this type of aerofoil. This assumption is only likely to be appreciably in error near the wing tip where the angle of attack is small or negative and the camber slight.

4.4 **Forces.**

4.4.1 **Elbow:**

The elbow is considered as a hinge joint of effective depth $d$ between the upper and lower bearings (Fig:30). Of the forces on the lower bearing Fig:31 $P(Z_1)$ and $P(X_1)$ are the pulls due to $M(Z_1)$ and $M(X_1)$ respectively and whilst $P(R)$ is the resultant pull $P(S)$ is the shear force due to the total load outboard of the joint and is the force tending to slide the forearm upwards with respect to the humerus. $\theta$ is the angle between $Z_1$ and $Z_2$ and $\alpha$ the angle the resultant makes with $Z_1$. 
Figure: 30  Hinge joint

Figure: 31  Forces on elbow joint (a) *Columba*  
(b) *Larus*

Figure: 32  Forces on wrist joint (a) *Columba*  
(b) *Larus*
TABLE III

<table>
<thead>
<tr>
<th></th>
<th>gf cm.</th>
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<th></th>
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<tbody>
<tr>
<td>M(Z1)</td>
<td>-282</td>
<td>-318</td>
<td></td>
</tr>
<tr>
<td>M(X1)</td>
<td>420</td>
<td>1735</td>
<td></td>
</tr>
<tr>
<td>θ</td>
<td>104°</td>
<td>145°</td>
<td></td>
</tr>
<tr>
<td>d</td>
<td>0.9</td>
<td>1.7</td>
<td></td>
</tr>
<tr>
<td>P(Z1)</td>
<td>312</td>
<td>186</td>
<td></td>
</tr>
<tr>
<td>P(X1)</td>
<td>466</td>
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</tr>
<tr>
<td>P(R)</td>
<td>561</td>
<td>1036</td>
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<tr>
<td>P(S)</td>
<td>97</td>
<td>164</td>
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<tr>
<td>α</td>
<td>32°</td>
<td>10°</td>
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</tbody>
</table>

In Fig:31 the forces are shown and (a) refers to *Columba* and (b) to *Larus dominicanus*.

The forces are resisted by the ligaments assisted by the muscles arising on the ventral surface of the humerus.

4.4.2 Forearm:

The forearm is subjected to a considerable positive moment, M(Z2) and is unable to obtain any appreciable support for this from the elbow joint. The major portion of the opposing moment must be supplied by M. supinator. Some assistance may be given by M.flexor carpi ulnaris and possible, in a minor degree, by the ventral colateral ligament (Fig:33).

During the up stroke of the wing when flapping, the moment on the forearm is reversed and must be opposed by the pronator muscles (M.M.pronator profundus et superficialis).
Figure: 33 Ventral collateral ligament of elbow

Figure: 34 Medial ligaments of wrist
ulno ulnare and ulnare
carpometacarpal

Figure: 35 Effect of droop of manus

Figure: 36 Ulnare and tendons
F.c.u. M.flexor carpi ulnaris
F.d.p. M.flexor digitorum profundus
F.d.s. M.flexor digitorum sublimus
The moments are for *Columba*, 294 gf.cm. and *Larus dominicanus* 400 gf.cm.

4.4.3 **Wrist:**

The moments at the wrist joint are $M(Z3)$ about the axis through the manus skeleton and $M(X2)$ about an axis parallel to $XX$. As in the case of the elbow, it is treated as a hinge joint of depth $d$. The angle between $Z2$ and $Z3$ is $\phi$ and the angle between the resultant and $Z3$ is $\beta$.

**TABLE IV**

<table>
<thead>
<tr>
<th></th>
<th>COLUMBA</th>
<th>LARUS DOMINICANUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>$M(Z3)$ gf.cm.</td>
<td>114</td>
<td>161</td>
</tr>
<tr>
<td>$M(X2)$ gf.cm.</td>
<td>194</td>
<td>490</td>
</tr>
<tr>
<td>$\phi$</td>
<td>120°</td>
<td>145°</td>
</tr>
<tr>
<td>$d$ cm.</td>
<td>0.7</td>
<td>1</td>
</tr>
<tr>
<td>$P(Z3)$ gm.force</td>
<td>163</td>
<td>161</td>
</tr>
<tr>
<td>$P(X2)$ gm.force</td>
<td>277</td>
<td>490</td>
</tr>
<tr>
<td>$P(R)$ gm.force</td>
<td>321</td>
<td>516</td>
</tr>
<tr>
<td>$P(S)$ gm.force</td>
<td>70</td>
<td>51</td>
</tr>
<tr>
<td>$\beta$</td>
<td>30°</td>
<td>18°</td>
</tr>
</tbody>
</table>

These forces and angles are shown in Fig:32 and, as above, (a) refers to *Columba* and (b) to *Larus dominicanus*.

The major load must be taken by the ventral ligament connecting the os ulnare to the ulna, through the former and to the carpometacarpus by the distal
ligament (Fig:34). It is interesting to note that the line of this connection lies more or less along the line of the resultant (Fig:32). The tendons of M.M.flexor digitorum sublimus et flexor carpi ulnaris can make some contribution and particularly the first two since they brace the os ulnare aft (Fig:36). M.flexor metacarpi posterior can also contribute a little and has a slight moment in the positive sense.

Mention has been made of the fact that the manus slopes downwards from wrist to tip when in the gliding mode. This enables the ligaments and tendons to exert a greater force since the effective depth, $d$, is increased (Fig:35).

The shearing force is quite low in both cases and presents no particular problems.

4.4.4 Phalangeal joints:

The loads diminish rapidly distal to the wrist and the joints are comparatively rigid. The actual loads are extremely difficult to assess since the wing is not a homogeneous body and only a few primaries are mounted directly on digit III. The load on, say, the first phalangeal joint may be affected to some extent by the primaries mounted on the carpometacarpus. The figures given below are, therefore, only rough approximations and must be treated with caution.
The angles the resultants make with Z3 are $\gamma$ and $\delta$ respectively.

**TABLE V**

**FIRST PHALANGEAL JOINT.**

<table>
<thead>
<tr>
<th></th>
<th>COLUMBA</th>
<th>LARUS DOMINICANUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>M(Z3)</td>
<td>gf.cm.</td>
<td>30</td>
</tr>
<tr>
<td>M(X3)</td>
<td>gf.cm.</td>
<td>87</td>
</tr>
<tr>
<td>d</td>
<td>cm.</td>
<td>0.35</td>
</tr>
<tr>
<td>P(X3)</td>
<td>gm.force</td>
<td>86</td>
</tr>
<tr>
<td>P(X4)</td>
<td>gm.force</td>
<td>248</td>
</tr>
<tr>
<td>P(R)</td>
<td>gm.force</td>
<td>262</td>
</tr>
<tr>
<td>P(S)</td>
<td>gm.force</td>
<td>39</td>
</tr>
<tr>
<td>$\gamma$</td>
<td></td>
<td>19°</td>
</tr>
</tbody>
</table>

**TABLE VI**

**SECOND PHALANGEAL JOINT.**

<table>
<thead>
<tr>
<th></th>
<th>COLUMBA</th>
<th>LARUS DOMINICANUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>M(X3)</td>
<td>gf.cm.</td>
<td>10</td>
</tr>
<tr>
<td>M(X4)</td>
<td>gf.cm.</td>
<td>30</td>
</tr>
<tr>
<td>d</td>
<td>cm.</td>
<td>0.3</td>
</tr>
<tr>
<td>P(Z3)</td>
<td>gm.force</td>
<td>33</td>
</tr>
<tr>
<td>P(X3)</td>
<td>gm.force</td>
<td>100</td>
</tr>
<tr>
<td>P(R)</td>
<td>gm.force</td>
<td>105</td>
</tr>
<tr>
<td>P(S)</td>
<td>gm.force</td>
<td>30</td>
</tr>
<tr>
<td>$\delta$</td>
<td></td>
<td>12°</td>
</tr>
</tbody>
</table>

Since, in both cases, M(Z3) at the joint is small compared with M(X4) the resultant is not at a great angle to the Z3 axis.
4.5 Conclusion.

The foregoing analysis is based on the lift of a rigid wing in the gliding mode only and no account has been taken of the drag since this is small enough to be neglected.

During the downstroke of flapping flight the loads are obviously greater but the moment $M(X)$ will be about an axis inclined to the $X$-axis of the bird since the resultant lift is inclined forward. At mid-stroke, when the inner wing ceases to move, the elbow is bent and the forearm rotated by the supinator muscles to allow further movement of the manus. M.M. flexor carpi ulnaris et flexor metacarpi posterior are responsible for this latter movement and for resisting the pronating moment.

On the up stroke the loading on the outer wing is reversed and M.M. extensor metacarpi radialis, extensor metacarpi ulnaris et extensor pollicis longus will be largely responsible for movement of the manus.
CHAPTER V.

FLIGHT.
CHAPTER FIVE

5. FLIGHT:

5.1 Introduction.

The subject will be discussed in five main divisions, namely, gliding, flapping, hovering, take-off and landing. There are of course distinct differences between the modes, but there is also considerable overlap as one fades into the other.

The positions of the wing and tail at various instants during flight are discussed and a correlation between the aerodynamics, myology and structure is made. It will be appreciated that although there is great difficulty in defining exact interactions between muscles, the origins, runs of tendon and insertions described above make it possible to reach some conclusions.

It is assumed that any normal manoeuvre will be effected with the greatest economy of effort and this assumption helps in the analysis.

