

## THE GEOLOGICAL HISTORY OF FLYING VERTEBRATES.

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*(Presidential Address, delivered February 5th, 1915.)*

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### I.—INTRODUCTION.

**A**MONG the multitudinous attempts which have been made by man during the past half-century to improve his powers of locomotion, few have been followed with greater public interest than his efforts to achieve the conquest of the air. While success, so far as the surface of the earth is concerned, has been attained, on the large scale, by the successive inventions of the steam engine, the electric motor, and the internal combustion engine, and on the small scale by the bicycle, the desire to rise from the surface and fly through the air above has ever been seething in the minds of men, and many ingenious brains have been continually puzzling over and grappling with the elusive problem.

During the last few years progress has been rapid, though marked by a terrible series of tragic accidents, and almost complete success appears to have been attained. The outbreak of war has greatly stimulated further research and has focussed public opinion upon the question to an extraordinary degree. To me it appears a horrible travesty of civilisation, that the first-fruits of man's latest, and, in some respects, greatest achievement should be devoted to the slaughter of his fellow creatures. The darkened streets through which you groped your way to attend this meeting are an eloquent testimony to the apprehension of this new terror of the sky. Under the circumstances I can only hope that man's mastery over nature is not yet quite so complete as some enthusiasts would have us believe.

From the consideration of the history of the development of flight by man, one is naturally led to the study of its develop-

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# A LIST OF FLYING VERTEBRATES WITH THEIR GEOLOGICAL RANGE.

(Among the Birds and Bats only those genera which have been found fossil are mentioned.)

|                                      | Trias. |         |        | Rhetic. | Lias.  |         |        | Oolites. |         |        | Cretaceous. |        | Eocene. | Oligocene. | Miocene. | Pliocene. | Quaternary.<br>E. Extinct. L. Living |
|--------------------------------------|--------|---------|--------|---------|--------|---------|--------|----------|---------|--------|-------------|--------|---------|------------|----------|-----------|--------------------------------------|
|                                      | Lower. | Middle. | Upper. |         | Lower. | Middle. | Upper. | Lower.   | Middle. | Upper. | Lower.      | Upper. |         |            |          |           |                                      |
| CLASS PISCES.                        |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| SUB-ORDER PROTOSPONDYLI.             |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| Fam. Semionotidæ.                    |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Dollopterus</i> ... .. × ... ..   |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| SUB-ORDER ISOSPONDYLI.               |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| Fam. Pholidophoridæ.                 |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Thoracopterus</i> ... .. × ... .. |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Gigantopterus</i> ... .. × ... .. |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| Fam. Pantodontidæ.                   |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Pantodon</i> ... .. × ... ..      |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| Fam. Chirothricidæ.                  |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Chirothrix</i> ... .. × ... ..    |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Telepholis</i> ... .. × ... ..    |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Exocoetoides</i> ... .. × ... ..  |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| SUB-ORDER OSTARIOPHYSI.              |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| Fam. Characinidæ.                    |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Gastroleucus</i> ... .. × ... ..  |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| SUB-ORDER PERSESOCES.                |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| Fam. Scombrisocidæ.                  |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Exocoetes</i> ... .. × ... ..     |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| SUB-ORDER HEMIBRANCHII.              |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| Fam. Pegasidæ.                       |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Pegasus</i> ... .. × ... ..       |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| SUB-ORDER ACANTHOPTERYGII.           |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| Fam. Dactylopteridæ.                 |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |
| <i>Dactylopterus</i> ... .. × ... .. |        |         |        |         |        |         |        |          |         |        |             |        |         |            |          |           |                                      |

CLASS AMPHIBIA.

ORDER ECAUDATA.

[illegible]

CLASS REPTILIA.

ORDER SQUAMATA.

SUB-ORDER OPHIDIA.

[illegible][illegible]

SUB-ORDER LACERTILIA.

Fam. Geckonidæ.

[illegible]

Fam. Agamidæ.

[illegible]

## ORDER PTEROSAURIA.

SUB-ORDER PTERODERMATA.

[illegible][illegible][illegible]

|                      |     |     |     |     |     |     |     |     |   |     |     |   |     |     |     |     |     |     |     |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|---|-----|-----|-----|-----|-----|-----|-----|
| <i>Scaphognathus</i> | ... | ... | ... | ... | ... | ... | ... | ... | × | ... | ... | × | ... | ... | ... | ... | ... | ... | ... |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|---|-----|-----|-----|-----|-----|-----|-----|

|                       |     |     |     |     |     |     |     |     |     |     |   |     |   |     |     |     |     |     |     |
|-----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|---|-----|-----|-----|-----|-----|-----|
| <i>Ramphocephalus</i> | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | × | ... | × | ... | ... | ... | ... | ... | ... |
|-----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|---|-----|-----|-----|-----|-----|-----|

|                       |     |     |     |     |     |     |     |     |     |     |     |   |     |     |     |     |     |     |     |
|-----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|-----|-----|
| <i>Ramphorhynchus</i> | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | × | ... | ... | ... | ... | ... | ... | ... |
|-----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|-----|-----|

SUB-ORDER ŌRNITHOCHEIROIDEA.

|                      |     |     |     |     |     |     |     |     |     |     |     |   |     |     |     |     |     |     |     |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|-----|-----|
| <i>Pterodactylus</i> | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | × | ... | ... | ... | ... | ... | ... | ... |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|-----|-----|

|                        |     |     |     |     |     |     |     |     |     |     |     |     |   |     |     |     |     |     |     |
|------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|-----|
| <i>Ptenodracon</i> ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | × | ... | ... | ... | ... | ... | ... |
|------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|-----|

|                      |     |     |     |     |     |     |     |     |     |     |     |     |   |     |     |     |     |     |     |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|-----|
| <i>Cycnorhamphus</i> | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | × | ... | ... | ... | ... | ... | ... |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|-----|

|                      |     |     |     |     |     |     |     |     |     |     |     |     |   |   |   |     |     |     |     |     |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|---|---|-----|-----|-----|-----|-----|
| <i>Ornithochirus</i> | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | × | × | × | ... | ... | ... | ... | ... |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|---|---|-----|-----|-----|-----|-----|

|                      |     |     |     |     |     |     |     |     |     |     |     |     |   |     |     |     |     |     |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|
| <i>Ornithodesmus</i> | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | × | ... | ... | ... | ... | ... |
|----------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|

|                   |     |     |     |     |     |     |     |     |     |     |     |     |     |     |   |     |     |     |     |     |
|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|
| <i>Pteranodon</i> | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | × | ... | ... | ... | ... | ... |
|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|

|                        |     |     |     |     |     |     |     |     |     |     |     |     |     |     |   |     |     |     |     |     |
|------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|
| <i>Nyctosaurus</i> ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | × | ... | ... | ... | ... | ... |
|------------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|---|-----|-----|-----|-----|-----|

# A LIST OF FLYING VERTEBRATES WITH THEIR GEOLOGICAL RANGE—*continued*.

(Among the Birds and Bats only those genera which have been found fossil are mentioned.)

|                                      | Upper Oolite. | Lower Cretaceous. | Upper Cretaceous. | Eocene. | Oligocene. | Miocene. | Pliocene. | Quaternary.<br>E, Extinct. L. Living |
|--------------------------------------|---------------|-------------------|-------------------|---------|------------|----------|-----------|--------------------------------------|
| CLASS AVES.                          |               |                   |                   |         |            |          |           |                                      |
| ORDER SAURURÆ.                       |               |                   |                   |         |            |          |           |                                      |
| <i>Archæopteryx</i> ... ..           | X             | ...               | ...               | ...     | ...        | ...      | ...       | ..                                   |
| ORDER CARINATÆ.                      |               |                   |                   |         |            |          |           |                                      |
| SUB-ORDER ODONTORMÆ.                 |               |                   |                   |         |            |          |           |                                      |
| <i>Ichthyornis</i> ... ..            | ...           | ...               | X                 | ...     | ...        | ...      | ...       | ...                                  |
| <i>Apatornis</i> ... ..              | ...           | ...               | X                 | ...     | ...        | ...      | ...       | ...                                  |
| SUB-ORDER EUORNITHES.*               |               |                   |                   |         |            |          |           |                                      |
| Grebes, <i>Colymboides</i> ...       | ...           | ...               | ...               | X       | X          | ...      | ...       | ...                                  |
| Penguins, <i>Palæudyptes</i>         | ...           | ...               | ...               | X       | ...        | ...      | ...       | ...                                  |
| <i>Palæopheniscus</i> ...            | ...           | ...               | ...               | X       | X          | ...      | ...       | ...                                  |
| <i>Paraptenodytes</i> ...            | ...           | ...               | ...               | ...     | X          | ...      | ...       | ...                                  |
| Albatrosses, <i>Diomedea</i>         | ...           | ...               | ...               | ...     | ...        | ...      | X         | L                                    |
| Gulls, <i>Halcyornis</i> ...         | ...           | ...               | ...               | X       | ...        | ...      | ...       | ...                                  |
| Gannets, <i>Odontopteryx</i>         | ...           | ...               | ...               | X       | ...        | ...      | ...       | ...                                  |
| <i>Argillornis</i> ... ..            | ...           | ...               | ...               | X       | ...        | ...      | ...       | ...                                  |
| <i>Prophæthon</i> ... ..             | ...           | ...               | ...               | X       | ...        | ...      | ...       | ...                                  |
| <i>Sula</i> ... ..                   | ...           | ...               | ...               | X       | ...        | ...      | ...       | L                                    |
| Pelicans, <i>Pelecanus</i> ...       | ...           | ...               | ...               | ...     | ...        | X        | ...       | L                                    |
| <i>Palagornis</i> ... ..             | ...           | ...               | ...               | ...     | ...        | X        | ...       | ...                                  |
| Hérons, <i>Proherodius</i>           | ...           | ...               | ...               | X       | ...        | ...      | ...       | ...                                  |
| <i>Ardea</i> ... ..                  | ...           | ...               | ...               | ...     | ...        | X        | X         | L                                    |
| Auks, <i>Mancalla</i> ... ..         | ...           | ...               | ...               | ...     | ...        | X        | ...       | ...                                  |
| Cranes, <i>Palæogrus</i> ...         | ...           | ...               | ...               | X       | ...        | ...      | ...       | ...                                  |
| Ibises, <i>Ibidopsis</i> ... ..      | ...           | ...               | ...               | X       | ...        | ...      | ...       | ...                                  |
| Cormorants, <i>Graculavus</i> ?      | ...           | ...               | X                 | ...     | ...        | ...      | ...       | ...                                  |
| Flamingos, <i>Agnopterus</i>         | ...           | ...               | ...               | X       | ...        | ...      | ...       | ...                                  |
| <i>Helornis</i> ... ..               | ...           | ...               | ...               | ...     | ...        | X        | ...       | ...                                  |
| <i>Palælodus</i> ... ..              | ...           | ...               | ...               | ...     | ...        | X        | ...       | ...                                  |
| <i>Phœnicopterus</i> ... ..          | ...           | ...               | ...               | ...     | X          | X        | ...       | ...                                  |
| <i>Scaniornis</i> ... ..             | ...           | ...               | X                 | ...     | ...        | ...      | ...       | ...                                  |
| Ducks, <i>Anas</i> ... ..            | ...           | ...               | ...               | ...     | ...        | X        | X         | L                                    |
| Geese, <i>Anser</i> (and others)...  | ...           | ...               | ...               | ...     | ...        | X        | X         | L                                    |
| <i>Cnemiornis</i> ... ..             | ...           | ...               | ...               | ...     | ...        | ...      | ...       | E                                    |
| Secretary birds, <i>Serpentarius</i> | ...           | ...               | ...               | ...     | ...        | X        | ...       | L                                    |
| Eagles, <i>Aquila</i> ... ..         | ...           | ...               | ...               | ...     | ...        | ...      | X         | L                                    |
| <i>Harpagornis</i> ... ..            | ...           | ...               | ...               | ...     | ...        | ...      | ...       | E                                    |

\* A large number of genera of fossil birds have been described, but as in many cases their identification and affinities are uncertain, I have given a selection only, grouped under the English names of their nearest allies.

