THE BIOLOGY OF CILIA AND FLAGELLA

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M. A. SLEIGH

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PERGAMON PRESS

OXFORD · LONDON · NEW YORK · PARIS

1962

PERGAMON PRESS LTD.
Headington Hill Hall, Oxford
4 & 5 Fitzroy Square, London, W.1

PERGAMON PRESS INC.
122 East 55th Street, New York 22, N.Y.

GAUTHIER-VILLARS
55 Quai des Grands-Augustins, Paris 6

PERGAMON PRESS G.m.b.H.
Kaiserstrasse 75, Frankfurt am Main

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PERGAMON PRESS LTD.

Library of Congress Card No. 62-19269

Set in Imprint 11 on 12 pt. and printed in Great Britain by
BELL AND BAIN, LTD.

. . . the general existence of the ciliary motion in the Animal Kingdom is already sufficiently established, . . . whoever has opportunities and inclination to cultivate this field of inquiry will find his labour rewarded by much curious and interesting discovery.

DR. W. SHARPEY, 1835

PREFACE

IMPORTANT advances in our knowledge of the structure and physiology of cilia have been made since Gray's classical monograph on *Ciliary Movement* was published in 1928. In particular, the improvement of techniques of electron microscopy in the last decade gave rise to a renewed interest in the structure of cilia which has been rewarded with the discovery of a widespread and consistent fibril pattern in all true cilia, flagella and sperm tails. A parallel growth of interest in the physiology of the beating and co-ordination of cilia has been taking place in these years, and has been given an added stimulus by the success of morphological studies. The primary purpose of this book is to review advances in these fields since 1928, for in these 34 years no attempt has been made to summarize fundamental work on cilia and flagella in a comprehensive way. A review by J. A. Rivera entitled *Cilia, Ciliated Epithelium and Ciliary Activity* was published while the present book was in the press; Rivera approached the subject in an entirely different way in summarizing the effects of various agents on ciliary activity from the point of view of the human physiologist, so that the two reviews scarcely overlap at all. In the present book modern ideas on structure are linked with modern ideas on physiology in an attempt to make a single coherent story.

The field of study has been divided into four parts: ciliary structure, the effects of various agents on ciliary activity, the physiology of beating of cilia and the physiology of co-ordination. The second of these is intended for reference and for the introduction of evidence used in the third and fourth parts. Summaries of the material included will be found at the beginning of Chapter II (structure of a typical cilium) and at the ends of Chapters IV (beating activity) and V (co-ordination).

The literature contains many thousands of references to ciliary structure and functioning, and, in order not to overload the book with bibliography, some selection had to be made. Only

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some 400 references are mentioned here, recent work being cited more fully (well over half the references date within the last 10 years), while key works are quoted from older studies to enable interested students to follow up other references.

While the review was written to satisfy the needs of the honours student of Zoology, students in other fields should also find it valuable. Research workers studying any topic related to ciliary organelles or their activity should find it useful as a fairly concise summary of the structure and physiology of cilia, particularly since most reviews tend to concentrate on either structure or physiology with little reference to the other part of the subject. Where good evidence is available I have tried to keep closely to established facts, but where our knowledge is very scanty I have tended to stray into the realms of speculation; I hope that the reader will be able to distinguish facts from speculative suggestions.

Few can fail to be convinced of the need for such a review at this time, and I hope that this attempt at a summary of the present position will satisfy the requirements of as many people as possible. If any of the ideas presented here will lead others to further research, then the author will be well satisfied that he has not laboured in vain.

ACKNOWLEDGEMENTS

I AM pleased to record my thanks to Professor J. E. Harris and Dr. J. A. Kitching of the University of Bristol, both for introducing me to the study of ciliary activity and for valuable comments on parts of the text of this book. I am also grateful for the advice and criticism of Professor J. O. Corliss of the University of Illinois, who, while visiting Professor of Zoology at the University of Exeter, has read the whole text and spent much time in fruitful discussions. My wife Peggy has given invaluable help in correcting manuscripts and proofs and in innumerable other ways. The help of these kind people has improved this book considerably, but the author must bear the responsibility for the shortcomings that remain.