As the actions of the leg and foot muscles of man during normal walking are semi-automatic (that is they are performed without conscious control) so are the movements of the wing and tail. The foot and leg react to changes in the nature of the surface and the wing and tail to changes in the aerodynamic forces.
The contribution of the tail to flight and control is considered where necessary but no detailed study has been made of this appendage.

5.2 Gliding.

The term gliding implies a mode of flight in which no thrust is supplied by the flying body other than that which may be due to the forward component of the gravity force.

Many authors distinguish between gliding and thermal soaring, but as will be realised from the above definition, the latter is much the same as the former except that there is a rising air current and the forward speed is generally lower. Dynamic soaring is a different matter since, in this case, use is made of the momentum of the creature and the variation of wind velocity with height. This subject is well discussed by Walkden (1925). However, in neither case is any thrust supplied by flapping the wings except occasionally to counteract some disturbance or irregularity in the air.

Gliding flight of birds does not appear to have attracted as much attention as flapping flight although Lilienthal (1911) studied the subject extensively and Storer (1948), has a fairly comprehensive account in his book on the general aspects of gliding and soaring. Raspet (1950)
and Pennycuick (1960) have also made valuable contributions to the subject.

Aymar (1938) attempts to make a comparison between a bird gliding against the wind and a sailing vessel beating upwind. This is open to several objections. While the camber of the wing, as with the sail, does increase the lift available there must always be a drag force acting in the same direction as the air flow. In the case of the ship two different media are involved with very different densities and viscosities. The resultant force on the sail when close hauled has one component along the axis of the hull and the other at right angles to this. The resistance of the hull to lateral motion through the water is high compared with that to forward motion so that the net result will be motion against the wind but at an angle to the axis. The bird, being immersed in one medium only, which is moving in the same direction throughout, cannot move forward indefinitely against this stream unless there is a force to propel it. If the air flow has an upward component then the component of the gravity force parallel to the flow may be sufficient to maintain the glide.

If the body be flying with fixed wings and tail the axis may or may not be parallel to the path. The four cases illustrated in Fig.37(a),(b),(c) and (d) assume the wings and tail to be fixed in the same relative position with respect
Figure: 37  Attitudes in flight
(a) Climbing
(b) Level flight
(c) Descending
(d) Riding an up-draught

Figure: 38  Illustrating wash-out
Wing viewed from distal end
to the body and the wind to be blowing with a steady uniform velocity, horizontal in (a), (b) and (c) and inclined upwards in (d). It is further assumed that these conditions obtain an instant after the thrust has ceased to act.

In Fig:37(a), the lift is greater than the weight so that a climbing path is being followed, that is the path is upward with respect to the wind and the ground. In (b) the path is parallel to the wind and the ground. In both these cases the forward speed of the bird relative to wind and ground will decrease since there is no thrust to maintain it. If the path be downward, as in Fig:37(c), the ground speed may decrease, remain constant or increase depending on whether the forward component of the gravity force, \( W \sin \theta \), is less than, equal to or greater than the drag.

The only steady propulsive effort available is that due to the forward component of the gravity force (Fig:37(c)) and this is \( W \sin \theta \) and the sinking speed, \( U \), is equal to \( V \sin \theta \).

Since the work done against the drag can only be supplied by the loss of potential energy,

\[ WU = DV \]

The sinking speed is a minimum when the power \( (DV) \) is a minimum, since the weight is fixed, and it can be shown that this occurs when \( \frac{C_L^{\frac{3}{2}}}{C_D} \) is a maximum.
The total drag of a wing is the sum of the profile drag and the induced drag. The profile drag coefficient, \( C_{D0} \), is a function of the aerofoil shape and the induced drag coefficient, \( C_{Di} \), is a function of the lift.

\[
C_D = C_{D0} + C_{Di}
\]

and

\[
C_{Di} = \frac{C_L^2 S}{\pi \epsilon b^2}
\]

where \( \epsilon \) is a span efficiency factor.

Thus \( C_{Di} \) is inversely proportional to the aspect ratio.

If the lift be equal to the weight

\[
W = C_L \frac{1}{2} \rho V^2 S
\]

hence

\[
C_L = \frac{W}{\frac{1}{2} \rho V^2 S}
\]

\[
\therefore C_{Di} = \frac{1}{\pi \epsilon \frac{1}{2} b^2} \cdot \frac{W^2}{\frac{1}{2} \rho V^2}
\]

\[
WU = C_{DO} \frac{1}{2} \rho V^2 S + \frac{1}{\pi \epsilon \frac{1}{2} b^2} \cdot \frac{W^2 V}{\frac{1}{2} \rho V^2}
\]

\[
U = C_{DO} \frac{1}{2} \rho V^3 S + \frac{1}{W} \cdot \frac{WV}{\frac{1}{2} \rho V^2}
\]

Thus it will be seen that the sinking speed is a function of the weight, the wing area and the span and not of weight and span only as stated by Maynard Smith (1953).
Figure: 39  *Larus novaehollandiae* gliding

Posterior view

Frame numbers given on right
The last figure of the four, (d), shows the effect of sloping ground. The air flow is deflected upwards and, if conditions be right, the bird can ride on this up current without changing its position relative to the ground.

The wing is normally twisted during flight of this type so that the angle of attack decreases towards the tip. In this configuration the wing is said to have washout and Fig:38 represents such a wing viewed from the distal end.

Examples of gliding flight shown in Figs:39 - 42 inclusive are taken from photographs of red-billed gulls (Larus novaehollandiae). The filming speed was 64 frames per second and the number given with each figure refers to the frame number so that an approximate time scale is available. It will be noted that the sequence of Figs:39 and 40 occupies a period of rather more than 0.75 sec.

Figs:39 and 40 are posterior views of the bird riding on up draught with little movement relative to the ground, Fig:41 shows a lateral view with similar condition and the last, Fig:42, a ventral view. Note that this bird is in moult and the position of the manus is rendered particularly clear because of this.

Considering Figs:39 and 40, first, the air flow is far from steady, there being variations in speed and direction as well as eddies so that constant adjustment is required in order to maintain stability.
Figure: 40 *Larus novaehollandiae* gliding

Posterior view
One of the primaries of the right wing shows a consistent tendency to separate and this is probably due to moulting or mechanical damage. There also appears to be another loose feather about half way along the posterior part of this wing, first remarked in Fig:40, f.27.

The first point of importance to be noted is that the outer wing, at least distal to phalanx 2 digit III, is supplying little lift. This is apparent from the fact that the primaries are not flexed upwards and is to be expected for two reasons. In the first place, as discussed above in Chapter 4, the closer the centre of lift is to the centre line of the body the less will be the muscular effort required to support the body. Secondly, if the angle of attack is small, as it will be for low lift, there is a reduction in the risk of a stall due to sudden changes of air flow over this important control surface.

In f 1 the wings are nearly symmetrical but the right is stalled close to the body. This condition, marked by the lifting of the feathers (indicated by the arrow) has almost ceased to exist in f 3 (roughly .03 sec. later) and the right wing has been slightly supinated by rotation at the shoulder. The fact that the wing has been supinated indicates that the wind direction has altered such that the angle of attack has tended to decrease since the attitude of the body has not altered. Between f 6 and f 10 the air flow has again become
steeper and both wings have been pronated by movement at the shoulder joint. This adjustment has prevented an increase in lift or stalling. It is to be noted that both wings have been pronated by nearly the same amount and that both hands have been pronated slightly with respect to the forearms. This latter is achieved by contraction of M.M.obliquus et extensor metacarpi ulnaris. It is difficult, in these posterior views, to see if there has been any extra flexing of the manus in the plane of the wing but, judging by the wing lengths, such flexing, if any, must be slight.

The banking in f 21 has been produced by a vagary of the air current as is shown by the fact that there has been no appreciable change in the wing settings. A correction has been made (f 27) by supinating the left wing thus increasing the lift on that side. Further supination of the left manus is shown in f 29 produced by relaxation of M.obliquus and contraction of M.flexor carpi ulnaris, while M.M.extensor pollicis longus et extensor metacarpi radialis remain in tension.

In f 36 the right wing has again been pronated and from the position two frames later (f 38) it is apparent that a gentle flap has developed with the greater thrust on the right wing. The downbeat has finished by f 42, both wings are supinating and a slight turn has been achieved. Considerable pronation of the right wing in f 44 has prevented
Figure: 41  *Larus novaehollandiae* gliding

Lateral view
banking and in f 50 a gust has caused stalling at the centre and the left wing has been allowed to rise to prevent rolling of the body.

The lateral views of Fig:41 occupying a little more than 0.3 sec. show the same general control features. The body and head show very little change of attitude other than a slight roll but the wings are in constant movement.

In ff 1,2,7 the right wing is being increasingly pronated, mainly from the wrist outwards, while the left wing is nearly constant in setting. In f 12 the left wing is pronating and there has been a slight roll to the right, continued in f 15. The body is again stable by f 16 and so remains for the last four frames. The left wing tip commences to extend in f 17 and in the last frame it is nearly at full stretch. The twisting of the right manus is shown particularly clearly in f 7 where the wrist joint (arrow) is quite prominent.

The final sequence, Fig:42 is a ventral view of the bird riding an up-current about fifteen feet above the ground and nearly stationary in space. Rotation of the wings cannot be seen clearly but the view does illustrate the flexing of the manus very well. From f 3 to f 8 the right manus is extended thus increasing the area. At the same time the elbow has been somewhat straightened so that M.M.tensor patagii longus et extensor metacarpi radialis come into play. Note that this
Figure: 42  *Larus novaehollandiae* gliding

Ventral view

Note that this bird is in wing moult
extension does not appear to have shifted the centre of lift of the wing in the fore and aft direction as is indicated by the tail, which has not been adjusted. From f 15 to f 68 there are minor movements with a brief flexing of the right manus in f 35. The next important variation occurs in f 70 to f 73 where the left manus is flexed considerably, lowered and supinated. M.M. flexor digitorum profundus, flexor metacarpi posterior, flexor carpi ulnaris et flexor digitorum sublimus will all be called into play and the elbow is flexed to reduce the pull on the extensor process of the carpometacarpus. Some of the flexing and extension of the manus may be helped by altering the angle of attack as is shown in Fig: 76, Appendix IV.