A LIST OF FLYING VERTEBRATES WITH THEIR  
GEOLOGICAL RANGE—*continued.*

[illegible]

# A LIST OF FLYING VERTEBRATES WITH THEIR GEOLOGICAL RANGE—continued.

|                          |  |     |     |     | Upper Oolite. | Lower Cretaceous. | Upper Cretaceous. | Eocene. | Oligocene. | Miocene. | Pliocene. | Quaternary.<br>E. Extinct. L. Living |
|--------------------------|--|-----|-----|-----|---------------|-------------------|-------------------|---------|------------|----------|-----------|--------------------------------------|
| ORDER RATITÆ—continued.  |  |     |     |     |               |                   |                   |         |            |          |           |                                      |
| SUB-ORDER RHEÆ.          |  |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | <i>Brontornis</i>                      | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ×        | ...       | ...                                  |
|                          | <i>Rhea</i>                            | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ?         | L                                    |
| SUB-ORDER STRUTHIONES.   |  |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | <i>Eremopezus</i>                      | ... | ... | ... | ...           | ...               | ...               | ×       | ...        | ...      | ...       | ...                                  |
|                          | <i>Struthio</i>                        | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ×         | L                                    |
| CLASS MAMMALIA.          |  |     |     |     |               |                   |                   |         |            |          |           |                                      |
| ORDER MARSUPIALIA.       |  |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | Fam. Phalangeridæ.                     |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | <i>Palæopetaurus</i>                   | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | E                                    |
|                          | <i>Petauroides</i>                     | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | L                                    |
|                          | <i>Petaurus</i>                        | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | L                                    |
|                          | <i>Acrobates</i>                       | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | L                                    |
| ORDER RODENTIA.          |  |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | Fam. Anomaluridæ.                      |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | <i>Anomalurus</i>                      | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | L                                    |
|                          | <i>Idiurus</i>                         | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | L                                    |
|                          | Fam. Sciuridæ.                         |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | <i>Petaurista</i> (= <i>Pteromys</i> ) | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | L                                    |
|                          | <i>Sciuropterus</i>                    | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | L                                    |
|                          | <i>Eupetaurus</i>                      | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | L                                    |
| ORDER INSECTIVORA.       |  |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | <i>Galæopithecus</i>                   | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ...      | ...       | L                                    |
| ORDER CHIROPTERA (BATS). |  |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | SUB-ORDER MICROCHIROPTERA.             |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | <i>Rhinolophus</i>                     | ... | ... | ... | ...           | ...               | ...               | ×       | ...        | ×        | ...       | L                                    |
|                          | <i>Alator</i>                          | ... | ... | ... | ...           | ...               | ...               | ×       | ...        | ...      | ...       | ...                                  |
|                          | <i>Pulzeonycteris</i>                  | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ×        | ...       | ...                                  |
|                          | <i>Nyctitherium</i>                    | ... | ... | ... | ...           | ...               | ...               | ×       | ...        | ...      | ...       | ...                                  |
|                          | <i>Nyctilestes</i>                     | ... | ... | ... | ...           | ...               | ...               | ×       | ...        | ...      | ...       | ...                                  |
|                          | <i>Vespertilio</i>                     | ... | ... | ... | ...           | ...               | ...               | ...     | ...        | ×        | ...       | L                                    |
|                          | <i>Vespertiliavus</i>                  | ... | ... | ... | ...           | ...               | ...               | ×       | ...        | ...      | ...       | ...                                  |
|                          | <i>Taphozous</i>                       | ... | ... | ... | ...           | ...               | ...               | ×       | ...        | ...      | ...       | L                                    |
|                          | <i>Necromantis</i>                     | ... | ... | ... | ...           | ...               | ...               | ×       | ...        | ...      | ...       | ...                                  |
|                          | <i>Provampyrus</i>                     | ... | ... | ... | ...           | ...               | ...               | ...     | ×          | ...      | ...       | ...                                  |
|                          | SUB-ORDER MEGACHIROPTERA.              |     |     |     |               |                   |                   |         |            |          |           |                                      |
|                          | <i>Archæopteropus</i>                  | ... | ... | ... | ...           | ...               | ...               | ...     | ×          | ...      | ...       | ...                                  |

ment in other animals, so I decided that "The Geological History of Flying Vertebrates" would be a subject particularly suitable for a presidential address at the present time.

At the outset it is worthy of remark that all animals which now have, or have ever possessed, the power of flight are, with one exception, vertebrates; but this exception—the Insects—is a class so numerous in type and so varied in structure that to have included it would have lengthened this address beyond all reasonable limits. It is also noteworthy that the assemblage of Flying Animals includes representatives of every one of the five great Classes into which vertebrates are divided—Fishes, Amphibia, Reptiles, Birds, and Mammals—although their proficiency in the art varies enormously.

Flying Animals fall naturally into two groups, the Fliers and the Gliders. The Fliers are those which, by the muscular motions of their limbs, are able to sustain themselves in the air and to alter the direction or altitude of their flight at will. The Gliders are those which possess specially modified skin coverings or appendages that can be spread out to form a parachute, and thus enable the animal to glide through the air without muscular effort. The glide can only be made in a downward direction, and is merely a prolonged kind of leap. The Gliders cannot alter the direction of their flight, but when flying against the wind can temporarily rise by altering the angle of the body so as to prolong the glide, but the extent of the flight primarily depends on the initial impetus of the leap. This is the passive type of flight. The gliding membrane consists of a double fold of skin which extends along the sides of the body, connecting, to a greater or less degree, the fore and hind limbs, and in some cases the tail also. Such a membrane is termed a "patagium." It is found in both reptiles and mammals.

The only animals possessing true flight are birds, bats, and pterodactyls. All the other so-called "flying" animals are merely gliders (with the possible exception of some of the fishes, see sequel). In the bats and the pterodactyls the patagium is converted into a true wing by modification of the bones of the fore limb. In the birds the wing is formed on a totally different plan.

Great attention has been paid of late to the study of the mechanical principles underlying the various forms of flight, but so far these are by no means thoroughly understood. Especially is this the case in the "soaring" flight by which vultures, for instance, can circle in still air for long periods with apparently motionless wings, rising, nevertheless, all the time. The latest writer on the subject, Dr. E. H. Hankin, whose book, "Animal Flight," was published last year, believes that it is not a question of mechanics alone, but that in some way the creature derives energy from the air, and, perhaps, also from the sun. Many

years' observation in India has shown him that there is a definite order in the time of day at which various birds begin to soar. As a rule, the heavier the bird the later the hour. He asserts that, at a given hour, which varies from day to day, the air may be "soarable" for one species but not for another, and this suggests that the amount of sunlight may have something to do with it. He shows that neither ascending currents nor heat eddies will explain the phenomenon, and his treatise, although somewhat inconclusive, is well worth studying, as showing the complexity of the problem.

On taking up the study of the evolution of Flight we find our investigations hampered by our old friend—or enemy—the imperfection of the geological record. To no branch of palæontological inquiry does this offer more serious obstacles. The great majority of flying animals are essentially land-dwellers, making temporary, although in some cases prolonged, incursions into the air, returning, however, to earth to rest. Only a few are able to go far from land, and so their fossilised remains are mostly confined to shallow marine, fresh water, or land deposits. When we consider how small a proportion the two last-named classes bear to the great mass of sedimentary rocks, it is not surprising that the sought-for remains are somewhat rare. Also, the bones of flying animals are extraordinarily light and thin, and therefore easily crushed and liable to destruction. Another difficulty is that in the whole of the "gliding" group the skeleton shows no special modification, so that it is not possible to recognise in the fossil remains the original capacity for flight which they might have possessed.

Nevertheless we shall find with regard to the various types of animals possessing true flight that there is sufficient fossil evidence to make up a fairly complete geological tale. I propose to deal with each zoological class separately and, after a rapid review of the living forms, to take the fossil forms on a stratigraphical basis.\*

## II.—FISHES.

It is hardly to be expected that flight should be developed to any great extent among the Fishes. Breathing, as they do, by gills, they are unable to remain long out of water, and although a few genera (such as are found in the Climbing Perch of India) have developed accessory breathing organs, while in the "Lung Fishes" (Dipnoi), *Neoceratodus*, *Protopterus* and *Lepidosiren*, the air bladder has been modified into a lung, none

\* A most instructive collection of all the animals possessing flight has been arranged by Dr. W. G. Ridewood at the Natural History Museum, South Kensington, and should be consulted by all interested in the subject.



of the known flying-fishes possesses any such modification of its breathing apparatus. All the larger forms are pelagic, and are very widely distributed in the warmer parts of the world. The function of their flight in most cases is to enable them to escape from their enemies, but it is possible that the fresh-water forms may also capture insects whilst in the air.

The flying organs of Fishes are usually the pectoral fins, which are very greatly enlarged, but in one fossil genus it is the ventral pair that has thus been altered. As a rule no other part of the skeleton has been modified, so that the identification of the fossil forms as flying-fishes depends entirely upon the chance preservation of the enlarged fins.

Whether or not the "flying" fishes really do fly is a point on which there is very great difference of opinion, and many papers have been written on both sides of the question. Most of the observers are agreed that there is some movement of the fins immediately after the fish leaves the water. But while some writers maintain that the flapping is continued at intervals, others assert that the fins are held rigid and merely act as planes, enabling the fish to glide through the air with the momentum gained by its initial leap from the water. If, however, as has been asserted, the fish has the power of altering its direction whilst in the air, the movement would appear to be rather more complicated than the latter view implies. It is very probable that the tail may occasionally touch the water at the crest of a wave, and by means of a flick the creature may alter the direction of the flight.

