The Biochemistry of Semen

PREFACE

WHEN I took up my studies on semen in 1944, on behalf of the Agricultural Research Council, I became painfully aware of the fact that information on the physiology of semen, its chemical aspects in particular, is rather difficult to come by; the older observations and records being hidden away in books and journals not readily accessible in any but the best equipped libraries, and moreover, scattered throughout an exceptionally wide range of publications, which embrace disciplines as far apart as say, agriculture, urology and cytology. Judging from numerous requests for information, received from fellow workers in the field, biochemists, clinicians, zoologists and veterinary officers alike, the absence of a fairly comprehensive and up-to-date treatise on the chemical physiology of semen must have proved a serious handicap to many in their scientific and practical pursuits. Therefore, I accepted gladly the invitation to write this book; having agreed to produce but a 'little book', I have often found it rather irksome to condense the vast mass of data into the allotted space; had it not been for the encouragement and ready help of colleagues—my wife not least among them, the task would have been even more burdensome.

Biochemistry of semen is a relatively modern, but rapidly expanding, field of physiology; consequently, many of our present views, particularly as regards the biological significance of various chemical constituents of semen, may have to be revised or modified in the near future. That being so, I like to look upon this book, or at any rate, those parts of it which deal with the newer, still fluid concepts, as something in the nature of an Interim Report, designed to furnish information and to convey ideas emerging from the state of knowledge as available at the time of writing, however imperfect that may be. In presenting the recently acquired evidence, I have tried to render justice to developments in the sphere of mammalian as

well as non-mammalian physiology, selecting examples from species as far apart as man and the sea-urchins, and occasionally, introducing plants as well. I have done my best to distinguish between established fact and tentative hypothesis, and, as far as possible, have refrained from the tendency, currently prevalent among workers in this field, to assign to every newly discovered chemical constituent of semen a major role in the process of fertilization.

I wish to acknowledge gratefully the help of those who gave me permission to reproduce plates and figures. In particular I wish to extend my thanks to Dr. C. R. Austin (Sydney), Dr. J. L. Hancock (Cambridge) and the Cambridge University Press for Plate I, to Prof. L. H. Bretschneider and Dr. Woutera van Iterson (Utrecht) and the Nederland Academy of Science for Plate II, to the Royal Society for Plate III, to Lord Rothschild (Cambridge) for Plate IV and for reading the manuscript, to the Royal Society of Edinburgh for Fig. 2, to Dr. E. Blom (Copenhagen) and the *Skandinavisk Veterinärtidskrift* for Fig. 3, to Dr. C. Huggins (Chicago) and the Harvey Society of New York for Fig. 5, to Dr. L. Jacobsson (Göteborg) and the *Acta Physiologica Scandinavica* for Fig. 11, and to the Cambridge University Press, Messrs. Churchill and Messrs. Macmillan for permission to reproduce Figs. 6–10, 12–14 and 16, from the *Biochemical Journal*, the *Journal of Agricultural Science*, and *Nature*, and Plate IV, from the Ciba Foundation Symposium on *Mammalian Germ Cells*. I should also like to thank Miss P. A. Northrop for helping me in the preparation of the typescript.

INTRODUCTION

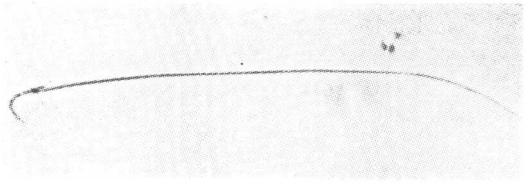
BEFORE I decided to embark upon the business of studying the metabolism of semen, my interest used to centre on very different biochemical problems; earlier on, in the laboratory of J. K. Parnas, I was youthfully grappling with the intricacies of intermediary carbohydrate metabolism in muscle, blood and yeast; later on, at the Molteno Institute, in happy association with D. Keilin, we were investigating the nature and function of metalloprotein enzymes in plant and animal tissues. When confronted with the opportunity of an extensive study of spermatozoa, I did not hesitate to give up my former pursuits in order to devote myself to experiments involving biological material which offers the investigator a chance, almost unique so far as mammalian tissues are concerned, of correlating chemical and metabolic findings with clearly defined and highly specific criteria of physiological activity, such as the motility and fertilizing capacity of the spermatozoa. Among other peculiarities which make semen such a fascinating and attractive object of study is that it represents an animal tissue with but a single type of cells, the spermatozoa, freely suspended in a fluid medium of some complexity, the seminal plasma, and not subject to cellular growth, division or multiplication; thus, making it feasible to express all one's metabolic measurements directly in terms of cell numbers, without recourse to cumbersome and often unreliable standards such as dry weight of tissue, nitrogen content, or indeed, any other of the commonly used metabolic indices. From the purely practical point of view, which matters greatly, the ability of spermatozoa to 'survive', i.e. retain their remarkable properties under conditions of long-term storage *in vitro*, is of great importance. This in turn, gives one a chance of exploring at will and under well-defined conditions *in vitro*, the intricate chemical mechanism underlying the viability, and ultimately, the senescence, of living animal cells.

