

EDWIN STEPHEN GOODRICH

1868-1946

On January 6th of this year, 1946, our beloved and revered Professor Goodrich died at Oxford in his seventy-eighth year, scarcely three months after he had retired from his long tenure of the Linacre Chair. He is acknowledged on all hands to have been one of the great masters of Zoology. His influence will not die with his passing: his contributions to our science have been fundamental and have added so many different and vital parts to its permanent framework. As well as a great master he has been one of the great servants of Science: for a quarter of a century he has been the devoted editor of our Quarterly Journal.

Only a few weeks before he died he had corrected the proofs of the last part of that remarkable review of his 50 years' work on nephridia and coelomoducts which forms parts II, III, and IV of the previous volume. The last part was printed but not issued when he died, and before it appeared Dr. Bidder added to it the mourning notice which bore these words:

Si monumentum quaeras, respice.

The *Quarterly Journal of Microscopical Science* for the last fifty years is indeed his memorial; apart from his editorship since 1920, no fewer than forty-three of his research papers, from 1893 onwards, have been published in its pages.

Edwin Stephen Goodrich was born at Weston-super-Mare on June 21, 1868, the son of the Rev. Octavius Pitt Goodrich, and was the last male descendant of John Goodrich of Energlyn, Glamorganshire, who came from Nansewood, Virginia, U.S.A., in 1775. John Goodrich's forbear, also John, had gone to America in 1630 and settled in Nansewood in 1635; he in turn was descended from John, the elder brother of Thomas Goodrich who was Lord Chancellor of England, Bishop of Ely from 1534 to 1545, then Ambassador to France and again Bishop of Ely in 1551. With Professor Goodrich's death this branch of the family is now extinct.

His father having died, his mother Frances Lucinda Parker (who lived until 1936 reaching the age of 98) took the children

to the south of France at the end of the Franco-Prussian war and they settled at Pau. His elder brother returned for education to England, going to Charterhouse and Balliol, but he himself was considered too delicate and was brought up in France; he attended first a French Lycée and then an English school at Pau. So it came about that he spoke French as perfectly as English.

From his earliest years he had a taste for natural history and, inheriting a family gift for drawing, produced in his boyhood beautiful coloured studies of birds and butterflies. His keen artistic sense, as will be stressed later, was an important factor contributing to his great qualities as a teacher and master of his science; it also made him an accomplished landscape painter in water colour.

At the age of twenty Goodrich returned to England and entered the Slade School of Art at University College, London, in 1888. What a fortunate event for Zoology that was! Ray Lankester, then at the height of his powers as an inspiring teacher, was Jodrell Professor at London and lecturing in a nearby classroom; so Goodrich with his interest in natural history went to hear him. He immediately fell under his spell; he decided then and there that zoology was his real career and changed his course of studies from art to become a pupil under Lankester. At that moment a very important link in the chain of zoological history was forged. Lankester was at once greatly impressed by Goodrich's ability and when in 1891 he was appointed to the Linaeum Chair at Oxford, he took Goodrich with him as his assistant. I am sure that in many Zoologists' minds the names of Lankester and Goodrich are closely linked—and with good cause. Lankester was the dominating force in the evolutionary comparative anatomy which arose and flourished after the publication of the *Origin of Species*. Goodrich more than anyone else has carried forward the torch, lit by Lankester, in this field of zoology; he has carried it from the last century up to nearly half of this and the flame burns as brightly in his last great paper just published, as it did in his early papers of the 'nineties. To say this is not to imply that Goodrich just continued lines of work started by Lankester—not at all: his genius and insight

continually opened up new lines of work bringing sense and order where hitherto had been confusion in both vertebrate and invertebrate zoology. Our Journal has of course developed and kept its fame under the guidance of these two great leaders: when Lankester gave up his long editorship in 1920, Goodrich was his natural follower.

On coming to Oxford from London Goodrich entered Merton College as an undergraduate in 1892 and while acting as Assistant to Lankester read for the final honour school in Zoology; he was awarded the Rolleston Memorial Prize in 1894 and graduated with First-class Honours the following year.

An account of his scientific work will come later, but while we are being biographical it should be recorded that when still an undergraduate he had become a most active researcher. He was of course somewhat older than the average undergraduate; he was twenty-four when he entered Merton and in that year he published his first two papers. His third paper, and his first in this Journal, came in 1893, two more in 1894, and before he took his final schools he must have completed the two papers published in 1895 which included his ever famous dissertation 'On the Coelom, Genital Ducts and Nephridia'. His wide range of interest was already clearly shown: apart from this classic, which covered the whole range of the Metazoa, his early papers had dealt with cephalopods, polychaetes, oligochaetes, fossil mammals and museum reform.

After graduation he went with the Naples Scholarship for six months to the famous Stazione Zoologica and in 1898 he was awarded the Radcliffe Travelling Fellowship, whereby he visited India and Ceylon. In the following year he was appointed Aldrichian Demonstrator of Comparative Anatomy and in 1900 was elected a Fellow of Merton. Apart from his world-wide travels in vacations Goodrich remained at Oxford all his life. W. F. R. Weldon had become Linacre Professor in 1899 when Lankester went to be Director of the Natural History departments of the British Museum and was in turn succeeded in the chair by G. C. Bourne in 1906. During the first world war when Bourne and other members of the staff were away on war service, Goodrich carried on the teaching and administration of the

department single-handed. A special Professorship of Comparative Embryology was made for him in 1919, and in 1921 he succeeded Bourne in the Linacre Chair, which he held until last year. All this time, until his death Goodrich remained a Fellow of Merton, becoming a Professorial Fellow when he took the Chair, and being elected an Honorary Fellow when he retired.