The gull has been chosen for this analysis because, while being capable of strong flapping flight, it spends a large part of its time in the air in gliding. In this position, as has already been stated, the centre of lift is kept close to the body and the outer part of the wing is lightly loaded. This is shown by the fact that the primaries are not flexed upwards and the manus, as a whole, droops.

An aircraft with fixed wings is designed to be inherently stable, that is, if its altitude is disturbed it will tend to return to the original state. The wings have a di-hedral setting for lateral stability, a fixed tail for longitudinal stability and a fin for directional stability.
The bird is not inherently stable, just as a standing man is not, and muscular action is required to correct any disturbance. The subject of stability is discussed below in Chapter VI.

The movements of the wings in these sequences are almost entirely due to muscular action since little help is available from aerodynamic forces other than that mentioned above.

The rotation of the wing about the shoulder is due to the pectoral and other muscles of this region. The twist is controlled by the pronators and supinators of the forearm and the extensors and flexors of the manus.

5.3 Flapping Flight.

Flapping flight constitutes the phase in which thrust as well as lift is supplied and this, of course, is used in take-off as well as in ordinary flight. The above definition is necessary in order to distinguish it from hovering as in the latter conditions are different.

This question has been discussed by a number of authors including Leonardo da Vinci (1452-1519), Marey (1883), Boel (1929), Guidi (1938), Storer (1948), Brown (1951), and Shestakova (1956).
Boel (1929) in his definition of an ornithopter states inter alia "whose angle of attack is always positive". As will be shown below, the angle of attack of some portions of the wing is negative for part of the stroke during strongly flapping flight. Also the statement that the angle of attack increases when the wing is opened and decreases as it is folded requires considerable qualification before it can be accepted. The primary adjustment of angle of attack is made at the shoulder joint, assuming that the inclination of the X-axis of the body is not altered.

Aymar (1938), in his discussion of aerodynamics of bird flight bases some of his conclusions on unsound data and insufficiently precise definitions. The statement that the force of the wing beat acts at right angles to the surface is not clear. If, by the surface, is meant the chord this statement is not true since the direction of the resultant is variable. Again, the often repeated statement that the primaries open in order to reduce resistance is incomplete and the matter is discussed below.

Brown (1951) produced an elegant analysis of the wing movements of a pigeon during flapping flight. In it he makes a brief mention of the functions of certain muscles but fuller information would have been helpful. For instance the statement that it may be shown that, in one type of flight, M.pectoralis minor, does not raise the wing. Presumably this
refers to the case where the lift on the wing is sufficient to raise it at the required rate without muscular effort. Doubt is also cast on the effect of M. pectoralis major in pronating the wing and this subject is discussed below in Appendix I.

The use of the term "angle of incidence" leads to some confusion hence the definition given in Chapter I. In Fig:1 of the above-mentioned paper the angle of incidence appears to refer to the setting with respect to the body.

In his paper on the flight of birds (1953) Brown gives the following table:-

<table>
<thead>
<tr>
<th></th>
<th>Take-off</th>
<th>Medium speed</th>
<th>Normal high speed</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Downstroke:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Wing tip:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Angle of attack</td>
<td>Positive</td>
<td>Positive</td>
<td>Positive</td>
</tr>
<tr>
<td>Angle relative to</td>
<td>1. Positive</td>
<td>Negative</td>
<td>Negative</td>
</tr>
<tr>
<td>direction of flight</td>
<td>2. Lift</td>
<td>Propulsion and lift</td>
<td>Propulsion and lift.</td>
</tr>
<tr>
<td>Function</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Inner Wing:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Angle of attack</td>
<td>Positive</td>
<td>Positive</td>
<td>Positive</td>
</tr>
<tr>
<td>direction of flight</td>
<td>4. Lift</td>
<td>Lift</td>
<td>Lift</td>
</tr>
<tr>
<td>Function</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
There are one or two points where the author disagrees with this table and these are listed below:-

1. If the angle of attack of the wing be positive with respect to the direction of motion the take-off will be backwards, a manoeuvre which is only executed in an emergency. In fact it is normally negative, see Fig:52, Fig:53, Fig:54, Fig:55, Fig:56.

2. Thrust is supplied as well as lift.

3,4. The inner wing may have a negative angle of attack relative to the direction of motion,
Fig:53, f 9 and Fig:55, f 6 being examples of this and in this case some thrust will be produced.

5, 6, 8, 9. The angle of attack is over 90° negative.

10. May, in some cases, have a negative angle of attack relative to the direction of motion.

11. On the up-stroke there can be some slight propulsive force and a little down force on the manus could be a small price to pay for thrust in these circumstances and could be balanced by extra lift on the inner wing. The exact setting of the wing tip is, however, exceedingly difficult to determine.

The author cannot agree that the inner wing can contribute little or nothing to the lift of the wing as a whole during take-off since this depends on the type of take-off. As long as the angle of attack is positive with respect to the air flow there must be some resultant force on the wing, part of which may be lift and part thrust. Boel's experiments with clipped wings do not, in fact, disagree with the above contention and Brown himself admits that birds so treated can only fly under take-off conditions for a short time.

It is agreed that the rotation of the primary feathers is not primarily under muscular control but it may be helped slightly by some of the slips or fascia inserted in the system surrounding their bases.
The maximum arc through which the inner wing moves varies widely with the different species thus, in the pigeon it is approximately 90° and in Larus dominicanus about 45° - 60°. In no case, however, does it appear that the humerus is depressed appreciably below the horizontal when in the extended position.

In all cases studied the inner wing as far as the wrist commences to rise before the manus and is supinated sufficiently to maintain a positive angle of attack. The manus then follows, the tip moving dorso-posteriorly during the process. If the movement be slow there is little or no thrust produced but the drag is reduced to a minimum.

Unless the wing reaches the vertical limiting position, as it sometimes does with the pigeon, lift is available throughout the stroke.

During the flapping phases of flight it would be better in some ways to consider the wing on airscrew theory rather than wing theory. In effect the wing becomes an oscillating propeller with some differences between the up and down strokes. The down stroke is similar to an ordinary airscrew providing thrust along the axis of rotation and torque reaction (lift) at right angles to this. During the up stroke the outer wing may still be a propeller but the inner wing, with the lift acting in the direction of motion,
Figure: 43  *Larus dominicanus* in flapping flight
Figures: 44 and 45  Strong flapping flight - 

*Larus novaehollandiae*
Fig. 44
has now become a windmill. The outer wing may, perhaps, be a windmill at times but, when not producing thrust, is probably "feathered". The wing has one great advantage over the conventional airscrew in that, not only is the pitch variable, but the twist may be adjusted to suit conditions. The variability of pitch is most clearly seen at take-off and landing when the forward speed is low and the thrust high.

Fig: 43 shows a gull (Larus novaehollandiae) in level flight and Figs: 44 and 45 a similar bird just after take-off.

Commencing with the wing at the beginning of the down stroke, Fig: 43, f 2, Fig: 44, f 1, the wing is fully extended and moves in one piece as a rigid body. The extensor muscles are taut and the elbow locked at the olecranon. Considerable pronation has occurred so that a reasonable angle of attack is maintained (Fig: 46(a)) and the resultant is upwards and forwards, giving lift and thrust. As this is the beginning of the stroke the loading is not high and the primaries are not disturbed. The downward movement is produced by the major pectoral muscles and the exact degree of pronation controlled by other shoulder muscles.

As the down stroke progresses the primaries become flexed and the wing pronates still further to maintain the angle of attack at a reasonable value (Fig: 46(b)). Since the airflow relative to the wing during the down stroke is
Figure: 46 Wing attituders - angular setting during different phases of the stroke

Figure: 47 Position of manus during stroke
(a) Dorsal view
(b) Anterior view - down stroke
(c) Anterior view - up stroke
Fig. 46

Fig. 47
inclined upwards and the lift is normal to the undisturbed air flow the latter will be inclined forward. Unless the horizontal component of the drag is equal to or greater than the horizontal component of the lift there will be thrust. For a pigeon flying level at a forward speed of 30 ft./sec. and a wing-beat frequency of about 5 cycles per second the average direction of the air flow at the wrist is about 5° and at the tip 20°. Thus whether thrust is produced or not depends on the direction of air flow relative to the wing and the lift/drag ratio only.

In order to emphasise the effect of the relative air flow consider Fig:46(e). The aerofoil is inclined at an angle θ to the horizontal and the air flow is inclined upward at an angle β, the angle of attack, α, is then equal to θ + β. If the resultant force on the aerofoil is inclined at an angle φ to the lift (to the normal to the air flow) thrust is produced provided β is greater than φ.

For an R.A.F. 33 aerofoil under certain test conditions α = 7° and φ = 3.5°, if the downward velocity is greater than 6.1% of the forward velocity the resultant will have a forward component. Thus a wing may produce thrust even though it may have a positive setting angle with respect to the horizontal. By the time the wing is horizontal the inner part, to the wrist, has ceased, or
almost ceased, to move and is supinated (Fig:46(c)). At this point the elbow and wrist are flexed slightly to allow the manus to continue in a downward and forward direction, Fig:43, f 9 and Fig:45 f 6. The manus remains pronated so that as it swings down through an arc, which may reach 90° from the horizontal, lift and thrust are still produced. The lift will fall steadily as the angle of the manus from the horizontal increases but the thrust will diminish as the angular velocity decreases.