Another difficulty is that the flight, which in the case of *Exocætus* may attain to 200 or 300 yards, is often maintained at a uniform level at a height of only a few inches, and rarely more than a few feet above the water. If so long a flight were due only to the initial leap, one would expect that a greater trajectory would be necessary. Possibly some day this question may be set at rest by the help of the kinematograph.

The best fliers are the various members of the genus *Exocætus* (which has been subdivided by some authors, who have added *Cypselurus*, *Fodiator*, and *Exonautes*, as generic names). They belong to the family Scombriscidæ, which comprises the Skippers (*Scombresox*) and Garfish (*Belone*). Their pectoral fins are long and narrow, but the various species differ considerably in respect of the size of these fins. In some species they reach to the root of the tail, but in others they are not above half that length. This genus has a very wide range and is found all over the world in tropical and sub-tropical regions. The best-known form is probably *Exocætus evolvans*, the "Flying Herring," which is only about 10 to 12 inches long, but the Catalina flying-fish *Exocætus* (or *Cypselurus*) *californicus* reaches a length of 18 inches. Although in *Exocætus* the skeleton has not been

modified, in one species Mr. Burne has found that the muscles which move the pectoral fins are about four times as heavy as those of other fishes of the same size.

The Flying Gurnard, *Dactylopterus*, is a more heavily built fish than *Exocoetus* with much more limited powers of flight, the usual distance being only from 15 to 20 yards. The pectoral fins are broad and rounded, and in some species are beautifully coloured. Moseley says of one species, which inhabits the Sargosso sea, that "when startled by the boat flew away before it, and as they did so, appeared to me to buzz their wings very rapidly." For comparison of *Exocoetus* and *Dactylopterus*, see Figs. A and B of Plate 20.

The remaining modern flying fishes are all very small, and are highly specialised members of various suborders whose other members are not modified in this respect. In these the pectoral fins are only slightly enlarged, and they are not indeed flying fishes in the ordinary meaning of the term, although their habits are of sufficient interest as to warrant their being mentioned.

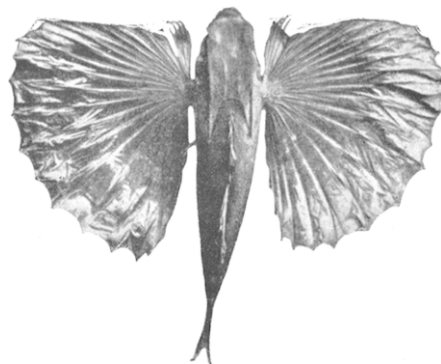
*Pantodon buchholzi*, the African Fresh-water Flying Fish, inhabits the Congo and Niger rivers. It merely springs out of the water, flutters along a little way and then falls back again. The first specimen known to have been caught by a European was taken in the air with a butterfly net. It is only about 3 inches long, and is the only species of its genus and family. One of its nearest relatives is the Barramunda of Queensland. Living specimens are at present to be seen in the Reptile House at the Zoological Gardens, Regent's Park.

*Gastrolepecus*, the American Fresh-water Flying Fish, is an aberrant member of the large fresh-water family, the Characinidæ, which includes some of the most powerful and ferocious fresh-water fishes known, such as the Dogs of the Water (*Hydrocyon*) of the Nile, and the Piranha (*Serrasalmo*) of South America. The family has a peculiar geographical distribution, being confined to the fresh waters of Africa and Central and South America.

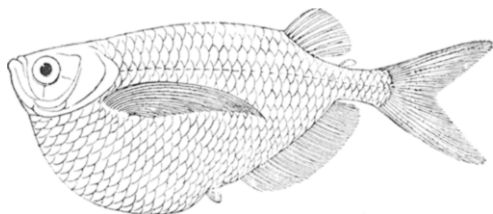
*Gastrolepecus* lives in the rivers of British Guiana. It is a small fish, a little over two inches long, with a very deep, narrow body. They dart along the surface of the water, with only the lower part of the body submerged, using their pectoral fins almost like oars, while the sharp keel of the body acts as a cut-water. After about 40 ft. of this mode of progression they leave the water entirely for a few feet, falling back when their original impetus is exhausted. This tiny creature is in one respect the most remarkable of all the "flying fishes," as being the only one in which the skeleton has been modified in accordance with its habits. The keel is strengthened internally by a thin, vertical, corrugated plate of bone, to the sides of which



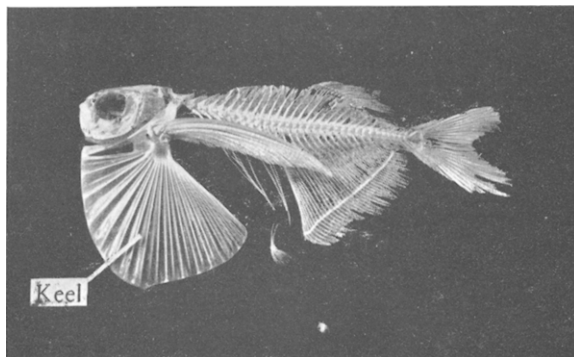
A.—*Exocoetidae*. About  $\frac{1}{3}$  nat. size.



B.—*Dactylopterus*. About  $\frac{1}{3}$  nat. size.



C.—*Gasteropelecus*. Nat. size.



D.—*Gasteropelecus*, skeleton. Nat. size.

THREE TYPES OF FLYING FISHES.

are attached the powerful muscles which move the pectoral fins.\* See Figs. C and D of Plate 20.

*Pegasus volitans*, which frequents flat, sandy coasts, in China and the East, has been called a flying fish, but, although its pectoral fins, when horizontally spread, look like wings, it can do no more than skim through the air for a short distance a little above the surface of the water. It has an angular, bony body about four inches long, and is allied to the Pipe-fishes and Seahorses of our own shores.

From the foregoing remarks it will be seen that the habit of flight in modern fishes has not been sufficiently developed as to cause a modification of the structure of the skeleton (with the exception of *Gastropolecus*), and the same thing applies, so far as is known, to the fossil forms also. The geologist, therefore, is greatly hindered in his investigations, because it is obvious that external appendages like fins are unlikely to be preserved, since they are easily removed on the death of the animal. Nevertheless, several fossil fishes have been discovered which had fins sufficiently large as to warrant the belief that they had a power of flight equal to that of any fishes living at the present day, and it is quite possible that many other forms might have possessed it equally well, although the evidence has not been preserved.

All the known forms of flying fish, both recent and extinct, belong to the highest group of the Bony Fishes, the Actinopterygii. This group first appears in the Lower Devonian with *Cheirolepis*, but no flying forms are known earlier than the Trias. *Dollopterus volitans*, from the Muschelkalk of Isserstadt, has been claimed by Compter† as a flying fish, but the evidence is not very satisfactory. The size of the fins in the figure which he gives seems hardly to warrant its being credited with the power of flight. Abel‡ places it in the family Semionotidæ, of which it would appear to be an aberrant member, as this family includes the well-known *Dapedius* and *Lepidotus* of the Lias and Wealden, both deep bodied, heavily built fishes, which were certainly not able to fly.§

In the Upper Trias we come to more definite evidence of flying forms. *Thoracopterus niederristi* and *Gigantopterus telleri* have been found at Raibl and Lunz, in Austria. Both are small fishes, not more than five inches in length, but the pectoral fins are very large. They belong to the Isospondyli and to the family

\* See paper by Dr. W. G. Ridewood, *Ann. Mag. Nat. Hist.* (July, 1913), p. 544, who says also that the pectoral muscles in *Gastropolecus* weigh one quarter of the whole weight of the body, whereas in its nearest ally, *Tetragonopterus*, the proportion is only 1 to 140.

† Zeitschrift für Naturwissenschaften, 64 Bd., (5 Folge 2 Bd.) Leipzig, 1891.

‡ Jahrbuch der k. k. Geol. Reichs-Aust., Wien, 56 Bd. (1906).

§ This fish was originally named *Dolichopterus* by Compter, but that name having previously been given to another animal, Abel subsequently re-named it *Dollopterus*.

Pholidophoridae, which ranges only from the Upper Trias to the Purbeckian.

A long gap now occurs. Not until the Upper Cretaceous is reached do we again meet with flying forms. Another family, the Chirothricidae, also belonging to the Isospondyli, then appears in the well-known fish beds of this age of Mount Lebanon and Westphalia. It contains only three genera, all of which probably had the power of flight. They were only small fishes, the largest, *Telepholis*, being not more than seven inches long, while the smallest, *Exocetoides*, was but a little over two inches long. A well-preserved specimen in the British Museum shows that the

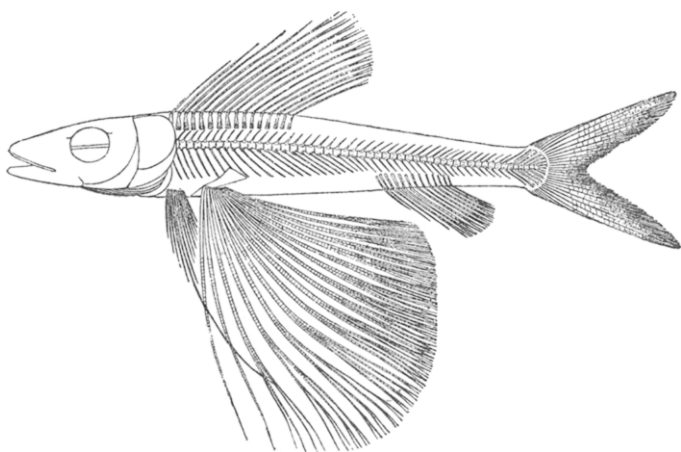


FIG. 16.—*Chirothrix libanicus*.  $\frac{2}{3}$  Nat. size. From the Upper Cretaceous of Mount Lebanon.

After A. S. Woodward, *Cat. Foss. Fishes, Brit. Mus.*, vol. iv, p. 281.

remaining genus, *Chirothrix*, was exceptional to the general rule that the flight fins are the pectorals, because Dr. A. Smith Woodward\* has proved that in this genus it is the pelvic pair that has undergone enlargement. The pectoral fins are quite small, but have one ray (the fifth) excessively elongated. This possibly may have acted as an organ of touch. (See Fig. 16.)

After the close of the Cretaceous period no flying fishes are met with until we come to the living species. This is not altogether surprising when we remember how little change fishes have undergone since early Tertiary times. *Dactylopterus plicocenicus* has been recorded from the Lower Pliocene of Tuscany, but its bones are said to be identical with those of

\* *Cat. Foss. Fishes, Brit. Mus.*, vol. iv, p. 280.

the existing *D. volitans*, and specimens of the allied but non-flying genus *Trigla* (Gurnard) are known from the Miocene.

### III.—AMPHIBIA.

The Amphibia are another group in which flying animals could hardly be expected to occur. Their present-day representatives are but relatively insignificant survivors of a race which reached its zenith in the Palæozoic period, when, as the earliest air-breathing vertebrates, they possessed the earth. The more progressive members, however, as they became more and more land-dwellers, developed long ago into Reptiles, and perhaps even directly into Mammals. No fossil flying amphibia are known, and there is but one living form to bear out the statement that flying representatives are to be found in every one of the Classes of vertebrates.