The book was written at the suggestion of Dr. G. A. Kerkut, to whom I am sincerely indebted. My thanks are also due to Dr R. Barton, Professor J. T. Randall and Dr. K. Vickerman who have passed on valuable information for this book in discussions of their unpublished work.

It is a pleasure to acknowledge the assistance of Mr. N. Barratt in preparing photographs of some of the illustrations, and of Miss B. Mortimer in typing parts of the script.

The generosity of the following workers who have lent or given copies of electron micrographs is acknowledged with gratitude: Dr. B. A. Afzelius, Dr. W. Bernhard, Dr. E. De Robertis, Professor D. W. Fawcett, Dr. J. G. Gall, Dr. I. R. Gibbons, Dr. E. G. Gray, Dr. A. V. Grimstone, Dr. D. R. Pitelka, Professor J. T. Randall, Dr. L. E. Roth, Dr. J. E. Shapiro, Dr. K. Vickerman and Dr. E. Yamada. Professor P. P. Grassé, Professor I. Manton and Lord Rothschild have kindly given permission for electron micrographs to be copied from published work.

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CHAPTER 1

INTRODUCTION

CILIA seem to have been seen for the first time by the Dutch microscopist Leeuwenhoek in 1675. In a letter to the Royal Society (Leeuwenhoek, 1677), he described the incredibly thin feet or little legs by means of which a small animalcule, which Dobell (1932) believes to have been a ciliated protozoon, moved through the water. Cilia, or the immediate result of their movements, were seen in metazoa at about the same time by de Heide (1684), who described a " motus tremulus " of the gill surface of *Mytilus*. These authors did not give these little legs any special name, and O. F. Müller (1786) seems to have been the first to use the name cilia, probably from the similar appearance of a group of cilia to eyelashes. The name flagellum seems to have a more recent origin, and is perhaps due to Dujardin (1841), who used the term flagelliform to describe the appearance of cilia on some protozoa.

By 1835 cilia had been found in most of the main animal groups, and the first comprehensive reviews about these organelles were written by Purkinje and Valentin (1835) and Sharpey (1835). To the former authors goes the credit for the discovery of cilia in mammals in 1834. Sharpey described cilia observed by himself and others in protozoa, sponges, coelenterates, ctenophores, turbellarians, rotifers, annelids, molluscs, echinoderms, ectoprocts, tunicates and vertebrates. In addition to reviewing the functions of the cilia in these various groups, Sharpey made some interesting comments on the structure and physiology of cilia. Some authors of that time, including Ehrenberg (1832) and Purkinje and Valentin (1835), seemed to be of the opinion that cilia were moved by small muscles attached to the bulbous base of the cilia, while Grant (1835) suggested that they might move by the flowing of water into and out of a tubular organelle. Sharpey, however, put forward the idea that the cilia actually "contain muscular substance throughout a greater or less part of their length, by which they can be bent or extended". He had indeed noticed that cilia may bend in the main part of their length as well as at the base, although the significance of this observation was not appreciated by some of his contemporaries. The same author observed metachronal waves (although the term metachronal was not used until later), and compared the appearance of these waves to those produced by wind in a corn-field; he explained the waves correctly as being the result of the undulations of the individual cilia composing the waves. Sharpey knew that in some cases cilia were compounded together, and he records that cilia varied considerably in length from $\frac{1}{500}$ in. on the branchiae of *Buccinum* to perhaps less than 0.000075 in. In his review he mentions results of experiments on cilia with electricity, varied temperature, acids, alkalis and various other substances carried out by himself and others, and, although the experiments were not recorded in detail, they demonstrate that the physiology of cilia was already exciting attention.