The flexing of the elbow brings the wrist forward, Fig:45, f 9, and slacks off the tendon of M. tensor patagii longus thus allowing the leading edge of the inner wing to curve as indicated in Fig:47(b) and this part of the wing is still supplying lift.

By the time the outer wing has reached the end of its stroke the inner wing is rising, Fig:43, ff 11, 12, Fig:45 f 6, followed by the manus. In these circumstances the air pressure is on the dorsal surface of the primaries, and, in extreme cases, causes the manus to twist so that lift and thrust are again supplied, Fig:45, f 7. This causes the primaries to separate and form a cascade. Owing to the arrangement of the primaries of the wing, shown in Fig:47(a), only the first two of these are parallel or nearly parallel to the leading edge and these are the only ones which can form a cascade in the true sense, as the axes of the
Figure: 43  Flapping flight - *Larus dominicanus*
primaries proceeding inwards lie at an increasing angle to the leading edge and bend, as is clearly shown in Fig:45, f 7.

Thus lift is supplied almost throughout the whole beat for the type of flapping discussed above. However, in the case of *Columba livia*, when very powerful flapping is required (e.g. at take-off) the wings rise to the vertical and actually touch so that no lift is given. Thrust cannot be supplied in the region of the rest points of the beat and is probably negligible during the up stroke of gentle flapping.

*Larus dominicanus* (Fig:48) with its longer wings does not normally lower the manus to the same extent as the smaller gull according to the evidence of photographs and extensive observation. The action in this case is somewhat different since the manus on the up stroke, having a smaller arc of movement, cannot supply so much thrust. However, as the mass of the bird is greater the momentum will be greater in proportion to $L^3$ (where $L$ is a linear dimension) whereas the drag is proportional to $L^2$, both for the same air speed. Hence continuous thrust is not so essential to maintain speed and height. The evidence of photographs suggests that during the up stroke of the manus it is set to an angle of attack giving minimum drag, zero or a few degrees negative for this type of aerofoil. This view is supported by the fact that the primaries do not separate.
It is to be noted that the wing tip describes a closed curve relative to the body and at the bottom of Fig:48 is shown the path followed plotted from photographs. The characteristic figure-of-eight pattern is not apparent in this particular case, probably because the bird is flying quite gently. The rate of wing beat is about three per second and the flying speed 25 - 30 m.p.h. Boel (1929) noted this and analysed the wing movements very well but failed to appreciate the fact that lift and thrust can be applied during the up stroke.

As noted in Chapter IV, when discussing the position of the centre of pressure relative to the supporting skeleton, there is a negative pitching moment tending to supinate the wing during the down stroke. Similarly, during the up stroke there is a tendency to pronate if the angle of attack is sufficiently negative. The above is based on the assumption that the centres of pressure are at the quarter points.

The advantage of this arrangement from the point of view of the bird is that the pronation or supination are resisted by elastic restrainers, that is, the ligaments. The muscles, then, can reinforce this resistance as required to give the correct settings and the resistance offered by the ligaments is proportional to the movement. The main pronator and supinator muscles in the forearm (M.M. pronator profundus, pronator superficialis et supinator brevis) will be active in
Figure: 49 Flapping flight - *Larus novaehollandiae*
this connection for the wing distal to the elbow.

Fig:49 gives further examples of wing configurations. *Larus novaehollandiae* can raise the wings to about $80^\circ$ from the horizontal when flapping strongly to gain height and forward speed. The tail is spread in this particular case in order to increase the lifting surface and to help maintain horizontal stability. The twisting of the manus is very marked in ff 8, 17 and the bending of the primaries in ff 1, 18.

5.4 Hovering.

The hovering flight of the humming bird, whose ability in this field is supreme among birds, has been fairly extensively studied and photographed. For other birds, whilst the principles involved are the same, the action is different and is more akin to flapping flight and has been less fully discussed. Between the species there are also differences in wing settings, leg action and tail position.

Figs: 50 and 51 are taken from photographs of a gull (*Larus novaehollandiae*) for one cycle of wing movement, occupying a time interval of about 0.25 second. A reference point is marked on each drawing and this reveals that there is little body movement in space.

In f 1, the wings are set with the chord almost horizontal so that the only force is nearly vertical, i.e.,
Figure: 50  *Larus novaehollandiae* hovering
little or no thrust is produced. The manus is brought forward by flexing of the elbow and the primaries are spread and flexed upwards. The body is inclined at about 45° and the tail spread with its plane parallel to the axis.

The inner wing, having its chord normal or nearly normal to the direction of motion, is equivalent to a plate placed at right angles to the air flow in a wind tunnel. In these conditions there is no lift, in the accepted sense of the word, but there is a high drag force. Thus, the wing moving downward at a high speed produces a strong upward force on the bird. The tail is spread wide and moving down to act as a stabiliser since the wings are rather more forward than for ordinary flapping. The end of the downstroke is reached in f 2, which is about .015 second later than f 1, and the wing is well forward; the manus is twisting (supinating) and the tail still being depressed. In f 3 and f 4 the inner wing is rising, comparatively slowly and the manus is still giving lift as it continues to move forward and down. The inner wing is considerably supinated in order to reduce the downward force on the bird and to prevent overall generation of thrust. As the inner wing continues to rise the manus commences to move posteriorly, f 5, and the pressure on the back has become sufficient to bend the primaries thus showing that considerable lift is being generated. At f 6,
Figure: 51  *Larus novaehollandiae* hovering
the wing begins to straighten mainly by contraction of M.M.scapulotriceps, humerotriceps et anconeus. This causes the manus to extend, by tightening the tendons of M.M.tensor patagii longus et extensor metacarpi radialis, and at the same time to twist (pronate). By f 7 the wing has lost much of its twist, the body has moved to a more vertical position and the tail has depressed even further. In this position of the latter, with its plane vertical, tends to prevent horizontal movement of the body. By f 10 the up stroke is nearly complete and the last part of the straightening movement causes the manus to flick over to its normal position very rapidly. The tilting of the body has been caused by the shifting of the centre of pressure to a point anterior to the centre of gravity thus providing an anti-clockwise couple.

In f 5 it may be noted that there is a distinct division between the distal secondary and the proximal primary and this emphasises the degree of freedom of the manus with respect to the forearm.

The forward movement of the wing takes place almost entirely from the elbow and because of this flexing the wrist joint gains greatly increased freedom of movement and the distal end of the ulna-radius assembly can be twisted by rotation of the latter about the former. M.flexor metacarpi posterior, in opposition to M.extensor metacarpi
radialis, serves to maintain the required degree of flexion.

The twisting or supination of the manus, as stated above, is primarily due to the air pressure having its centre posterior to the carpus and digits, the force being on the dorsal surface. Control of this twist is exercised by M.obliquus as a powerful pronator and, to a lesser extent, by M.extensor metacarpi ulnaris. M.M.extensor digitorum communis et extensor indicis longus are in tension causing slight supination of the phalanges and bracing the digit against flexion in the ventral direction.

In f 11, as the wings have started to move downward and the centre of pressure is posterior to the centre of gravity, the body has reverted to the 45° position. The remaining three drawings show progress towards the horizontal and reveal nothing of special note.

5.5 Take-off.

The take-off procedure varies not only with the species and habitat but also with the exigencies of the moment. Thus, a gull (novaehollandiae or dominicanus) taking off from land when not pressed, takes a few leisurely steps along the ground as the wings open and the first down beat carries it off the surface. The forward velocity gained by the run helps to reduce the power required for the first wing stroke. If pressed, however,
Figure: 52 Normal take-off - *Columba livia*

Figure: 53 Normal take-off - *Larus novaehollandiae*
they jump and the wings are ready for the downbeat by the
time the feet leave the ground.

While the Reynolds number during the initial stages
of take-off is low by normal aircraft standards the roughness
of the leading edge of the wing is probably sufficient to
give a turbulent boundary layer and this latter is necessary
for good performance. The average values of $R$, taken at the
wrist, for the first down stroke of the pigeon (Fig:52) and
the gull (Fig:54) are approximately 17,000 and 72,000
respectively.

Examples taken from species other than the six
specifically chosen for this work are used in addition in
order to give a more general picture.

Fig:52 shows *Columba livia* during a normal, unhurried,
take-off and the series are taken from consecutive frames at
approximately $1/64$th second intervals. In $f\, 1$ and $f\, 2$ the
wings are beginning to open but the feet have not moved. By
$f\, 3$ the right foot is moving forward and the step is completed
by $f\, 8$, at which point the wings are nearly fully raised to
the vertical position. Between $f\, 9$ and $f\, 10$ full stretch is
reached and both wings are pronated by rotation at the
shoulder and at the same time the leg stretches and raises
the bird on tiptoe. The first part of the down stroke
produces little lift, since the wings are nearly vertical,
but produces considerable thrust and by $f\, 11$, when the lift
Figure: 54  Jump take-off  -  *Larus novaehollandiae*
has developed the feet are just leaving the ground. The remainder of the beat is similar to that described in flapping and hovering flight with strong lift and thrust during the up stroke. The normal take-off from a ledge or branch is similar to that of other birds of this type. If, however, the take-off be from a ledge or crevice with the bird facing a vertical surface the position of the wings needs to be modified. Instead of being pronated during the first downbeat the wings are supinated thus the take-off is backwards, since the thrust has been reversed, and as soon as sufficient clearance has been achieved to allow a turn the flight will become normal.