*Rhacophorus nigropalmatus*, the Flying Frog of Borneo, is one of several arboreal species which have greatly enlarged feet with webs extending to the tips of the toes. By using the out-stretched feet as planes the animals are able to make great gliding leaps from branch to branch and from tree to tree; but it is not known whether the feet are also used for beating the air. Owing to the mistake originally made by Wallace in giving the total expansion area of the four feet as the area of each foot, grossly exaggerated figures of this animal have been published. Several species of *Rhacophorus* have been described from Eastern Asia and the larger Pacific Islands, but only a few have fully webbed hands and feet. It is an interesting circumstance that in Borneo and the other Malay Islands the tree-frogs (*Hyla*) are entirely absent, their place being taken by *Rhacophorus*, which is more closely allied to the ordinary frogs (*Rana*).

### IV.—REPTILES.

We come now to the Reptilia, and in this Class meet for the first time with a group of animals which had undoubted, and, in some respects, unrivalled powers of flight. The type, however, does not seem to have been a successful one, for it enjoyed but a comparatively short existence.

At the present day there are but few flying reptiles, and all of them are of the gliding type. The most interesting is *Draco*, the so-called "Flying Dragon" of the Malay Peninsula and the great islands of the Pacific. About twenty species have been described. They are all small, arboreal in habit, and exceedingly elegant and beautiful animals. *Draco volans*, the typical species, is about 6 in. long, with a tail of about the same length. Fringing each

side of the body, but not attached to either the fore or hind limbs, is a wide membrane consisting of a double fold of skin. Such a fold of skin is termed a "patagium," and we shall find it developed under many modifications, as the gliding organ both among reptiles and mammals. In *Draco* the patagium is strengthened and supported in a very remarkable manner by an extraordinary elongation of the upper ribs, six of which actually project beyond the body and extend to the margin of the membrane. The patagium can be expanded and closed at will, and when not in use lies close along the side of the body. (See Plate 21.A.) *Draco* darts from bough to bough so rapidly that the opening of the parachute can hardly be noticed. It can also make glides of 50 yds. in length at a falling gradient of about 1 in 4. It is said to have the power of avoiding obstacles by canting the "wings," and when about to alight can make a short upward glide to break the force of the fall.\*

The Flying Gecko, or Fringed Gecko (*Ptychozoon homalocephalum*) has merely fringes of skin along the sides of the body, limbs and tail. It has been suggested that these may break its fall as it leaps from bough to bough. Although they are no more than exaggerations of the similar fringes of skin possessed by certain other Geckos, which are considered to be examples of concealment by protective coloration, it is possible we have here the patagium in its most elementary condition.

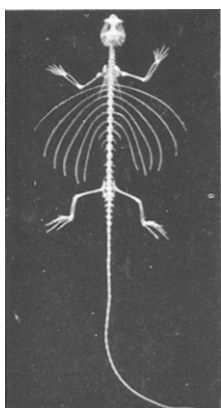
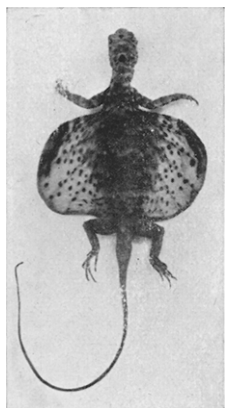
Finally, two snakes, *Chrysopelea* and *Dendrophis*, found in India, Borneo, and the East, have been described as "Flying Snakes." Shelford† says that they can descend from branches of trees to the ground obliquely by keeping the body straight and rigid. He describes their ventral scutes as having two transverse hinges, which enable the snake, by muscular contraction, to form a concavity along the length of its body, and asserts that this arched hollow acts as a parachute in breaking the force of the fall.

This meagre list gives no inkling of the importance of flying reptiles in the past. It is only when we study the fossil forms that we begin to appreciate the possibilities and achievements of reptiles as flying animals. During the Mesozoic Period reptiles dominated the whole earth, and for the major portion of that period were not only masters of the land and sea but were equally sovereign in the air. Beginning in the Lias and ending with the Cretaceous, a group is found having such special structural characters that it forms an Order of itself.

This Order, the Pterosauria or Ornithosauria, or more familiarly the Pterodactyls, after the name of the genus first described, had large membranous wings formed of a double

\* Dr. H. N. Ridley, of Singapore, quoted by Hankin, op. cit.

† *Proc. Zool. Soc.*, 1906, p. 227.



A.—*Draco spilopterus*. 1. Patagium expanded. 2. Skeleton showing elongated ribs. 3. Patagium closed.



B.—*Galæopithecus volans*, clinging to tree trunk.

TYPES OF PATAGIUM.



fold of skin which was stretched from the sides of the body to the extremities of the greatly lengthened fore limbs. All the bones of the hand were lengthened, but especially the phalanges of one of the fingers, which were enormously elongated. This finger gave support to the patagium and changed it into a true wing. The elongated finger is considered by most authorities to be the fifth or "little" finger, but Professor Williston, in a recent paper,\* has re-opened the question, and contends that it is the fourth. He thus reverts to the original view held by Cuvier, who was the first anatomist to describe a pterodactyl. The point is evidently difficult to decide with certainty. Williston himself, in 1902, in the chapter on Pterosauria in Zittel's "Text Book of Palæontology," described it, without any reservation, as the fifth finger (vol. ii, p. 249), and both Von Meyer and Owen appear to have been equally undecided about it. The thumb is either absent or is represented by a small pointed bone turned backward to strengthen the fore edge of the patagium between the wrist and the shoulder. This "pteroid" bone is believed by some authors to be one of the wrist bones abnormally developed, while others regard it as an ossified tendon analogous to the calcar of bats. The other fingers were small and were frequently fused, like splint bones, to the large wing finger. Their extremities were free and clawed, and could probably be used for grasping objects. The hind limbs were feeble and could have been of very little service for walking. In some genera the tail was very long, while in others it was practically absent.

The wings were long and narrow, resembling in shape those of a gull. They probably included the hind limbs and base of the tail. A beautifully preserved impression of the wing of *Rhamphorhynchus*, from the Lithographic Stone of Bavaria, shows that the skin membrane was quite smooth and devoid of hair, scales or feathers, thus resembling that of a bat.

The Pterodactyls are usually divided into two sub-orders: the Pterodermata, with long tails and toothed jaws, and the Ornithocheiroidea, with short tails, some of which had teeth, while others, especially the latest forms, were entirely toothless. This is not a very satisfactory classification, as it is impossible to be certain into which group certain genera should be placed, the tail not having yet been discovered. The grouping, and even the naming, of the genera can only be regarded as tentative, but it is probably safe to say that the earlier forms were long tailed, and the later gigantic forms which heralded the disappearance of the group were short tailed.

Although the structure of the wing is totally different to that of birds, in many respects they were extremely bird-like, but it cannot be too strongly insisted that, for reasons which will appear

\* *Journal of Geology (Chicago)*, vol. xix (1911), p. 695.



later on, they can in no sense be regarded as the ancestors of birds.

The following points of resemblance may be noted :

*Pneumaticity of the bones.*—Many of the bones, especially those of the fore limb, contained large hollow spaces which contained air. In some cases the substance of the bone was extremely thin in proportion to its length and diameter. Specimens over 1 in. in diameter, obtained from the Chalk of Burham and Snodland in the Medway Valley, show the bone to be no thicker than a visiting card.

*The flattened breast-bone or sternum.*—This, however, was not so large as in birds, and although in the largest forms a keel was developed, it never became the important structure it is in birds (*Ornithodesmus* had an exceptionally large and bird-like keel).

*The skull.*—This has an extraordinary resemblance to that of birds. It is as a rule very large in proportion to the size of the animal. It is fixed at right angles to the vertebral column, and the jaws are prolonged into a very bird-like beak, which, in the later forms, is devoid of teeth. The brain is small in proportion to the size of the skull, but in the arrangement of its parts resembles that of a bird. This is well shown in a very perfect natural cast of the brain-case of *Scaphognathus purdoni*, obtained by the Rev. D. W. Purdon from the Upper Lias of Whitby, and described by Mr. E. T. Newton.\* This shows the presence of the flocculus, a structure found in birds, but not in other reptiles. The teeth, when present, are fixed in separate sockets, generally irregularly spaced. They are simply conical in shape, and in the earlier forms are of large size. The eye is large, and was surrounded by a ring of sclerotic plates. Fig. 17, from a Paper by Mr. E. T. Newton, which was published in our PROCEEDINGS for 1887-8,† gives a comparison of the skulls of the following genera of Pterodactyls :

- |                  |                    |
|------------------|--------------------|
| 1. Pterodactylus | 5. Pteranodon      |
| 2. Cynorhamphus  | 6. Rhamphorhynchus |
| 3. Scaphognathus | 7. Dimorphodon.    |
| 4. Ptenodracon   |                    |

It must be remembered that these figures are drawn to widely different scales.

With respect to habitat and mode of life, the smaller forms would appear to have frequented the banks of rivers or lakes and the shores of the sea, while the larger kinds roamed far from land. All were carnivorous, surface swimming fish being most probably their principal diet, which they may have been able to snap up while on the wing, as do the fishing birds of to-day.

\* *Phil. Trans. Roy. Soc.*, vol. clxxix. b, p. 503.

† *Proc. Geol. Assoc.*, vol. x, p. 407.

The earliest form to appear is *Dimorphodon*, the single species of which (*macronyx*) had a grotesquely large head and formidable teeth. This is known only from the Lower Lias of Lyme Regis. The allied genera *Dorygnathus*, *Campylognathus* and *Scaphognathus* appear in the Upper Lias. *Ramphocephalus* has been described from the Great Oolite and Stonesfield Slate, while *Rhamphorhynchus* is represented by several species in the Lithographic Stone (Kimmeridgian) of Bavaria and Württemberg. This form had an expansion of skin at the end of the tail, and it is probable that the hind limbs and tail were included in the patagium. In O. C. Marsh's restoration, which has been widely copied by writers, the hind limbs and tail are included in the patagium, but in those by Von Stromer, they are shown as free. The skull in *Rhamphorhynchus* was very bird-like and was furnished with long and irregular teeth which did not extend quite to the tip of the jaws. This is the latest of the long-tailed forms.