So far as the nutrition of spermatozoa is concerned, semen resembles more a suspension of microorganisms in a nutrien medium, than other animal tissues which rely for their nutrients

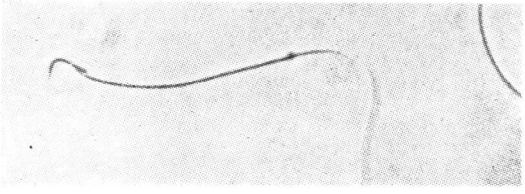
on the blood supply. Nature has endowed the spermatozoa with the means of very efficient utilization of extraneous sources of energy, such as are accessible to the sperm cells either in their natural environment, the seminal plasma, or in the artificial storage media.

As will be evident from what follows later, the present century has witnessed much that is new in the field of semen biochemistry. By and large, however, the situation is not very different from what it was two centuries ago, when Charles Bonnet addressed the following remarks about spermatozoa to Spallanzani:

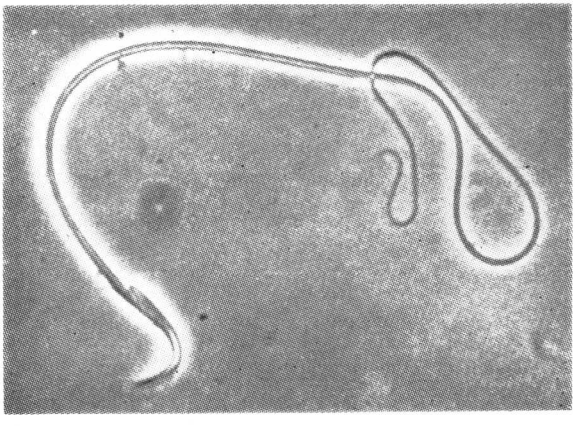
'They are, of all animalculi of liquids, those which have most excited my curiosity: the element in which they live, the place of their abode, their figure, motion, their secret properties; all, in a word, should interest us in so singular a kind of minute animated beings. How are they found there, how are they propagated, how are they developed, how are they fed, and what is their motion? What becomes of them when the liquid they inhabit is reabsorbed by the vessels and returned to the blood? Why do they appear only at the age of puberty; where did they exist before this period? Do they serve no purpose but to people the fluid where they are so largely scattered? How far are we from being able to answer any of these questions! And how probable it is, that future age will be as ignorant of the whole, as our own!'