The normal take-off of Larus novaehollandiae is shown in Fig:53. Between f 1 and f 4 the wings start to open and the run commences with the left foot while between f 4 and f 9 the wings continue to open and four steps are taken. In f 9 the pronations of the wings at the beginning of the downstroke can be very clearly seen. The wings are inclined forward at this point so that the downward motion has a backward component, thus increasing the thrust. In f 10 the feet have just left the ground and from then on flight continues in the usual manner.

The same species in a jump take-off is shown in Fig:54. The wings commence to open, f 1, and the legs being to bend f 2, when the former are about half spread. As
Figure: 55 Take-off - *Passer domesticus*
the wings approach the top the legs straighten, ff 3,4 and
by f 5, when the downbeat begins, the feet are about to
leave the ground and they are just clear one frame later,
f 6. In this particular case the bird was jumping for a
piece of food and required to move vertically, hence the
wings are not pronated in f 6 and f 7. In f 8 it will be
noted that the wing is considerably twisted so that the manus
is giving some forward thrust. To counteract this the inner
wing is supinated to give reverse thrust and the result is
lift only. Four frames later, f 12, the body has taken up
an almost vertical position, the manus is turned over and the
wing moving backwards so that the manus is giving lift. The
action is similar to that for hovering with the difference
that, in this case, the lift exceeds the weight and the body
moves vertically.

Fig:55 shows a sparrow (*Passer domesticus*) taking off
from a wire. Here the jump is forward and the feet leave
the support just as the wings start the down stroke, f 6.
The position of the tail is to be noted, in f 7 it is up
while the wings are moving down, probably to counteract a
clockwise pitching moment on the body due to the centre of
pressure of the wings being aft of the centre of gravity.
It has been depressed by f 8 and now seems to be acting as
an auxiliary lifting surface (see also ff 9, 10). Frame
f 16 is of interest in that, the manus, while it has the
usual vertical position at the end of the down stroke, is
Figure: 56 Take-off - *Phala crocorax varius*
drawn back instead of forward as in the other cases considered and the body axis is at a considerable angle to the horizontal.

A shag (Phalacrocorax varius) is shown in Fig. 56 at an early stage in its take-off run on water. This particular bird took about 100 yards before it was finally clear of the water although for the last 50 yards only the feet touched occasionally. At the beginning of the downstroke, f 1, one foot has just entered the water and the tail is fully raised. During the next six frames there is the ordinary downbeat of the pronated wing, the broad webbed feet give a strong forward thrust and the tail is lowered until its trailing edge touches the water. By f 8, the end of the down stroke, the feet are clear but the tail still gives some support since it is trailing in the water. As the wings rise, f 11, the feet reach forward and again enter the water in f 14 and are well immersed by f 16, the top of the stroke. For about half the take-off the tail continues to touch the water thus giving some support. The twist of the manus is well marked in f 21 and the fact that the air pressure on the back (dorsal) surface is clearly seen.

It is to be noted that during take-off and rapid acceleration the comparatively small M. pectoralis minor must be under extreme strain since there is little help from aerodynamic forces in raising the wing. The fact that the
Figure: 57 Normal landing  -  *Columba livia*
manus does not rise appreciably until the inner wing is well up is certainly an aid since the centre of pressure is thus brought well inboard.

5.6 Landing.

As with take-off, the landing technique varies with the species and with the particular conditions obtaining at the time.

A bird landing on the ground need move forward very little after touch-down and, of course, when landing on a branch or twig all horizontal motion must cease when the perch is gripped. When landing on water, birds like ducks and swans usually run forward much as does a seaplane although they are able to stop almost dead if necessary.

In Fig:57 Columba livia is making a normal landing in still air and the forward velocity is very small. At an earlier stage than the beginning of the sequence the creature has stalled to cut its forward velocity. It is worth noting that stalling for a bird presents no difficulties since the centre of resistance can be shifted so quickly by moving the wings or tail or both.

Thus having lost practically all forward speed, it is possible to float gently down with the wings and tail spread against the air flow. In f 13 the tail is fully open and the wings spread, with the left moved somewhat rearward. In f 2 the left wing is extended to counteract a roll and it is
Figure: 58  Landing on water - *Larus novaehollandiae*
also moved forward to prevent the head dropping. The next frame shows the wings raised and pronated in order to increase the forward velocity slightly. By f 9 a roll to the left has developed and the left wing is beating down (shown by the bending of the primaries) to correct this. Having once more achieved an even keel, the wings are raised in order to give them sufficient latitude of movement during the final landing operation, f 10, f 11. A very quick up beat, (ff 12, 13, 14) steadies the body and allows a slow down-beat f 17 to f 26, where touch-down occurs. The wings are again raised so that they are ready in case a steadying flap is required or in case immediate take-off becomes necessary. The final three frames show the wings and tail folding and a forward step is beginning. The head begins to come up about frame f 20, when there is only an inch or two to go before the ground is reached. The sinking speed is of the order of one to two feet per second.

*Larus novaehollandiae* landing in a pool is shown in Fig:58. Frame f 1 is the last of the steady glide in and again illustrates the small amount of loading on the outer wing, shown by the lack of bending of the primaries and the down-droop of the manus. The next three, ff 2, 3, 4 show the beginning of a slight turn. First, the manus of the right wing is pronated and shows very clearly the point made above, that the manus can be rotated at the wrist joint by an appreciable amount even when the wing is nearly fully
extended. At the same time the tail, being fully spread, is twisted anti-clockwise and lowered so that it acts as a rudder turning the bird to the right as the bank develops. In f 17 about half the turn has been completed and the right manus is being supinated. The stall commences in f 43 and, in order to continue the turn the left wing is supinated, folded and raised somewhat to reduce the resistance on that side (f 50). This latter movement also serves to correct the bank and bring the lateral axis level again. From f 53 to f 62, the final approach, there is some movement of the tail to the left to stop the turn and minor wing movements to keep the balance. Touch-down occurs in f 63 with a simultaneous slow down-beat of the wings. The final settling f 67 to f 75, is interesting as it shows the head submerging immediately after touch-down. There is nothing in the beak when it emerges f 75, so that there are several possible explanations for this. First, the bird may have been after some food and missed, but this seems unlikely in view of the unhurried approach to the landing. Secondly, it may have been an accident due to misjudgement. Thirdly, it may have been done to prevent sinking too deeply, tail first, by allowing the full length of the body to reach the water at the same instant. Of the three the last appears to be the most probable.
Figure: 59 Normal landing on ground - *Larus novaehollandiae*
Fig. 59
Fig:59 gives a few views of a landing on the beach by a similar gull. The stalling is again clearly shown in f 27 and frame f 34 shows further braking just before touch-down. This is achieved by supinating at the shoulder, thus sweeping the rear portion of the wing forward. Touch-down takes place in f 38.

The next figure (Fig:60) is of *Larus dominicanus* landing on a post and the dotted line represents the horizon which serves as a reference for height, while the post first appears in f 74. There is a light breeze blowing against the bird and the first fifteen frames show the adjustments necessary to reduce the forward velocity almost to zero by the time the edge of the post is reached. Frames f 3 to f 23 show the elevation of the head and the gain in height, due to the increased angle of attack, required for the final approach. The increased angle of attack also causes an increase in the drag and a consequent loss of speed, since there is no thrust being produced. From frame f 30 to frame f 71 the final approach is made and the position of the head indicates the watch that is being kept on the post while at the same time the wings are pronated in order to lose height by reducing the lift. By f 74 the landing point has almost been reached, the legs are lowered and the wings relaxed. The forward speed is now almost zero, as may be seen by noting the body position relative to the post, and by f 87 the legs are reaching forward for the landing, the wings are beginning to fold and
Figure: 60 *Larus dominicanus* landing on a post
the descent is vertical. The feet finally touch in f 91 and the position chosen, on the edge of the split, gives the best chance of gripping. By f 112 the bird is firmly established on the post and is raising the head to look round. The final phase, up to f 153, take the sequence almost to completion with the wings nearly folded.

This sequence illustrates extreme accuracy of control and the advantages taken of the wind. The point at which thrust ceases must be nicely judged so that the momentum is just sufficient to enable the post to be reached without undue wing movement. The whole operation has been carried out in quite a leisurely manner and with no great muscular effort.

5.7 Conclusion.

The main phases of flight have been considered and the action of the flight apparatus analysed for particular species.

Except for hovering, the general wing movements in flight have been discussed by a number of authors (see Chapter I, section 1.2) but here a more detailed assessment has been made of certain aspects. In some cases there is disagreement with previous work and where this is so particular care has been taken to ensure that the deductions agree with aerodynamic and mechanical principles.
Figure 61

(a)(b) Position of manus during down and up strokes - gull
(c) Manus moving back - gull
(d) Twisted manus - gull
(e) Normal glide - Brahminy kite
(f) Twisted tail - Brahminy kite
(g) Soaring - Alpine chough
(h) Landing - Alpine chough
Some differences in technique have been noted as well as the variations in geometry and a few further examples of particular configurations are given in Fig:61, described below.

The angle of attack of the manus is clearly shown in (a) and (b) for the down and up strokes of a gull flying normally.

In (c) the manus is moving backwards and outwards and the wide separation of the primaries is very marked. There is obviously considerable lift as well as thrust being produced by the manus in this position.

The twisting of the manus about the wrist joint is shown in (d) and it appears that the elbow has been appreciably flexed in order to allow this movement. The wing is near the top of the upstroke and has commenced the backward kick produced by straightening.