In the same beds as *Rhamphorhynchus* occur the earliest of the short-tailed group, the type genus *Pterodactylus* being represented by several species. This form was the first flying reptile discovered, and was described by Cuvier in 1809. Its name has been popularly given to the whole group. *Pterodactylus* varied in size from that of a blackbird to that of an eagle. The teeth were small and confined to the anterior part of the jaws. *Ptenodracon* has been separated by some authors from *Pterodactylus* on account of the shortness of the head. It is the smallest of the group, being no larger than a sparrow. *Ornithochirus* is a genus of indefinite limits, all the specimens which have been referred to being imperfectly preserved. Probably, when better specimens are discovered, it will be found necessary to break it up into several genera, each with a more restricted range in time. At present it is said to range from the Upper Jurassic to the Upper Chalk. In general structure it resembled *Pteranodon*, but differed from it in the possession of numerous and formidable teeth. Its latest members attained to a very large size, and with it the Pterosauria became extinct in Europe.

*Ornithodesmus* was, until lately, a very imperfectly-known genus, but Mr. R. W. Hooley\* has recently described a specimen from the Wealden, near Atherfield Point, in the Isle of Wight, which adds greatly to our knowledge. He shows that the skull resembles that of *Scaphognathus*, and suggests that a new classification of the group, based on the structure of the skull, would be more satisfactory than the present one.

*Pteranodon*† from the Upper Cretaceous of Kansas displays specialisation carried to extreme limits. It is by far the most

\* *Quart. Journ. Geol. Soc.*, vol. lxi (1915), p. 372.

† Or *Ornithostoma*, Seeley.

gigantic flying creature that ever existed. Beside it the condor and albatross appear insignificant. With a body no larger than that of a goose, it had wings with an expanse of about 20 feet. It could probably sustain flight for great distances, its remains having been found in deposits estimated at over 100 miles from the nearest shore. Its hind limbs were extremely feeble, and quite useless for walking or swimming, and it probably had great difficulty in rising from the surface, either on land or water. The albatross is said to have to make a flapping run on the surface of the sea for 70 or 80 yards before it can get up sufficient impetus to spread its wings, and *Pteranodon* would probably have had still more difficulty in doing so, for its feet were not webbed and its legs were hampered by being included in the patagial membrane. The skull is long and entirely toothless. In two species, *P. ingeus* and *P. longiceps*, the back part is prolonged into a large bony crest, the function of which is conjectural. It



FIG. 18.—*Pteranodon occidentalis*. Span of wing 18 to 20 ft.

has been suggested, with some confidence, that this was of use in steering or balancing; but if this was its sole function it is difficult to understand why these two species alone needed it, since none of the other Pterodactyls possessed such an organ. In the smaller but closely allied genus *Nyctosaurus* (or *Nyctodactylus*) found in the same deposits there is no vestige of a crest. Others have supposed that it formed a support for muscles giving power to the grip of the jaws when holding slippery and struggling fish. A similar crest, but on a much smaller scale, is found in two living animals which feed on such prey, the Cormorant and Snapping Turtle, but the analogy is not conclusive, for the Chameleon, which lives on totally different food, also possesses a crest. Laterally the skull was remarkably compressed, and was more dagger-like than that of any other animal.

A point of great interest has been raised by Williston in regard to *Nyctosaurus*.\* He asserts that this animal had ribs of two different kinds. The first four pairs were short and curved.

\* Field Columbian Museum, Geological Series, vol. ii (1903), p. 125.

The remainder (four or five pairs) were much longer, very slender, and nearly straight. The fifth rib, the longest, was "about 75mm. in length, 2mm. across its somewhat expanded head, 0.8 across the shaft a little beyond the capitular thickening, and but 0.4 near its distal extremity." Williston suggests that these lower ribs were not confined to the body cavity, but protruded through it and helped to support the patagium exactly as in the *Draco* of to-day. The suggestion is interesting, but it must be remembered, however, that *Nyctosaurus* had an expanse of wing of about six feet, and therefore that these three-inch ribs would be very small in proportion to the size of the wing, whereas in *Draco* they extend to the margin of the wing membrane. Furthermore, their extreme tenuity, roughly  $\frac{1}{8}$  inch in diameter, would render them of comparatively little value as a support of so large a surface. Additional evidence is therefore needed before this theory can be accepted with confidence.

#### V.—BIRDS.

In birds we have a totally different type of vertebrate flight, and one which has proved extraordinarily successful. This is evidenced by their immense numbers, their world-wide distribution, their astonishing variety of form, of size, of colour, of habitat, of mode of life, of power of flight and even of mental capacity. But with all this wealth of variation there is a surprising similarity in bodily structure. Indeed, it has been well said that there is no more essential difference in the most diverse forms of birds than there is between a rat and a rabbit, both of which belong to the Rodentia, the most compact of the orders of mammals.

The variety and similarity of modern birds being so great, it is impossible to deal with them in any detail. For our present purpose it is sufficient to note that the organ of flight is again the modified fore limb, but in this instance the hand is degenerate, and the bones which remain are fused together into a completely immobile structure. The possession of feathers distinguishes birds from all other vertebrates, and the specially developed flight feathers which are borne on the fore limb (wing) serve the same function as the patagium of the Pterodactyls in being the air-beating organ which sustains the body in flight. Microscopical examination of the feathers of the wing reveals a complicated mechanism of interlocking hooklets and ridges for converting the whole into a light but exceedingly efficient apparatus for striking the air.

Other important modifications are, (a) The possession of a well-developed breastbone or sternum, which in the vast majority of birds has a thin vertical plate of bone projecting from its outer surface. This is the carina or keel, and to it the muscles of the

wings are attached. (*b*) The shortening and fusing together of several of the last joints of the tail into the "ploughshare bone" or pygostyle, from which the tail feathers can be spread out fan-wise. (*c*) Saddle-shaped cervical vertebræ: these give great strength to the neck while retaining for it considerable flexibility; and (*d*) Toothless jaws; no birds later than those found in the upper chalk have teeth in the jaws. It is interesting to recall that the latest of the Pterodactyls were also toothless.

Birds are usually divided into two great groups according to the presence or absence of a keel on the sternum. These groups are of vastly different importance, for, of living forms, those possessing a keeled sternum (the Carinates) number some 12,000 species, while those in which the keel is absent (the Ratites) are only twenty in number. The latter are quite abnormal, inasmuch as they are completely devoid of the most important avian characteristic—the power of flight. This grouping, however, is an artificial one, for there is little doubt that the Ratites are descended from Carinate ancestors.

The earliest known fossil bird, *Archæopteryx*, occurs in the Lithographic Limestone of Bavaria, the formation already referred to as yielding many Pterodactyls. Only two specimens are known, so that their value to Palæontology is inestimable. The specimen in the British Museum was discovered by Andreas Wagner at Solenhofen in 1861, and another specimen was found in 1877, of which the museum possesses a cast. This bird, which was about the size of a pigeon, had many reptilian characters. The bones of the hand were quite free and were provided with claws. The tail was long and composed of about twenty separate joints, from each of which sprang a pair of feathers. Both jaws were furnished with teeth, and there was a sclerotic ring around the eye. Unfortunately, it is not known whether the sternum had a keel or not, but it had a well-developed U-shaped furcula. The shape of the skull was very bird-like, but the most distinctive avian character was the possession of feathers, and, indeed, the name *Archæopteryx* was first given, before the bones were discovered, to an impression of a feather found in the stone.

After the Jurassic period, no birds are known until we come to the Upper Cretaceous, when in the chalk of Kansas, again contemporary with Pterodactyls (*Pteranodon* and others) we find two forms which had made considerable advance towards the purely avian type. Both had numerous teeth in both jaws, and their discoverer, O. C. Marsh, endeavoured to use this as a character for classification, proposing for them a new order, *Ornithodontes*. But as in other respects they differ considerably, this arrangement has not been generally adopted.

One, *Hesperornis* (Fig. 19), was a large swimming bird, standing about 3 ft. high. The structure of the wing is unknown, the humerus only having been found. The wing, however, was

most probably degenerate, if not completely absent, as the broad flat sternum has no trace of a keel. The teeth are conical and inserted in a groove. The sacrum is extremely long, and there are 12 joints in the tail, the last 3 being apparently fused into a pygostyle.

The other, *Ichthyornis* (Fig. 20), was a bird of very different build. Unlike *Hesperornis* it was a powerful flier, as shown by the strong wing bones and the deep keel to the sternum. There were several species, the largest of which was not above 10 inches



FIG. 19.—*Hesperornis regalis*.  
Height about 3 ft.



FIG. 20.—*Ichthyornis victor*.  
Height 10 in.

high. The tail shows a further reduction in number of joints, there being only five free joints and a small pygostyle. In this genus the teeth were planted in separate sockets. Other toothed birds have been described under the names of *Baptornis* and *Apatornis* from the Cretaceous of Kansas, and *Enaliornis* from the Cambridge Greensand, but the remains are so fragmentary that their precise position is doubtful.

The list of Mesozoic birds is completed by some fragmentary remains in the Chalk of South Sweden, which have been referred by Dames to the Flamingoes under the name of *Scaniornis*. *Telmatornis* and *Graculavus*, from the American Cretaceous, have



been doubtfully referred to the Rails and Cormorants respectively. These are the earliest appearances of the modern type of birds, and the only ones previous to the advent of the Tertiary Period. The Flamingoes are possibly survivors from a primitive stock from which the Storks and Ducks are also descended.

With the arrival of the Tertiary Period modern birds appear suddenly in great variety. Several groups are known to have been well differentiated in Eocene times, and most of the forms found have strong affinities with existing types. A selection only is given here.

In the London Clay are found representatives of Gannets (*Odontopteryx*, with a powerful beak armed with strong and jagged denticles (not teeth) which were probably of service in catching fish, *Argillornis* and the still-living *Sula*), Falcons (*Lithornis*), and Herons (*Proherodius*).

The Upper Eocene Phosphorites of Southern France have yielded Storks (*Propelargus*), Trogons (*Archatrogon*), Game Birds (*Filhornis*, allied to the Hoatzin) and Rails (several genera), while Ibises (*Ibidopsis*) and Grebes (*Colymboides*) have been found in the Upper Eocene of Hordwell in Hampshire.

The Miocene Strata in various parts of Europe have afforded remains of Ducks (*Anas*), Geese (*Anser*), Pigeons (*Columba*), Flamingos (*Agnopterus*, *Heliornis*, *Phenicopterus*, and *Palaelodus*), Pelicans (*Pelecanus* and *Palagornis*), Secretary Birds (*Serpentarius*), and Parrots (*Psittacus*). On account of the recent extermination of the flightless Great Auk of the North Atlantic it is interesting to note that the earliest known Auk (*Mancalla*), from the Upper Miocene of California, was also highly specialised and flightless.