In spite of this flowering of interest in cilia, little serious work on ciliary activity was carried out until the end of the nineteenth century, when Verworn, Schäfer, Parker and Heidenhain were notable contributors to our knowledge of ciliary functioning, and there was renewed interest in ciliary structure. Much of this earlier work has been summarized by Gray (1928) in his well-known monograph; only the more important of these older works will be mentioned here, while more recent work will be treated in greater detail.

Since the time of Sharpey many workers have added further to our knowledge of the distribution and functions of cilia and flagella. Some idea of the wide occurrence of cilia and flagella may be gained from Table 1. The information given there can only be of a provisional nature in that some records require checking, and in some cases the fine structure of the organelle requires to be examined in the electron microscope to show that it conforms to the standard pattern. This applies particularly to the sensory cilia, which are only recorded as present when there is evidence both that the structures are cilia and that they have a function in the receptor organ, while a question mark indicates that one or other or both of these facts is not established, although the structures are usually regarded as cilia and are reputed to have a sensory function. Cilia or flagella are known to be present in all the major animal groups except the Nematoda, and it is possible that some sensory structures there may reveal their ciliary origin in studies of their fine structure.

The normal function of cilia and flagella is the movement of fluids relative to the attachment of the organelle. If the body bearing the organelle is free to move and is small enough, the movement of cilia or flagella will move the body, otherwise the fluid will be moved over the surface of a stationary body. It would be an easy matter to fill a book of this size with accounts of the ways in which cilia and flagella are used in organisms of all the groups mentioned in Table 1, so that we shall have to be satisfied here with a few general comments of wide application and some reference to useful reviews and other works of value in this context, which are listed in an Appendix on p. 201.

Perhaps it is first necessary to emphasize that the difference

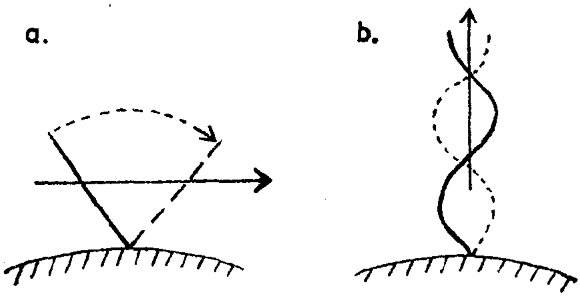

FIG. 1. Diagrammatic representation of the characteristic movement of **a**, a cilium, and **b**, a flagellum. The solid arrow indicates the movement of water and the dotted lines the movement of the organelles.

between cilia and flagella is a purely functional one. Both structures show an identical structural plan in electron microscope studies, but their mode of use is slightly different. It is characteristic of cilia *sensu stricto* that the resultant movement of fluid caused by their beating is at right angles to the long axis of the cilium when it is at the middle of the active part of the beat (Fig. 1a), and therefore parallel to the surface bearing the cilia. "Typical" flagella, on the other hand, produce a resultant

Table 1. The occurrence of cilia and flagella in various systems and organs of animals and plants.