The Brahminy kite (Haliastur indus) shown in (e) and (f) is gliding slowly and uses the tail as a rudder in some circumstances. In (f) it is twisted through an angle of about 45° while remaining flat, and is bent to the left.

The last two are drawings of an Alpine chough (Pyrrhocorax graculus) soaring (g) and about to land (h). Both the kite and the chough, unlike the gulls, appear to use the tail as an auxiliary supporting surface when gliding.
CHAPTER VI.

CONTROL.
CHAPTER SIX.

6. STABILITY AND CONTROL.

6.1 General.

Rotation about the vertical axis (YY) is defined as yaw, about the transverse axis (ZZ) as pitch and about the longitudinal axis (XX) as roll (Fig:62).

This chapter is supplementary to Chapter V since a number of control aspects have been mentioned in discussing flight.

It must be reiterated, when considering the question of control, that most aircraft are stable whereas a flying animal is not.

6.2 Yaw.

Directional control for an aircraft in horizontal flight is maintained by the fixed vertical fin and the rudder and the system is inherently stable but, as the bird has no vertical fin, other means must be employed. Directional stability is also aided by sweepback of the wings and this the bird can supply.

A study of the gull when gliding reveals that the tail is closed for most of the time and bent into a conical surface, concave upwards as shown in Fig:64(a). The axis of this cone is normally parallel to the X-axis but may be moved from side to side at will by rotation at the base. If
Figure: 62  Definitions of control axes

Figure: 63  Stability - (a) longitudinal
            (b) lateral

Figure: 64  Use of tail as a rudder
it be swung to one side the average direction of the air flow through it is no longer parallel to $XX$ and a side thrust is developed tending to swing the body about $YY$. In Fig:64(b) the base of the tail has been rotated in a clockwise direction thus moving the axis of the cone to the left and producing a force, on the tail, to the right. Since, in general, the amount of fortuitous yaw should be small only small correcting forces are required.

The yawing moment may be greatly assisted, if required, by adjustment of the wings. Thus if, say, the right wing be extended and the left retracted and adjusted to give the same lift (in order to prevent roll) there will be a net moment about $YY$ due to the movement of the centres of drag on the wings. Although the increased angle of attack of the left wing necessary to produce the required lift, will result in increased drag the resultant is closer to the body so that the moment about $YY$ can still be less than for the right wing.

6.3 Pitch.

In the steady state the total lift balances the weight and the lines of action both pass through the centre of gravity (Fig:63(a)), thus the system is in equilibrium. Since the wings are at the top of the body the resultant lift can be above the centre of gravity, in which case the system is in stable equilibrium.
Control in pitch is, therefore, very easily achieved by moving the resultant lift forward or aft as required and this may be done by moving the whole wing from the shoulder or the manus alone as circumstances require.

The tail may be raised or lowered and thus act as the elevators on an aircraft but this is usually only done when landing, taking off or hovering in the species discussed at length herein. However, note the comments on the Brahminy kite and the Alpine chough at the close of Chapter V which also apply to many other species.

In the steady state, the resultant lift of the two wings will be equal and the same distance from the centre line so that equilibrium obtains (Fig:63(b)).

6.4 Roll.
Rolling may be corrected or induced by one of three methods.

(a) Folding one wing slightly, thus reducing the area and lift and bringing the resultant closer to the body.
(b) Altering the angle of attack of the whole wing.
(c) Altering the angle of attack of the manus only thus using it as an aileron.

Any combination of these methods may be used and, as discussed in the section on gliding in Chapter V, such combinations appear to be the normal procedure.
Figure: 65  Effect of roll on lift

Figures: 66 and 67  Forces involved during turn
The fact that the wings droop towards the tips and therefore have, in effect, a negative dihedral shows that the system is not stable. If the wings be considered as rigid any departure from the horizontal position will cause the lower wing to lose lift due to the reduction in projected area and the upper to gain lift due to increased projected area. In Fig: 65, (a) is the level state and (b) is the rolled. In both cases $l_1$ may be taken as the projected area of a wing and in (b) $l_1$ is obviously greater than $l_2$. This instability makes for a high degree of manoeuvrability and is no disadvantage since the whole mechanism is so flexible.

6.5 Turning.

This is a manoeuvre in its own right since it involves both yaw and roll. In a correctly executed turn an aircraft is rolled so that the resultant of the weight and the centripetal forces acts along the Y-axis of the machine. Presumably, in general the same will apply to a bird and, in any case, it would be difficult for the latter to execute a flat turn since there is no vertical rudder to produce the necessary force. In Fig: 66, $L$ is the total lift force, $W$ the weight and $C.F.$ the centripetal force necessary to keep the animal following a curved path.

A bird may execute a turn in the following manner, using both wings and tail.
1) A roll is initiated by altering the balance of lift between the two wings.

2) Once the Z-axis is inclined, if the resultant lift of the wings be moved forward of the centre of gravity, there will be a moment about ZZ tending to pull the head round in the direction of the roll. Fig: 67(a).

3) If necessary, in the rolled position the tail may be used to assist turning by moving it in a dorsal direction. Fig: 67(b).

6.6 **Conclusion.**

Only a general picture of some control actions is given above. There are many combinations which may be used as required. In an emergency, for instance, the bird can stop very quickly by stalling and then, by a vigorous thrust of one or other wing, fly off in a new direction.
CHAPTER VII.

CONCLUSION.
CHAPTER SEVEN.

7. **CONCLUSION.**

The wing may be likened to a system of mechanical linkages and actuators such as is used in an aircraft except that it is, of course, far more complex than the latter.

The bones and joints are such that the wing is sufficiently strong and rigid yet is light and may take any shape, within limits, required by circumstances. The muscles are the actuators and the primary means of setting the wing and some of them supply the motive power necessary to propel the animal through the air.

The experimental work on the anatomical side has been concerned with determining the effect of muscle contraction, the exact route followed by the tendons and the points of insertion with respect to the articular surfaces. With this information it is possible to deduce the direction of the forces on a component and the interaction of these with the aerodynamic forces. The analytical side of the work was devoted to the study of a large number of high speed cinematograph films of birds in various flying modes in order to determine the aerodynamic actions.
The analysis of the forces on various parts of the wing, while being qualitative rather than quantitative in any strict sense, is necessary in order to ensure that muscle actions are not misinterpreted. For instance it is shown that the pronators and supinator of the forearm are primarily used for resisting the moment about the latter caused by the loading on the wing distal to the ulna axis. Again, during the upstroke when this is being used propulsively, there is a forward force on the distal phalanx of digit III. Forward flexion of the joint is not desirable and the form is such that this would, in any case, be difficult without straining the posterior ligaments. This, then, partly explains the tendon run and insertion of M. interosseus palmaris. Since it runs over the posterior edge of the post-distal extension of phalanx 1 (see Fig:21) to insert on the posterior edge of phalanx 2 it acts as a powerful reinforcement to the ligaments.

If the direction of the forces and the plane of the moment are known, the form of the joint can be shown to be eminently adapted thereto.

The elbow joint must be able to resist a moment in a plane at right angles to the axis of the forearm and yet not be so rigid as to preclude rotation of the wrist. A simple hinge joint would satisfy the first requirement but not the second and would also cause difficulty in folding. In the
folded position the distal end of the forearm falls below the head of the humerus in order to allow the manus to lie ventro-dorsally along the side of the body. While this could be done with a simple hinge having an inclined pin the wrist would be constrained to move in a plane at right angles to the pin. In these circumstances the position of the wrist with respect to the humerus in the partly flexed wing would be rigidly prescribed and general flexibility lost.

At the wrist one of the most notable features is the os ulnare which lies post-ventral to the main joint. The depth of the joint proper is not very great but there is a considerable moment here when the extended wing is moving rapidly downwards. Hence some additional strengthening is required and this is provided by the os ulnare. During the upstroke the outer wing lags behind the inner until near the upper limit of movement so that there is a downward flexing at the wrist. The os ulnare in no way interferes with this since it tends to move posteriorly out of the way. This compound joint at the wrist consisting of the two carpals and their connecting cartilage, the distal ends of the radius and ulna and the metacarpus permits a large angular movement during folding. The downward droop of the manus often noted in birds when gliding does not conduce to aerodynamic stability, which later has been shown not to be important, but it does decrease the load on the ventral muscles and ligaments produced by the upward force on the
outer wing.

The second phalangeal joint is a further illustration of good design. The load here is almost entirely due to the first primary feather since this and some coverts are all that is mounted thereon. The only movement required of the feather in flight is a slight rotation and for this provision has been made (Fig: 6). A simple swivel joint would be unsuitable since there must be provision for some flexing in order to prevent breakage due to accidental encounters with external objects. The four muscles, M.M.extensor indicis longus, flexor digitorum profundus, interosseus palmaris et interosseus dorsalis are so arranged that they can produce slight rotation of the phalanx as well as bracing it against flexing.

Analysis of the photographs and visual observation backed by the mechanical concept of the wing have brought several interesting points to light.

The wings of a bird in a steady glide are usually spread in the form of a shallow M as viewed along the X-axis. In these conditions it is noted that the primaries, in all species here examined with the exception of Hemiphaga, show no upward bending. Hemiphaga has been excluded in the above because, being rare, observations have been few and inconclusive but there is no obvious reason why the same
pattern should not hold in this case. The fact that the primaries are not bent indicates that the loading here is light and confirms the original conjecture that the centre of pressure for the wing as a whole will be as close to the body as possible in order to reduce the load on the wrist joint and on the pectoral muscles.