Other extinct birds of doubtful affinities have been grouped by some writers under the name of *Stereornithes*, but it is probable that they are aberrant or ancestral forms of several orders. Among them may be mentioned *Gastornis*, from the Lower Eocene (London Clay of Croydon, etc.), which approached the size of an ostrich, but which, in some respects, was allied to the geese\*; *Dasornis*, from the London Clay of Sheppey, and *Diatryma*, from the Eocene of New Mexico. In the same group have been put some extraordinary birds found by Ameghino in the Miocene of Patagonia, *Phororhachos*. This genus was remarkable for the enormous size of the head, which was greatly disproportionate to the rest of the body. The skull of the largest species was nearly two feet in length and had a strongly-hooked beak. It may have been a running bird of prey. Dr. C. W. Andrews considers that it was a carinate bird whose wings had undergone reduction, and that it may have been related to

\* A specimen found by Mr. H. M. Klaassen was described in our PROCEEDINGS for 1885-6 by Mr. E. T. Newton. *Proc. Geol. Assoc.*, ix, 349.

the ancestral form of *Cariama* (the Crested Screamer of South America), the exact affinities of which, however, are still uncertain. *Brontornis*, sometimes classed with the *Stereornithes*, was more probably related to the Rheas.

Notwithstanding the fact that the avian type of flight has proved so successful, some birds have adopted habits which have rendered the use of their wings unnecessary, or even disadvantageous. Several groups have been profoundly modified owing to this cause, which has eventually produced partial or total loss of the power of flight. Beside simple disuse a change of manner of using the wings may lead to this result. This aspect of the subject deserves a little examination.

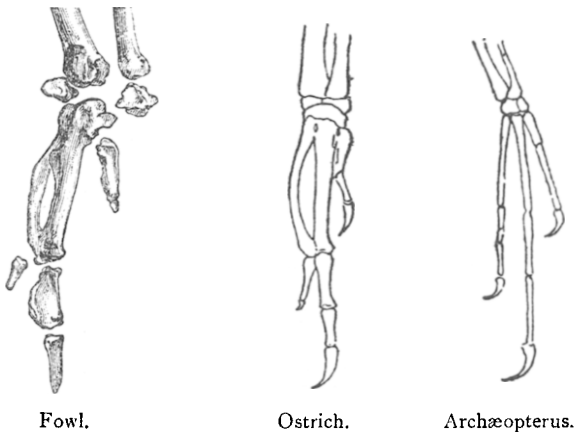


FIG. 21.—BONES OF HAND OF BIRDS.

I have already mentioned that the second great group into which birds are divided, the Ratites, or "raft-breasted" birds, are probably derived from Carinate ancestors. This group consists only of the Ostrich and its allies. In these birds the sternum is broad and nearly flat, and has no projecting keel, hence the name "raft-breasted." The wing is degenerate and quite useless for flight, but it is constructed on exactly the same plan as in Carinate birds. The primitive character of claws on the digits is, however, retained. Fig. 21 shows how much the avian hand of both Carinates and Ratites differs from the reptilian hand of *Archæopterus*. The plumage is loose and fluffy or even hairy, owing to the entire absence of the interlocking barbs and hooklets. The head and brain are relatively small, especially in the extinct family of the Moas. They are all totally unable to fly.

The geographical distribution of the Ratites as a group is very

wide, but the range of each genus is, on the contrary, greatly restricted, as the following list shows :

- Ostrich (*Struthio*), North and South Africa and Arabia.
- Rhea (*Rhea*), Southern part of South America.
- Cassowary (*Casuarius*), Northern Australia and New Guinea.
- Emu (*Dromæus*), Southern Australia.
- Kiwi (*Apteryx*), New Zealand.

Both the Ostrich and a variety of Cassowary (*Hypselornis*) have been found in the Lower Pliocene of the Siwalik Hills in India, and the Ostrich has also been obtained from beds of similar age in the Isle of Samos, but the other genera are only known in the fossil state from the superficial deposits of the regions inhabited by the living forms.

Two other extinct members of this group are known :

- Moas (group), New Zealand.
- Æpyornis*, Madagascar.

The Moas are an extinct group of Ratites found in large numbers in the superficial deposits of New Zealand, and are known to have been exterminated by the Maoris. Some were of gigantic size. The largest (*Dinornis*) was about half as large again as an ostrich, ranging up to 12 ft. in height. *Pachyornis*, although not so tall, was very massively built, while *Anomalopteryx* the smallest, was slenderly built, and no larger than a turkey. Not only are the bones met with, but the eggs and cartilage rings of the windpipe have been found in large numbers in swamps, while mummified remains are occasionally found in caves. In these cave relics the ligaments, skin, and even the feathers are sometimes preserved.

*Æpyornis* has not been long extinct in Madagascar. One species, *Æ. titan*, probably exceeded *Dinornis* in size. Its egg, not uncommon in marshy places, was enormous, having a capacity of over two gallons.

The existing Ratites are all good runners, and, with one exception, *Apteryx*, range over large stretches of open country. They are in all probability derived from Carinates which had taken to running as their chief means of locomotion. There are important differences between the genera, and it is possible that each genus may have descended from a separate stock.

This view of the origin of Ratites is supported by known facts of the degeneration of the keel of the sternum through disuse in undoubted Carinates. It is well known that in small oceanic islands both birds and insects have a tendency to lose their powers of flight. This is believed to be due to the liability of being blown out to sea during gales. If, therefore, we presuppose the comparative absence of predatory enemies and the presence of an abundant food supply, those birds which least exercised

their powers of flight would have the greatest chance of surviving and leaving progeny. The subsequent introduction of fresh enemies, however, would probably lead to rapid extermination. This sequence of events is well illustrated by the actual cases of the Dodo and Solitaire. Both of these were pigeons, which, under the conditions outlined above, completely lost the use of their wings, and at the same time grew to abnormal dimensions. The Dodo (*Didus ineptus*) of Mauritius was a clumsily built bird, larger than a turkey, with greatly degenerate wings and a mere ridge representing the keel on the sternum. An allied species (*D. borbonicus*) lived in Réunion. The Solitaire (*Pezophaps*), known only from Rodriguez, was of more upright build, larger than a swan and standing some 30 in. high. These large pigeons were inactive and defenceless, consequently on the introduction of pigs into the islands by man they were soon exterminated. The Dodo appears to have become extinct by the end of the 17th century, and the Solitaire about 50 years later.

Two other interesting cases are found in New Zealand, the home of so many strange animals. One a Rail (*Aptornis*), the other a Goose (*Cnemiornis*). In both the keel is degenerate. They were probably preyed upon by a large and powerful eagle (*Harpagornis*), which after exterminating these two weaker species appears itself to have become extinct. Other causes, however, may have contributed to this, as the present New Zealand avifauna is probably almost as rich as it ever was, but Professor Newton\* bitterly laments the rapidity with which species are now being exterminated.

Besides *Aptornis* the Rail family (*Rallidae*) contains a remarkably large number of genera which have more or less completely lost the power of flight, and these show the keel in various stages of degeneration. The family is one of the most ancient of modern birds, and is very widely distributed, while a considerable number of the genera are extinct.

The Tinamous (*Crypturidae*) are an abnormal family which, while possessing a well-developed keel to the sternum, have many resemblances to the Ratite group. They run with remarkable speed, and can only be flushed with difficulty. Although they can fly both strongly and swiftly, with a rapid whirring motion of the wings, they have but little power of direction and are often killed by collision with obstacles. They are confined to South America and Mexico. Most authors are now inclined to place them with the Ratites rather than with the Carinates.

Finally, an example of complete loss of flight due to change of habit is seen in the Penguins. Here the wing has become converted into a paddle, but in this case the keel of the sternum is retained, because the limb is still fully used, and is merely changed in function.

\* A. Newton, "Dictionary of Birds," 1893, p. 224 (footnote).

## VI.—MAMMALS.

Coming now to the Mammalia we find that the power of flight has been developed in no less than four of the Orders into which mammals are divided. Marsupials, Rodents, Insectivores, and Bats possess it in varying degrees of perfection. Of these the Bats alone are true fliers, all the others being merely gliders.

In the two first-named orders the modification caused by the adoption of the flying habit has proceeded along identical lines and a general similarity of appearance has resulted. The patagium, or flying membrane, is a double fold of skin covered with fur. It extends along the sides of the body connecting the fore and hind limbs. The tail is invariably long and is not included in the patagium. The flying genera are all modified from allied normal arboreal forms which have the habit of jumping from branch to branch of trees, but these, by the help of the extended patagium, are able to take greatly prolonged gliding leaps, extending, in some species, up to a distance of 70 or 80 yards. They are mostly nocturnal animals, and are all very beautiful creatures, some of the species being among the most brilliantly coloured of the mammalia. Beyond some lengthening of the bones of the limbs there is no structural modification of the skeleton. It would, therefore, be difficult to recognise their remains in the fossil state, and none have as yet been recorded.

## MARSUPIALS.

All the Flying Marsupials are found in one family only, the *Phalangeridæ*, which is a division of the Diprotodont section of the Marsupialia. The Phalangers are thick-furred animals with long prehensile tails. These animals are arboreal in habit, and are plentifully distributed throughout the whole Australian region. The flying varieties, however, are confined to New Guinea and the eastern part of Australia.

*Petauroides volans*, the Taguan Flying Phalanger,\* is the only species of its genus. It is also the largest of the Flying Marsupials, measuring about 20 inches from the snout to the root of the tail. Its fur is long and silky. The greater part of the tail is thick and bushy, but the tip is naked and prehensile. The patagium extends from wrist to ankle, but is very narrow beyond the elbow and knee joints.

*Petaurus* (3 species) is a much smaller animal, with exceedingly soft and beautiful fur. The patagium is, relatively, broader than in *Petauroides*, while the tail is thick and bushy to the tip and is not prehensile.

\* The name Taguan is also applied to the Flying Squirrels and the Flying Lemur.

*Acrobates pygmaeus*, the only species of its genus, is one of the smallest Marsupials known, being no larger than a mouse. It is a most beautiful little creature. The tail is as long as the body, and is remarkable in having a fringe of long hairs on each side, which give it a feather-like appearance. Notwithstanding its small size the female has a well-developed pouch containing four nipples. The patagium is narrow, extending only from the elbow to the flank, but the animal is said to be extremely agile. It feeds on insects and on honey obtained from flowers.

These three genera of Marsupials are not genetically connected. Each appears to be a specialised form derived from a closely allied non-flying genus, which has a somewhat similar geographical distribution. They may be contrasted as follows :

| FLYING FORMS.                      |                           | ALLIED NON-FLYING FORMS.             |                           |
|------------------------------------|---------------------------|--------------------------------------|---------------------------|
| Genus.                             | Geographical Range.       | Genus.                               | Geographical Range.       |
| <i>Petauroides</i><br>(1 species). | Eastern Australia.        | <i>Pseudochirus</i><br>(10 species). | Australia and New Guinea. |
| <i>Petaurus</i><br>(3 species).    | Australia and New Guinea. | <i>Gymnobelidus</i><br>(1 species).  | Victoria only.            |
| <i>Acrobates</i><br>(1 species).   | Eastern Australia.        | <i>Distæchurus</i><br>(1 species).   | New Guinea only.          |

It will be noticed that the geographical range of *Petauroides* is more restricted, while in both *Petaurus* and *Acrobates* it is more extended, than that of the parent form. This suggests that the two latter genera have been benefited by the adoption of the volant habit, and so have succeeded better than their ancestral forms in the struggle for existence, while *Petauroides* has so recently acquired the habit that it has not yet had time to spread over the whole area covered by the ten species of its parent genus.