Phylum	Class	Locomotion larval adult	Feeding	Digestive system	Respiratory system	Excretory flame cells nephridia	Sensory	Gametes	Reproductive system	Coelomic circulation	Surface cleaning
Animal kingdom											
Protozoa	Mastigophora	/P	P	/	/	//	P	P	/	/	P
	Rhizopoda	–P	–	/	/	//	/	P	/	/	–
	Sporozoa	—	–	/	/	//	/	P	/	/	–
	Ciliata	PP	P	/	/	//	P	/	/	/	P
Parazoa		P–	P	/	/	//	·	P	/	/	–
Cnidaria		P–	P	P	/	//	P	P	/	/	P
Ctenophora		PP	P	P	/	//	P	P	/	/	P
Platyhelminthes	Turbellaria	PP	–	–	/	P/	?	P	P	/	P
	Trematoda	P–	–	–	/	P/	?	P	P	/	–
	Cestoda	P–	–	/	/	P/	?	P	P	/	–
Nemertina		PP	–	P	/	P/	?	P	–	/	P
Aschelminthes	Rotifera	/P	P	P	/	P/	?	P	P	/	P
	Gastrotricha	/P	P?	–	/	P/	?	?	–?	/	P
	Kinorhyncha	—	–	–	/	P/	?	P	–	/	–
	Priapulida	—	–	–	/	P/	?	?	–	/	–
	Nematoda	—	–	–	/	//	?	–	–	/	–
Acanthocephala		—	–	/	/	P/	·	P	–?	/	–
Entoprocta		P–	P	P	/	P/	?	P	P	/	–
Sipunculoidea		P–	P	P	/	/P	?	P	P	P	–
Annelida		PP	P	P	P	/P	?	P	P	P	P
Mollusca		PP	P	P	P	PP	P	P	P	?	P
Arthropoda		—	–	–	–	/P[x]	P[z]	P[z]	P[x]	–	–
Ectoprocta		P–	P	P	/	//	?	P	P	P	–
Brachiopoda		P–	P	P	P	/P	?	P	P	P	P
Phoronida		P–	P	P	/	//	·	P	P	–	–
Echinodermata		P–	P	P	P	//	?	P	P	P	P
Pogonophora		P–	P?	/	/	/P	·	P	P	·	?
Chaetognatha		/–	–	P	/	//	?	P	P	P	–
Chordata											
Hemichordata		P–	P	P	P	//	?	P	/	P	P
Urochordata		—	P	P	P	//	?	P	P	–	–
Cephalochordata		—	P	P	P	P/	?	P	/	–	–
Vertebrata		P–	P	P	P	/P	P	P	P	P[y]	P
Plant kingdom											
Algae and fungi		P–	/	/	/	//	P	P	/	/	–
Bryophyta, Pteridophyta and Gymnospermae		/–	/	/	/	//	/	P	/	/	–

movement of fluid along the length of the flagellar axis (Fig. 1b), i.e. normal to the surface bearing the flagellum. It is also interesting that a beating flagellum moves fluid continuously, while a cilium is only moving the fluid usefully during part of its beat. In practice, there is no hard-and-fast line to be drawn between the two, for although one can usually see when an organelle is producing a typical ciliary beat, the beat of organelles generally described as flagella may vary from the sine wave pattern shown by some sperm tails, which results from equal and alternate waves of bending on the two sides of the flagellum, to a pattern that is virtually the same as a cilium, in most respects, being asymmetrical and sometimes extremely unilateral. This latter form of beating is common in those protozoa that bear few flagella, but the organelle may show several complete bending waves within its length (see p. 136), which one never finds in true cilia. It is perhaps realistic to regard the flagellum as the original type, which has been specialized in the majority of cases to give the ciliary type of beat.

On the basis of this functional distinction between cilia and flagella, it is interesting that a single cilium would be useless for moving a sperm head, while a flagellum is ideal. Similarly, a few flagella are much more efficient than a few cilia in moving a small protozoon. Large numbers of organelles with a flagellar beat may occur in those cases where they can be used effectively by virtue of their orientation in the functional position. Where many flagella occur on the bodies of some multiflagellate protozoa, their basal structures may be arranged in such a way that the flagellar shafts leave the surface at a fairly acute angle and the flagellar beat can only act to move the body in one direction, so that all the flagella of the body work together to move the organism forward (Pitelka and Schooley, 1958). The same may be true of the multiflagellate sperm of some plants. In sponges the flagellate cells are positioned so that the water currents produced by flagellar beating draw

P, present in at least some members of the group; –, absent; /, system or stage missing in the group; ?, uncertain (for sensory structures, cilia are presumed to be sensory or the sensory structures are presumed to be cilia); ^{x}, in Onychophora; ^{z}, in Insecta; ·, not known; y, in cerebrospinal cavity and therefore not strictly in the coelom.

Data mostly from Hyman (1939–59) and Grassé (1948–61), with additional information from other references quoted in this book.

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