When landing, the X-axis of the body is steeply inclined and the wings sweep forward in a nearly horizontal plane with the chord almost vertical. If the body axis is not sufficiently inclined this wing movement is achieved by dropping the elbows during the forward sweep. The wings are subsequently raised with the chord parallel to the resultant air flow over them thus giving minimum downward force on the body and little thrust. This action is difficult to exhibit in a series of still figures (Fig: 59), but is quite clear when running slow-motion films. It is said that the aerodynamic force on the wing at any instant is, in general, applied in such a position that it tends to alter the wing setting in the direction of decreasing load. This applies to all joints except the shoulder and here the statement does not always hold good. In cases when the statement is true the requisite muscles act in opposition to this and permit a greater or less change according to their tensions. As an example, the moment about the skeleton of the manus is, for gliding say, such as to produce
pronation with a consequent decrease in angle of attack and load. This movement is restrained chiefly by \textit{M. flexor carpi ulnaris} acting through the \textit{os ulnare}. During an upstroke, when the pressure is on the upper surface, the tendency to supinate is opposed by \textit{M. obliquus}, the tendon of which runs over the anterior face of the \textit{os radiale} to an insertion on the ventral surface of the metacarpus and has a powerful pronating action.

The wing is light, strong, flexible and appears to be extremely efficient as an aerofoil. The camber may be altered by muscular action so that, when required, increased lift is available and the form remains such as to give a high value of the lift/drag ratio. The trailing edge is extremely thin and capable of flexion without damage. This flexibility allows the trailing edge to bend upwards thus forming a reflex aerofoil (see Fig: 1(c)) which has several advantages. The fore and aft movement of the centre of pressure, due to changes in angle of attack, is far less than with the more conventional aerofoil and the point of separation of the flow over the upper surface is moved much closer to the trailing edge and thus reduces the drag.

In the photographs of birds gliding there is no sign of the coverts lifting, as would be probable if breakaway of the flow had occurred, except at high angles of attack caused by up gusts.
<table>
<thead>
<tr>
<th>Author(s)</th>
<th>Year</th>
<th>Title</th>
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<tbody>
<tr>
<td>BERGER, Andrew J.</td>
<td>1954</td>
<td>The Myology of the Pectoral Appendage of three genera of American Cuckoos.</td>
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<tr>
<td>BORELLI</td>
<td>1710</td>
<td>De Motu Animalium. 2 Vo.</td>
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<thead>
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<th>Author(s)</th>
<th>Year</th>
<th>Title</th>
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<th>Author</th>
<th>Year</th>
<th>Title</th>
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<table>
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<th>Author</th>
<th>Year</th>
<th>Title and Details</th>
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<tr>
<td></td>
<td>1960</td>
<td>Biophysics of Bird Flight.</td>
</tr>
<tr>
<td>R &amp; M No.72</td>
<td>1913</td>
<td>Experiments on Models of Aeroplane Wings. H.M.S.O. London.</td>
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<td></td>
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<td></td>
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<td></td>
<td>1916</td>
<td>Test of Four Slotted Aerofoils (Handley-Page). H.M.S.O. London</td>
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<td></td>
<td>1922</td>
<td>Test of Four Thick Aerofoils H.M.S.O. London</td>
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<td>SHESTAKOVA, G.S.</td>
<td>1890</td>
<td>Myology of the Raven. London.</td>
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<tr>
<td></td>
<td>1953</td>
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<tr>
<td></td>
<td>1954</td>
<td>The Effect of Wing Inertia on the Wing-stroke frequency of Moths,</td>
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<tr>
<td>STRESEMANN, E.</td>
<td>1934</td>
<td>Handbuch der Zoologie.</td>
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<td>Name</td>
<td>Year</td>
<td>Title</td>
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<td>THOMSON, A.</td>
<td>1964</td>
<td>A New Dictionary of Birds,</td>
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<td></td>
<td>New York.</td>
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<td>THOMSON, J.A.</td>
<td>1923</td>
<td>Biology of Birds,</td>
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<td></td>
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<td>London.</td>
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<td></td>
<td></td>
<td>Ed. J.T. Bonner C.U.P.</td>
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<td></td>
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<td>Cambridge.</td>
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<td>WALKER, G.T.</td>
<td>1925</td>
<td>The Flapping Flight of Birds.</td>
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<tr>
<td>WALKDEN, S.L.</td>
<td>1925</td>
<td>Experimental Study of the Soaring Albatrosses.</td>
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<td></td>
<td></td>
<td>Quart. Rev. Biol. 6: 84-98.</td>
</tr>
<tr>
<td>WHITE, G.</td>
<td>1720-1793</td>
<td>The Natural History of Selbourne.</td>
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</tbody>
</table>
WING LOADING.

The load curves (Figs: 68 and 69) are quite arbitrary except in that they satisfy the observed wing shape and give reasonable forces at the joints. The first trial curve was sketched in and modified slightly to bring the resultant centre of pressure nearer to the body. The loading near the root was increased when it was realised that, with the very sweet blending of the wing into the body, the lift could be high in this region. It is possible that this latter lift could be even higher but it was judged better not to work on this assumption until experimental verification is available.

It should be noted that, for a rigid untwisted wing, the drag is a minimum when the spanwise loading curve is an ellipse. However, again for a rigid wing, this loading may be modified by introducing twist and the drag be thereby reduced to a minimum for one particular angle of setting (see "Elements of Aerofoil and Airscrew Theory", Glauert 1948). Since the twist and camber of the bird's wing may be varied at will it seems reasonable to suppose that the drag is normally kept at the minimum value.

The load curves and quarter point positions are given in Fig: 68 for Columba and in Fig: 69 for Larus dominicanus.
Figure: 68 Geometry of the wing and loading distribution - *Columba livia*
All the quarter points, except those inboard of the elbow, and the centre of pressure are forward of the Z axis in both species.

The data for *Columba* is given below and in Table VII.

*Columba livia*

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
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<tr>
<td>Half weight</td>
<td>150.1 g.</td>
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<tr>
<td>Wing length</td>
<td>30 cm.</td>
</tr>
<tr>
<td>Wing area</td>
<td>261.7 cm(^2)</td>
</tr>
<tr>
<td>Average wing loading</td>
<td>0.575 gf/cm(^2)</td>
</tr>
<tr>
<td>Mean lift coefficient</td>
<td>0.51</td>
</tr>
<tr>
<td>Total drag</td>
<td>12.9 gf(^1)</td>
</tr>
<tr>
<td>Centre of pressure from XX</td>
<td>6.5 cm.</td>
</tr>
<tr>
<td></td>
<td>from ZZ</td>
</tr>
<tr>
<td></td>
<td>0.24 cm. (ant.)</td>
</tr>
</tbody>
</table>

The following table (Table VII) gives values of the various functions and parameters at the different stations.

**N.B.** 1 The symbol gf. is used to indicate a force (= 981 dynes) as opposed to g. for a mass.
**TABLE VII.**

<table>
<thead>
<tr>
<th>Station</th>
<th>Load (gf)</th>
<th>Loading (gf/cm²)</th>
<th>M(X) (gf/cm)</th>
<th>M(Z) (gf/cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.3</td>
<td>.04</td>
<td>8.2</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>0.4</td>
<td>.04</td>
<td>10.2</td>
<td>-0.1</td>
</tr>
<tr>
<td>3</td>
<td>0.6</td>
<td>.05</td>
<td>14.0</td>
<td>-0.3</td>
</tr>
<tr>
<td>4</td>
<td>1.4</td>
<td>.09</td>
<td>29.9</td>
<td>-1.3</td>
</tr>
<tr>
<td>5</td>
<td>1.8</td>
<td>0.11</td>
<td>34.8</td>
<td>-2.0</td>
</tr>
<tr>
<td>6</td>
<td>2.3</td>
<td>0.133</td>
<td>39.7</td>
<td>-2.8</td>
</tr>
<tr>
<td>7</td>
<td>3.4</td>
<td>0.18</td>
<td>51.9</td>
<td>-4.2</td>
</tr>
<tr>
<td>8</td>
<td>5.0</td>
<td>0.22</td>
<td>66.1</td>
<td>-7.3</td>
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<tr>
<td>9</td>
<td>9.2</td>
<td>0.39</td>
<td>102.9</td>
<td>-11.2</td>
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<tr>
<td>10</td>
<td>19.5</td>
<td>0.76</td>
<td>178.6</td>
<td>-19.8</td>
</tr>
<tr>
<td>11</td>
<td>25.7</td>
<td>0.94</td>
<td>183.2</td>
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<tr>
<td>12</td>
<td>27.0</td>
<td>1.09</td>
<td>137.7</td>
<td>0</td>
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<tr>
<td>13</td>
<td>27.0</td>
<td>1.63</td>
<td>82.9</td>
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<tr>
<td>14</td>
<td>26.5</td>
<td>1.7</td>
<td>27.6</td>
<td>+19.3</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>967.7</td>
<td>-35.7</td>
</tr>
</tbody>
</table>

For *Larus dominicanus* the data is given below and in Table VIII.

**Larus dominicanus**

- Half weight: 370.6 g.
- Wing length: 62.5 cm.
- Wing area: 757.2 cm²
- Average loading: 0.49 gf/cm²
- Mean lift coefficient: 0.44
- Total drag: 29.9 gf.
- Centre of pressure from XX: 14.5 cm.
  - from ZZ: 0.85 cm. (ant.)
Figure: 69  Geometry of wing and loading distribution - Larus dominicanus
Table VIII below gives further details.