#### RODENTS.

Among the Rodentia we find flying members in two distinct but allied families, the *Anomaluridæ* and the *Sciuridæ*.

The *Anomaluridæ* are a group intermediate between the Sciuromorpha or squirrel-like rodents and the Hystricomorpha or porcupine-like rodents. Forms connecting them with the true squirrels have been found in strata of Lower Tertiary age. Such are *Theridomys*, *Sciuroides*, and *Pseudosciurus*, which occur in the Upper Eocene in various parts of Europe, and *Ischyronys* from the Lower Miocene of Colorado.

To the *Anomaluridæ* belong the genera *Anomalurus* and *Idiurus*, or African Flying Squirrels, which differ from the true Flying Squirrels principally by the presence of a row of large spiny scales on the inferior surface of the root of the tail which are said to be of use in climbing up the trunks of trees. There are also

certain differences in the structure of the skull and teeth. In this family the patagium is supported in front by a rod of cartilage, which arises from the elbow. Several species have been described. The average length is about a foot, not including the tail. An allied genus, *Zenkerella*, has no flying membrane, and this probably represents the ancestral type from which the other two genera have descended.

Among the true squirrels (*Sciuridæ*) three genera possess a well-developed patagium. In all nearly thirty species have been

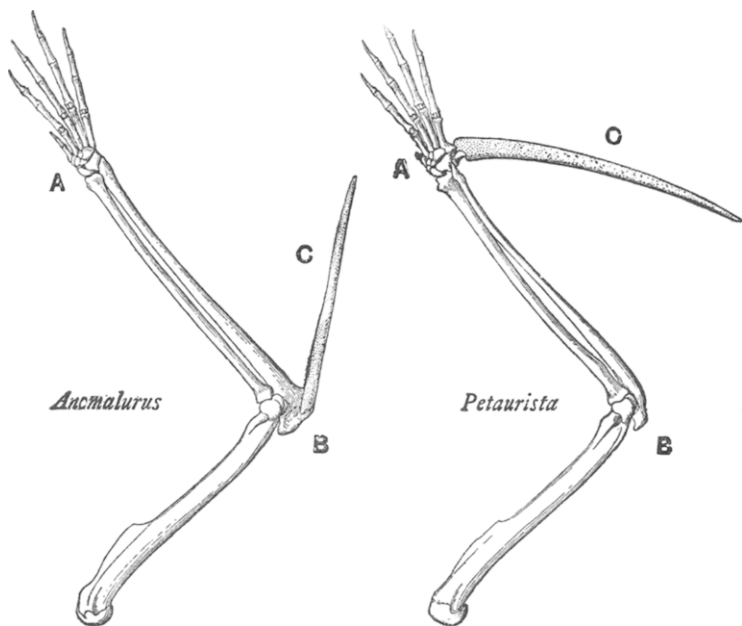


FIG. 22 —FORE LIMB OF FLYING SQUIRRELS.

In *Anomalurus* the rod of cartilage (*c*) springs from the elbow, in *Petaurista* from the wrist.

described, which, with two exceptions, are confined to the Indo-Malayan region. In this group the front part of the patagium is supported by a rod of cartilage which springs from the wrist, and not from the elbow as in the *Anomaluridæ*. (Compare A and B of fig. 22.)

In *Sciuropterus* the patagium extends to the wrists and ankles. The tail, however, is quite free, but it is very wide and horizontally flattened, and probably acts as a supplementary flying organ.

The species vary in size from 5 in. to 12 in. in length, exclusive of the tail. One species occurs in the United States, and

another in Siberia and north-east Europe, the remainder having the usual distribution of the group.

In *Petaurista* (= *Pteromys* of earlier authors) the tail is cylindrical, and is usually longer than the body, a small portion of the root being included in the patagium. It is of larger average size than *Sciuropterus*. Some of the species range up to 18 in. in length, exclusive of the tail, which may measure as much as 24 in. in addition.

*Eupetaurus cinereus*, the only species of the genus, is a large and extremely rare species from Kashmir. It fully equals the largest species of *Petaurista* in size, but has a much more bushy tail. The claws are short and blunt. Its habits are not well known, but it is believed to frequent rocky cliffs rather than trees.

The three genera of flying squirrels are regarded by some writers as constituting a sub-family of the *Sciuridae* on account of the complex character of the molar teeth and certain differences in the skull, and it is possible they may have descended from a branch of the main group, now extinct. No fossil forms are known.

#### INSECTIVORES.

The Order Insectivora contains only one genus which has the power of flight, the so-called Flying Lemur, Cobego, Kaguan, or Taguan, *Galaxiophilus*. This is one of those anomalous animals which will not fit in satisfactorily with any of the accepted definitions of classification, and some authorities have proposed that it should be considered as constituting an Order by itself. It was formerly classed by some zoologists with the Bats, and by others with the Lemurs, but it is now generally regarded as an aberrant type of the Insectivora.

In this animal the passive parachute-like type of patagium is developed to a greater extent than in any other vertebrate. Not only does it extend the whole length of the limbs, even to the tips of the toes, but the hind legs and tail are also completely connected. The bones of the legs, feet and tail are all greatly elongated, but the skeleton is not otherwise modified. The feet can be widely spread and the toes are webbed. (See plate 21.B.)

In certain other important respects *Galaxiophilus* is exceptional. Unlike all other insectivora it is a vegetable feeder, living upon leaves and fruit. Unlike the majority of flying mammals it is diurnal in habit, while its lower incisor teeth are unlike those of any other animal. These teeth are broad and thin and are cut vertically by a number of parallel slits so that they resemble little combs.\*

There are two species of *Galaxiophilus*, both about the size of a cat but with a more slender body. One occurs in the

\* The nearest approach to this type of tooth in other Orders is found in the exceedingly minute incisors of the blood-sucking Bats, *Desmodus* and *Diphylla*.



Malay Peninsula and the great islands of the Pacific, while the other is confined to the Philippine Islands. It is not known in the fossil state.

### BATS (CHIROPTERA).

As already mentioned, Bats alone, among the Mammalia, possess the power of true flight. In this Order the patagium has been developed into a wing, with which the animal beats the air and supports itself at will. Not only does the patagium completely envelop all the limbs and tail, as in *Galeopithecus*, but the bones of the fore limb have undergone extreme modification.\* The fingers have been enormously elongated, and serve as radiating supports to the wing-membrane. The patagium is destitute of hair, very thin and delicate, and richly furnished with blood-vessels. In the majority of forms the margin of the inter-femoral membrane, as the membrane stretching between the hind legs is called, is strengthened by a cartilaginous rod, the calcar, which arises from the inner side of the ankle joint. The tail may be long, short, or completely absent. When present, it is included in the patagium in some genera, while in others it perforates and projects beyond it. The skeleton is very lightly built, the bones being of extreme tenuity and slenderness. They are not, however, pneumatic. The sternum, although small, has a projecting keel for the attachment of the wing-muscles.

The Bats evidently represent a very successful type of flight-structure, their distribution being wider than that of any other Order of Mammalia. They are met with all over the world, even within the Arctic circle. In New Zealand and many of the remote islands of the Pacific they are the sole indigenous mammals. It is somewhat remarkable, however, that only one species, the Serotine, *Vesperugo serotinus*, is found in both the Old and New Worlds.

Some 450 species of Bats have been described, many of which have extraordinarily interesting bodily peculiarities which it is impossible to deal with here. They fall into two great groups, distinguished both by their size and the character of their food, the Microchiroptera being insect-eating, while the Megachiroptera are fruit-eating Bats.

The Microchiroptera are all comparatively small in size. The tail is usually long, and the ears large, sometimes enormously so. In many genera the nose has elaborate foliaceous expansions of skin surrounding the nasal apertures. These are the "nose-leaves," which are exceedingly delicate organs of touch, being probably sensitive to the most minute vibrations of the air. The molar teeth have numerous sharp cusps well adapted for crushing insects. The two abnormal blood-sucking

\* In one group, the Molossine division of the Emballonuridæ, the hind limbs are free and not included in the wing-membrane.

genera, *Desmodus* and *Diphylla*, both belong to this group. To the Microchiroptera belong by far the greater number of species of Bats, and they are distributed throughout the world.

The Megachiroptera, on the contrary, are found in the warmer parts of the Old World alone. As the name implies, they are mostly of large size. The largest species, *Pteropus edulis*, the "Flying Fox" of Java, has an expanse of wing of fully 5 ft. In this group the tail is usually either absent or very short. They are all fruit eaters, and their molar teeth have smooth crowns instead of the sharp cusps found in the insect-eating group.

Unfortunately fossil remains of Bats are extremely rare, but they are known to occur as far back as the Upper Eocene. The Phosphorites of Central France of that age have yielded *Rhinolophus*, *Alastor*, *Vespertiliavus*, *Taphozous*, and *Necromantis*. *Nyctitherium*, a form closely allied to *Vesperugo*, occurs in the Upper Eocene of the Paris Basin. This has also been found with *Nyctilestes* in the Upper Eocene Bridger group in the United States. *Rhinolophus* also occurs, with *Phyllorhina*, *Vespertilio* and *Palaeonycteris*, in the French Miocene at Cayeux (Tarn et Garonne). The remains of Bats are not uncommon in cave deposits, but these invariably belong to living genera.

All the above genera belong to the Microchiroptera. They appear to be closely allied to existing forms, but the remains are so scanty and ill-preserved that precise determination is difficult. They are, however, unmistakably Bats. Fossil remains of *Megachiroptera* are practically unknown, but recently Meschinelli has described *Archæopteropus*, from the Oligocene of Monteviale, as belonging to this group.

In many points of essential structure Bats are so closely allied to the Insectivora that there can be little doubt but that they have been derived from some of the earlier forms of that Order. *Galaxopithecus* shows the way in which the transformation may have been effected, although it cannot be regarded as being in the direct line of descent. Of the two groups of Bats the Microchiroptera are evidently the more primitive, and may be regarded as the parent stock from which the Megachiroptera have been derived, although the discovery of *Archæopteropus* proves that the separation took place at an early period in the history of the race. It is interesting to note that in another genus of the Megachiroptera, *Pteralopex*, the sharply cusped molar teeth of the ancestral type are still retained.

The remaining Orders of Mammals contain no members which have any reasonable pretensions to flying powers. The claim has been advanced on behalf of certain of the Primates, but the only one worthy of examination is that of the Sifaka, *Propithecus*. It is a Lemur, and one of the many strange animals inhabiting Madagascar. There are several species, all confined to that

island, each with a very small and rigorously confined local distribution. It is a long-legged, monkey-like creature of arboreal habit. Its hind limbs are very powerful, and it can take, without apparent effort, leaps of 30 ft. or more from tree to tree or along the ground ; at the same time it throws its arms above its head, and thus, according to Grandidier, appears almost to fly through the air.