c



d



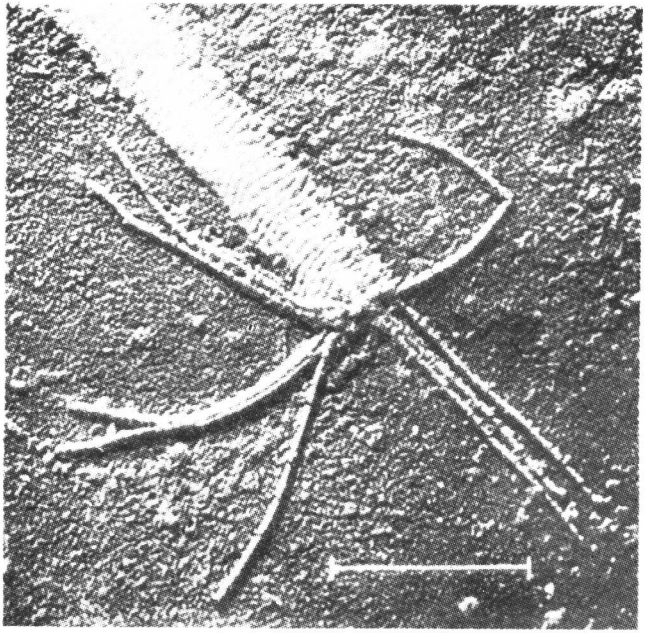
e

S OF SPERMATOZOA

c. Rat spermatozoon.
d. Rat spermatozoon with a kinoplasmic droplet at the posterior end of the middle-piece.
e. Rat spermatozoon. Mag. × 1500.

(By courtesy of Dr. C. R. Austin and Dr. J. L. Hancock)

PLATE II

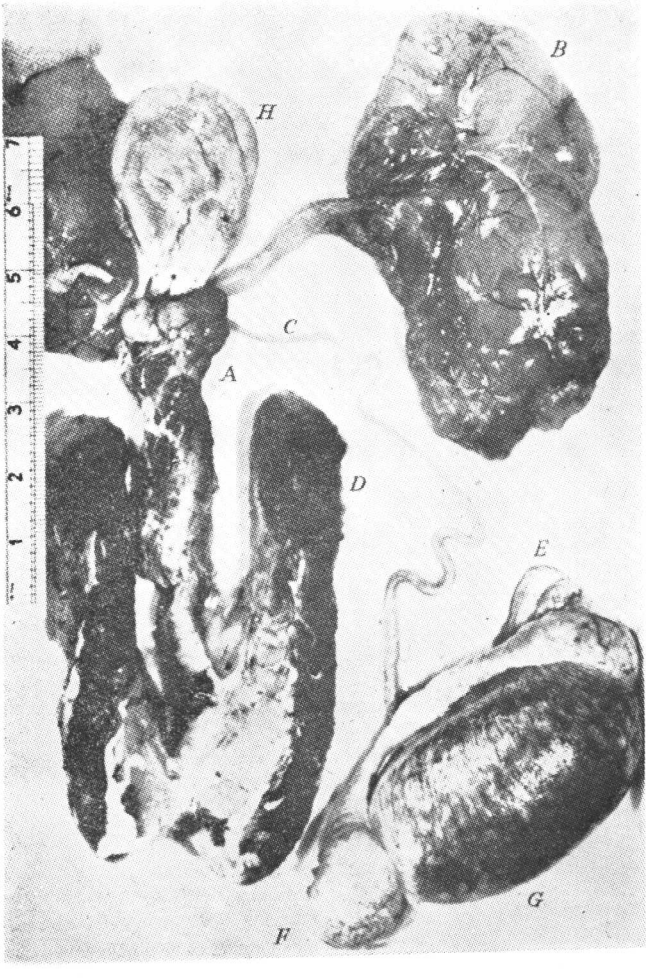


ELECTRON MICROGRAPH OF SPERM-TAIL

Broken end of tail from a bull spermatozoon, showing the tuft of fibrils of the axial filament, and the helical structure of the tail sheath; |——| indicates 1 μ.

(By courtesy of Prof. L. H. Bretschneider and Dr. Woutera van Iterson)

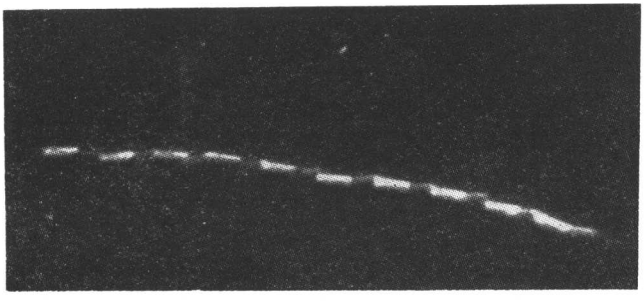
PLATE III



REPRODUCTIVE TRACT OF THE BOAR

A, prostate; *B*, seminal vesicle; *C*, vas deferens; *D*, Cowper's gland; *E*, caput epididymidis; *F*, cauda epididymidis; *G*, testis; *H*, bladder. Scale in inches.