**TABLE VIII.**

<table>
<thead>
<tr>
<th>Station</th>
<th>Load (gf)</th>
<th>Loading ( \frac{gf}{cm^2} )</th>
<th>( M(X) ) (gf/cm)</th>
<th>( M(Z) ) (gf/cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.5</td>
<td>0.037</td>
<td>30.0</td>
<td>-0.6</td>
</tr>
<tr>
<td>2</td>
<td>1.0</td>
<td>0.043</td>
<td>55.2</td>
<td>-2.3</td>
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<td>3</td>
<td>1.4</td>
<td>0.048</td>
<td>70.7</td>
<td>-4.7</td>
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<tr>
<td>4</td>
<td>2.2</td>
<td>0.053</td>
<td>100.5</td>
<td>-8.1</td>
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<tr>
<td>5</td>
<td>3.5</td>
<td>0.060</td>
<td>143.4</td>
<td>-14.5</td>
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<tr>
<td>6</td>
<td>6.0</td>
<td>0.094</td>
<td>217.1</td>
<td>-24.9</td>
</tr>
<tr>
<td>7</td>
<td>11.0</td>
<td>0.150</td>
<td>345.7</td>
<td>-46.0</td>
</tr>
<tr>
<td>8</td>
<td>25.0</td>
<td>0.317</td>
<td>666.8</td>
<td>-97.2</td>
</tr>
<tr>
<td>9</td>
<td>49.0</td>
<td>0.582</td>
<td>1073.6</td>
<td>-149.5</td>
</tr>
<tr>
<td>10</td>
<td>64.0</td>
<td>0.793</td>
<td>1097.6</td>
<td>-59.2</td>
</tr>
<tr>
<td>11</td>
<td>70.0</td>
<td>0.927</td>
<td>866.6</td>
<td>+31.5</td>
</tr>
<tr>
<td>12</td>
<td>69.0</td>
<td>0.928</td>
<td>529.2</td>
<td>+47.6</td>
</tr>
<tr>
<td>13</td>
<td>68.0</td>
<td>0.944</td>
<td>161.8</td>
<td>+10.2</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>5358.2</td>
<td>-317.3</td>
</tr>
</tbody>
</table>

If the whole of the load at the shoulder be taken by M.pectoralis there will be a considerable positive moment about ZZ due to the projection of the deltoid crest forward of the axis. However M.M.latissimus dorsi, subscapularis et subcoracoideus not only help in supporting the body but, being inserted posterior to ZZ, tend to neutralise the moment due to M.pectoralis.

Fig: 70 is a dorsal view of the humeral head in which (a) and (b) are the co-ordinates of the mean pectoral
Figure: 70  Positions (estimated) of the effective insertion points of certain muscles

Figure: 71  Effect of extending the manus and moving the wing tip forward
insertion while (c) and (d) are the estimated values for the mean insertion of the other three muscles considered as a single unit.

The values are estimated to be as follows:

\[ a = 1.35 \text{ cm.} \]
\[ b = 0.25 \text{ cm.} \]
\[ c = 0.5 \text{ cm.} \]
\[ d = 0.4 \text{ cm.} \]

Moving the wing tip forward by extension of the manus only (Fig: 71) causes an increase in \( M(Z) \) as a supinating moment without having any appreciable effect on \( M(X) \). A forward movement of the wing tip of 3.3 cm., as in the figure, changes \( M(Z) \) from \(-36 \text{ gf.cm.} \) to \(-84 \text{ gf.cm.} \) with consequent change in the distribution of the forces between the muscles as shown below.

1. \( \text{M.pectoralis alone} \)
   \[
   \text{Load (pect.)} = \frac{M(X)}{a} \cdot \frac{968}{1.35} = 717 \text{ gf.}
   \]
   \[ M(Z) = 717 \times 0.25 = 179 \text{ gf.cm.} \]

2. \( \text{All muscles} \)
   \[
   \text{Load (pect.)} = 609 \text{ gf.}
   \]
   \[
   \text{Load (others)} = 291 \text{ gf.}
   \]
   \[ M(Z) = 0.25 \times 609 - 0.4 \times 291 = 35.9 \text{ gf.cm.} \]

The net moment about \( ZZ \) is reduced to a very small value.
3. As in 2. above but with wing tip moved forward 3.3 cm.

Load (pect.) 645 gf.
Load (others) 194 gf.

\[ M(Z) = 0.25 \times 645 - 0.4 \times 194 = 83.7 \]

The net moment about ZZ is small as before.

The angle of glide, that is the angle between the flight path and the horizontal in still air, is approximately 5° in both cases.
Figure: 72 The effect of the Alula

(a) raised alula

(b) aerodynamic fence
Fig. 7a.
APPENDIX II.

A NOTE ON THE ALULA.

There has been considerable speculation as to the function of the alula and, until an experimental technique has been devised and data obtained, it will be difficult to be definite on the subject.

When the alula is raised it forms a slot along the leading edge of the proximal part of the manus. The proportion of the manus thus treated varies but it is always short compared with a similar device on aircraft.

In some birds, notably the larger gliding sea birds (Albatross and the like), the alula appears to open seldom, if ever, but with land gliders (eagle, hawk) it is in constant use. When open it is often flexed upwards to a considerable degree thereby reducing the effective length of the slot still further, as shown in Fig: 72.

The following is a possible explanation of its function, which does not appear to have been propounded elsewhere, based on the fact that there can be a very rapid change in angle of attack in the vicinity of the wrist.

When gliding it is important that the wing tips should not stall for, if they do, lateral control is lost. Stalling of the inner wing, however, does not matter so much and is,
in fact, frequently used when landing in order to reduce forward speed. In this case there is considerable turbulence over the inner wing and it is necessary to prevent this from disturbing the flow over the tip.

In aircraft a fence is sometimes fitted to the wing as shown in Fig: 72 in order to confine the disturbance to the stalled portion. It may well be that the slot formed near the wrist produces a sufficiently strong unstalled flow near the wrist to act as a fence. When the alula is flexed as in Fig: 72 its function is probably changed to that of a vortex generator which has the same effect as the fence in keeping the flow from breaking away from the wing surface.

In this case the alula provides an aerodynamic fence by one means or the other and this tends to confine the disturbed flow to the inner wing.
WING-BEAT FREQUENCY.

The subject of wing-beat frequency in relation to the natural frequency of a vibrating system has been discussed by Sotavalta (1947, 1954), Pringle (1957) and Greenewalt (1960) with respect to insect wings. Greenewalt has extended the subject to include some consideration of bird wings, chiefly those of the humming bird.

The insect wing is more nearly analogous to a vibrating rigid cantilever than that of the bird, since the latter is much more flexible.

In any case the minimum work will be done by the muscles if the beat rate is close to the natural frequency of the vibrating system.

For the simplest case the wing is considered as a cantilever (Fig: 73) with all the mass concentrated at \( m \) and restrained by the springs \( S_1 \) and \( S_2 \) representing the shoulder muscles. The fundamental frequency of this system is given by:

\[
f = \frac{1}{2\pi} \sqrt{\frac{x}{ml^2}} (S_1 + S_2)
\]  

This corresponds to the case of the wing moving as a whole, as is the case during the first part of the downstroke.
Figure: 73 Wing as simple system

Figure: 74 Wing as compound system

\[ S_1 \text{ depressor muscles of shoulder} \]
\[ S_2 \text{ levator muscles of shoulder} \]
\[ S_3 \} \]
\[ S_4 \} \text{ muscles of wrist} \]
Since the mass and the distance $x$ are fixed the frequency is affected by any alteration of $l$, $S_1$, and $S_2$, the latter representing the tensions of the muscles in opposition.

If the wing be in two parts flexibly connected Fig: 74 replaces the system of Fig: 73. The frequency of the outer wing about the wrist joint at $m$ is given by:

$$f_w = \frac{1}{2\pi} \sqrt{\frac{y^2(S_3 + S_4)}{m^2(l_2 - l_1)^2}}$$  \hspace{1cm} (2)

and for the wing as a whole, about the shoulder:

$$f = \frac{1}{2\pi} \sqrt{\frac{x^2(S_1 + S_2)}{m_1l_1^2 + m_2l_2^2}}$$  \hspace{1cm} (3)

The wing is, therefore, not a simple oscillator and the periods of the two half strokes can be very different. During the first half of the downstroke the wing is rigid and equation (3) applies. During the remainder of this period equation (2) will, to some extent, apply but it must be remembered that the wrist starts its upward movement before the manus has reached the limit of its downward movement.

The air pressure produces a damping force and, whatever the complication of the beat the muscular energy required will normally be a minimum.
Figure: 75 Aerodynamic Extension of Manus

(a) $-5^\circ$ angle of attack
(b) $+5^\circ$ angle of attack
(c) $+9^\circ$ angle of attack
(d) forces on section of primaries
EXTENSION OF THE MANUS.

In order to determine the effect of aerodynamic forces on the manus, the wing of a fresh swan (*Cygnus atratus*) was severed at the shoulder and set in plaster to the elbow. The elbow joint was set in the fully extended position so that the extensor muscles and tendons of the man are as taut as possible.

The wing was then mounted in the wind tunnel on a turntable and tested at an air speed of about 50 ft./sec.

As the angle of attack was varied from a few degrees negative to a high positive value the manus extended, this being due to aerodynamic force alone.

Fig: 75 shows the wing in three positions. In (a) the angle of attack is approximately $-5^\circ$ and it will be seen that is considerable sweep back of the leading edge. As the angle of attack is increased to about $+5^\circ$, (b), the leading edge advances and the primaries spread to some extent. Increasing the angle of attack to $+9^\circ$, (c), the extension has reached the normal limit of forward movement.

This shows conclusively that the reaction on the leading primaries is in a forward direction.

Fig: 75(d) represents a section near the tip and shows the overlapping primaries and the direction of the forces on these.