### SUMMARY.

We may now proceed to compare and contrast the various types of flight as developed in vertebrates. It is evident that all through the ages Nature has been experimenting in this matter, and that most of the experiments have been failures. In other words, in one animal after another, members of quite unrelated groups, variation has originated and heredity has preserved accumulating differences tending to produce a structure which would temporarily sustain the body in the air. It is not altogether strange that this should be so. It is to the interest of every organism to extend its food-collecting area and evade its enemies, and the advantage of the power of flight is obvious.

The first to make the essay were, so far as our certain knowledge goes, the fishes. In the Trias, *Thoracopterus* and *Gigantopterus*, if not indeed the slightly earlier but doubtful flier, *Dollopterus*, developed enlarged pectoral fins, a type of flight-organ which has been produced at intervals, spasmodically and independently, in other families, and is found in all the flying fishes of to-day.

Amongst reptiles and mammals the patagium, in one form or another, is the flight-organ. For reasons already given, geology cannot provide us with evidence of its evolution in the past, but a complete series of stages is found among living animals.

In its elementary forms it is not of great utility, but when supported and actuated by the limbs it becomes a very efficient structure. In the Flying Gecko we have its simplest condition. The enlargement of such flaps of skin would result in their coalescence and development along the limbs. This is exhibited in varying degrees of completeness in the Flying Marsupials and Rodents, and attains its greatest perfection in *Galæopithecus*. In all these forms the body is kept rigid during the flight. If, however, the animal acquired the habit of waving or jerking the limbs during its initial flights, modification of the skeleton might take place and a true wing ultimately be produced. This has actually occurred in two very different classes of animals, the Pterodactyls and the Bats. The wide separation of these two classes would alone lead us to infer that their

wings had been independently evolved, and this is confirmed by the fact that the modification has taken place in different parts of the limb. In the Pterodactyls one finger only, in the Bats the whole hand, has been modified.

The gradual perfecting of the mammalian patagium may be tabulated thus :—

| Order.                                  | Membrane. | Patagium connects :—   | Tail.   | Strengthening structure.                             |
|---|-----------|------------------------|---|--|
| Marsupials                              | Hairy     | Fore with hind limbs   | Long, free  | None   |
| Rodents                                 | Ditto     | Ditto                  | Ditto   | Cartilage rod from wrist or elbow                    |
| Insectivores ( <i>Galaxophilhecus</i> ) | Ditto     | Connects all the limbs | Long, included in patagium  | None   |
| Bats                                    | Hairless  | Ditto                  | Long, short, or absent. When present may or may not be included in patagium | Elongated bones of hand and cartilage rod from ankle |

Plate 22 illustrates the two types of patagium wing contrasted with the feather-bearing wing of birds, which is essentially different in construction.

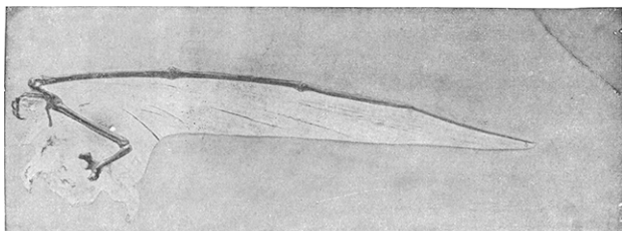
The patagium of *Draco* may be regarded as an unsuccessful attempt to produce a wing. In this case the membrane is undoubtedly strengthened by the elongation of the ribs, but the continued movements necessary for its use as a wing would probably cause much discomfort to the animal. It is unlikely, therefore, to become a permanent type, and it is apparently one of those elaborate contrivances not uncommon in Nature which, perfect in detail but faulty in design, are of no real benefit to the race. It will be noticed that in *Draco* it is the upper ribs that have been elongated, whereas in *Nyctosaurus* Williston's suggestion is that the lower ribs have been modified. (See Plate 21.)

It is interesting to compare the dimensions reached by the largest members of each Class of the Flying Vertebrates. The following lines show the relative expanse of wing on a scale of 6 ft. to 1 in.

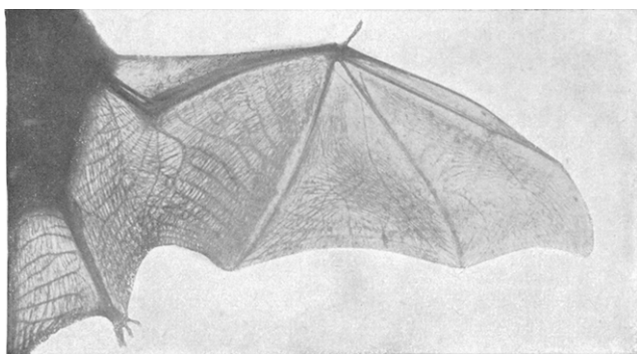
Reptile.—*Pteranodon*, 20 ft.

Bird.—*Diomedea* (Albatross), 11 ½ ft.

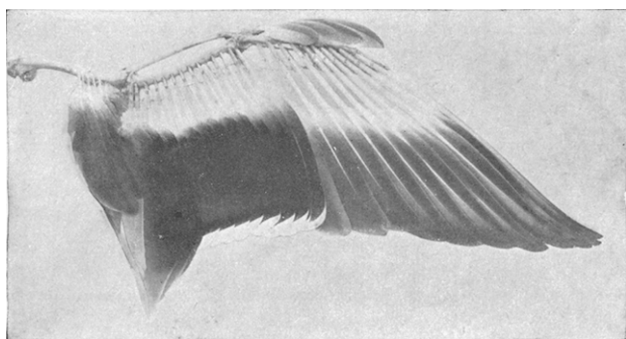
Mammal.—*Pteropus* (Bat, "Flying Fox"), 5 ft.



A.—PATAGIUM-WING OF PTERODACTYL, SHOWING ENLARGEMENT OF ONE FINGER.



B.—PATAGIUM-WING OF BAT, SHOWING ENLARGEMENT OF FOUR FINGERS.



C.—FEATHER-BEARING WING OF BIRD, SHOWING REDUCTION OF BONES OF HAND.

(From Sir E. Ray Lankester's "*Extinct Animals*," p. 233.)

TYPES OF WING-STRUCTURE.

Pterodactyls, the earliest group to appear, attained to the largest size and dramatically disappeared with its largest members. The largest members of the other two groups are found among those living to-day.

Birds made their appearance a little later than Pterodactyls, and were contemporaneous with them for a considerable period. They do not appear to have made much headway against their formidable and well-established rivals, and, indeed, *Hesperornis* and the other Odontolæ show that some of them had found it to their advantage, even thus early, to abandon the air for the water. With the disappearance of their enemies at the close of the Cretaceous era, birds increased rapidly in importance and variety, and by later Eocene times most of the modern types had become well differentiated. Much later than the *Hesperornis* group, and after the primitive character of toothed jaws had been completely lost, several other groups of birds independently adopted running habits, and these became the ancestors of the various types of existing Ratites.

Last of all came the Bats, but of their ancestry we know nothing. During the great development of mammalian life that took place with the advent of the Tertiary period, they appear to have broken away from the ancestral stock of the Insectivora. The transformation was comparatively rapid, for by Upper Eocene times their earliest known representatives had become highly specialised and differ but little from those now living.

Two interesting parallelisms of adaptation should be noted. The first is the shortening of the tail, which is found in all three Classes. In each the earliest members had long tails, but in the later Pterodactyls and bats it has vanished completely, while in birds its place has been taken by the feathers attached to the shortened pygostyle. Apparently a long tail as a steering organ is not a necessity. The second and perhaps more remarkable parallelism is the gradual loss of teeth and the development of a beak that is found in Pterodactyls and birds. Whether the same thing will happen in the bats of the future it is impossible to say, and it is not easy to understand why this particular modification of the jaws should be of service to flying animals. It is, however, one of the great charms of biology that it is continually presenting to us problems difficult of solution, and of such a nature that our explanatory hypotheses frequently but unfold still other problems requiring elucidation.

In conclusion, a few words with regard to Man as a flying animal may not be out of place. His earliest and most persistent efforts naturally tended towards the direct imitation of Nature in the form of flapping flight by means of artificial wings. All attempts in this direction have been complete failures, and the fate of Icarus has overtaken every experimenter who has been

rash enough to put his invention to the supreme test. Modern aeronautics have proceeded along two entirely distinct lines; the floating or "lighter than air" principle, of which the balloon is the type, and the gliding or "heavier than air" principle, exemplified by the aeroplane.

For many years the balloon seemed incapable of improvement, and its unwieldiness and uncontrollability caused it to fall into disfavour. Beyond the substitution of gas for heated air and a few mechanical details it remained essentially as designed by the Montgolfiers in 1783. Latterly, however, through improvements in steering and propulsion and the provision of a rigid metallic envelope, largely due to the ingenuity and perseverance of Count Zeppelin, it has become of great importance as a means of transporting considerable weights.

The mechanical principles involved in the construction of the aeroplane were early well understood, and we may be proud that the pioneers were mostly Englishmen. The great difficulty has always been the provision of an adequate propelling power, and until a light yet powerful engine was available little real progress could be made. As long ago as 1809 Sir George Cayley laid before the Institute of Civil Engineers designs for an aeroplane fitted with a propeller very similar to that in use at the present day. In 1842 Henson and Stringfellow constructed one which was remarkably like the modern Antoinette monoplane in appearance. This machine is preserved in the Victoria and Albert Museum. Six years later Stringfellow actually drove a model monoplane a short distance by means of a small steam engine. Although it was of no practical use he was, in after years, awarded £100 by the Aeronautical Society for his ingenious invention. In 1871 Otto Lilienthal began his important series of experiments in the manipulation of gliding machines constructed on the principle of the box-kites. He made many flights, ultimately extending to several hundreds of feet in length. Having no motive power his flight was always in a downward direction, and the distance travelled was dependent upon the height of his starting-point and the strength of the opposing wind, just as in the case of the gliding animals. After twenty-five years successful experimenting he at last became too venturesome, and on a gusty day in 1896 he met with an accident which proved fatal. His experiments were of great practical value, as through them the subsequent invention of the light petrol-driven motor has enabled modern aviators to achieve their remarkable results.

Circumstances are now putting the rival principles to stringent tests. At the present time each seems to have its special advantages and disadvantages, and time alone will show whether either can claim such general superiority over the other as to

completely exterminate it. Possibly, as with the birds and bats, both types will continue to exist side by side.

NOTE. —My thanks are due to the Trustees of the British Museum for permission to reproduce Figures 16, 18, 19, 20, 22, and C on Plate 20, and to Messrs. Constable and Co. for those on Plate 22. The illustration D on Plate 20 and all those on Plate 21 are from photographs specially taken by my cousin, Mr. W. P. Young, F.R.M.S., from specimens in the Natural History Museum.