PLATE IV

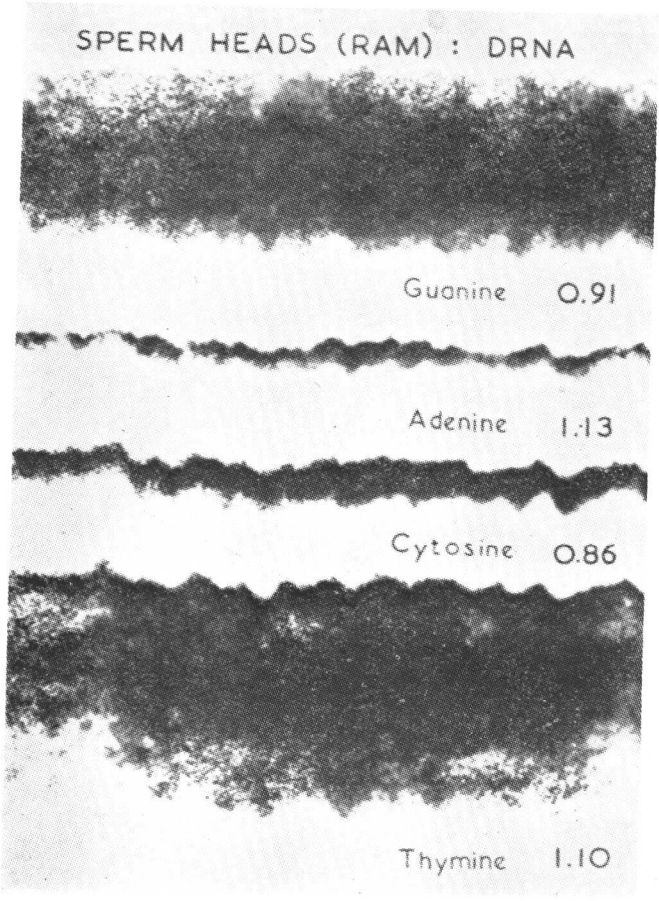


TRACK OF THE SPERM-HEAD

Cinematograph of a bull spermatozoon (in semen diluted 1 : 450) moving forward at a speed of about 0·15 mm./sec. Photographic plate exposed for 1 sec., using dark ground illumination. Mag.×673. Only the projection of the movement of the sperm-head is seen, the tail leaving no track. As the sperm-head is shaped like an elliptical disc, intense light scattering occurs only when the thin edge of the head is visible; during 1 sec. exposure ten images of the head were recorded which means that it rotated or oscillated backwards and forwards ten times.

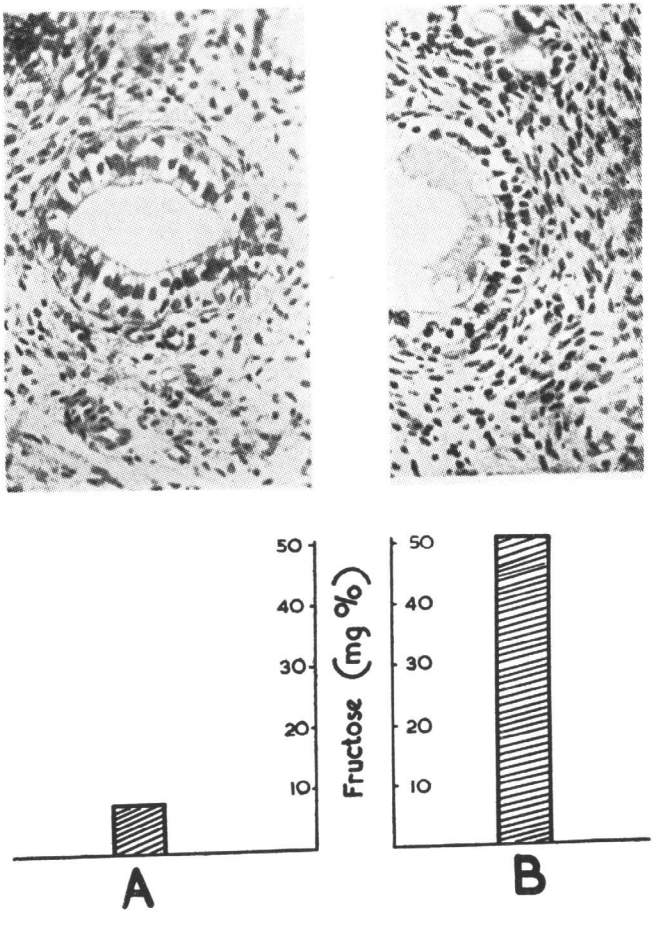
(By courtesy of Lord Rothschild)

PLATE V



PURINE AND PYRIMIDINE BASES IN SPERM DEOXYRIBONUCLEIC ACID

Contact print, taken with ultraviolet light, of a paper chromatogram from the acid hydrolysate of ram sperm-heads. The figures indicate the molar ratios.



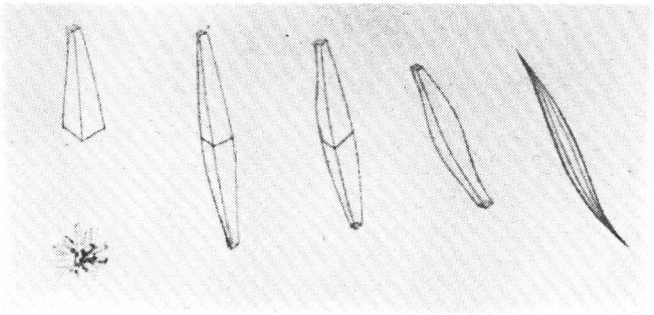
EFFECT OF CASTRATION AND TESTOSTERONE ON BULL SEMINAL VESICLES

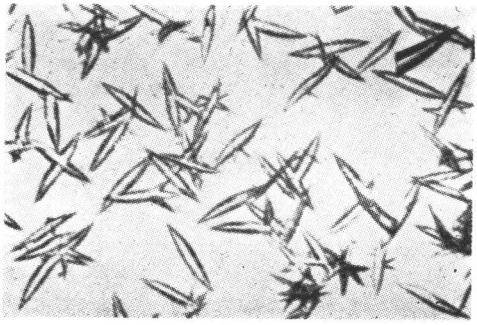
Histological sections from a tubule (mag.×437), and the fructose content of seminal vesicle.

A. from a bull-calf castrated when three weeks old, and killed when nine months old.

B. from a bull-calf castrated when three weeks old, left untreated till eight months old. and then implanted with testosterone (0·5 g.); killed one month later, simultaneously with calf A.

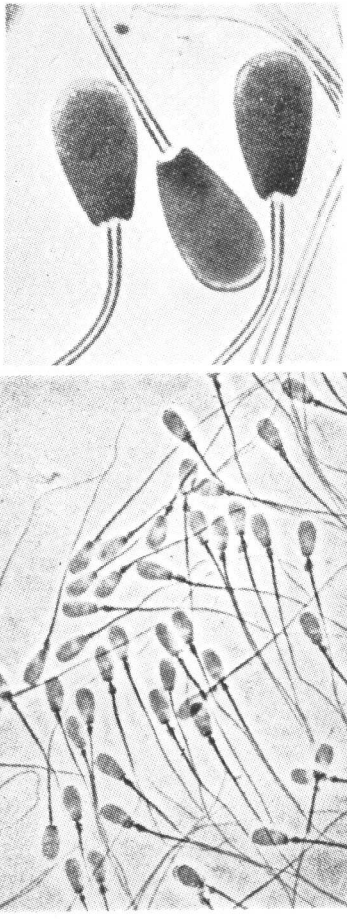
dicta materia paucillum temporis steterat, in ea observabantur trilaterales figuræ ab utraque parte in aculeum desinentes, quibusdam longitudo minutissimæ arenæ, aliquæ aliquantulum majores, ut fig. A. Præterea, adeo nitidæ ac pellucidæ, ac si crystallinæ fuissent.





SPERMINE PHOSPHATE

Crystals in human semen as seen (from top to bottom) by Leeuwenhoek (1677), Fuerbringer (1881) and Poehl (1898).



PHOTOMICROGRA

a. Normal bull semen; photographed in ultraviolet light at 2750 A. Mag. ×. 2700.

b. Semen from an infertile bull; the spermatozoa are 'unripe' and show kinoplasmic droplets at the anterior ends of the middle-pieces; nigrosin-eosin stain.

CONTENTS