In 1918 he married Helen Pixell, the eminent protozoologist, and more will be said of this very happy partnership later. Here I want to refer to something that is so characteristic of his modesty: he would not take his D.Sc. degree until some years after his wife had taken hers and then only when persuaded to the extent of her paying the necessary University dues and providing the gorgeous and costly robes!

Many were the honours that came to him. He was elected a Fellow of the Royal Society in 1905, when still in his thirties, served on the Council twice (1923-5 and 1931-2) and as Vice-President during 1930-1, and was awarded the Royal Medal in 1936. From 1915 to 1923 he was Zoological Secretary of the Linnean Society of London, helping to keep it alive through those lean and difficult years of war; in 1932 he received the Society's Gold Medal. He was given an Honorary LL.D. by Edinburgh University and an Honorary Sc.D. by Dublin. He was Hon. Member of the New York Academy of Sciences, Member of the Royal Swedish Academy, Membre Correspondant de la Société de Biologie de Paris, Associé de l'Académie Royale de Belgique, Foreign Member of the Academy of Sciences of U.S.S.R., Leningrad, Hon. Fellow of the National Institute of Sciences of India, Member of the International Institute of Embryology of Utrecht and Member of the Royal Society of Sciences of Upsala.

On his seventieth birthday, in 1938, his colleagues and pupils expressed their admiration for his work by presenting him with a congratulatory volume of essays edited by Dr. (now Professor) G. R. de Beer and entitled *Evolution: Essays on Aspects of Evolutionary Biology*.

With this brief biographical summary let us now turn to consider his contributions to zoological knowledge and his influence as a teacher. Appended to this account of his work will be found

a complete list of his publications arranged in chronological order, which was kindly prepared for me by Mrs. Goodrich; to her also I am much indebted for notes regarding his career.

Goodrich's first paper, published in the *Journal of the Marine Biological Association* in 1892 was a precise account of a large and rare squid *Ommastrephes pteropus* Stp. which had been captured off Salcombe; but he was not content with presenting just a careful description, for he added to it a valuable table giving the chief characters of all the genera of recent Oigopsid Cephalopoda in the form of a key. Four years later, in his tenth publication, he wrote a report on a collection of 162 Cephalopoda belonging to 28 genera, collected by H.M.S. Investigator in the Indian Ocean; he described and figured eleven entirely new species belonging to nine genera and recorded four genera not hitherto taken in the Indian region.

In 1892 he also published a note on a new species and genus of oligochaete *Vermiculus pilosus*, which he discovered at Weymouth, and in 1895 gave a full account of it in this Journal; he showed that it has a number of characters which place it in a very isolated position including a dense covering, from head to tail, of remarkable 'sense hairs'. He wrote further notes on oligochaetes with a description of a new species *Enchytraeus hortensis* in 1896, here paying particular attention to the coelomic corpuscles.

As soon as he came to Oxford he began to assist Lankester in an entire rearrangement of the zoological collections in the University Museum. He described these reforms in the now extinct monthly journal *Natural Science* in 1894. It is clear from his writing how enthusiastically he took up this task.

'Here', he writes, 'one need seek neither to attract the nursery-maid nor to amuse children, nor again need one trouble to satisfy the idle curiosity of the sightseer. There is, then, no necessity for tragic groups of stuffed animals, for birds perched on cardboard rocks among artificial flowers. On the contrary, the exhibits are to be strictly scientific, forming series at once instructive and interesting to the general educated public, and more especially to the real student of

zoology. Surrounded as it is by the various chemical, physical, and biological laboratories, the central court is in the first instance a place of study. In such educational collections it is essential that each object should be exhibited for a definite purpose, should show what it is meant to show as clearly as possible, and should be fully labelled in language technical so far as is necessary for accuracy. The observer is not to be bewildered by a number of specimens, but rather impressed by a few well-chosen examples.'

He was responsible for the greater part of the vertebrate exhibits. As a Professor from another University remarked to me recently 'there is no other museum in which a student can learn so much sound comparative anatomy by walking round and studying the exhibits and their labels—thanks to Goodrich'.

This rearrangement of the museum led to Goodrich's first published work in palaeontology: his paper (1894) on the fossil Mammalia of the Stonesfield Slate. How characteristic of him is the manner in which he came to undertake it. In this paper he writes: 'Through the kindness of Professor Green and Professor Lankester, who placed the Oxford fossils in my hands for the purpose of displaying them in a museum case in a manner more worthy of their interest and value, I had the opportunity of examining and handling our six specimens.' These were the famous lower jaws of the first Mesozoic mammals to be discovered; they had been found about 1814 and examined and described by a succession of authors including Buckland, Cuvier, Owen and Osborn. Their particular interest apart from their early origin lay in the nature of their teeth and the light they shed on the evolution of mammalian dentition. Goodrich was not content simply to display the specimens with explanatory labels setting out the current theories concerning them; he must thoroughly re-examine them himself to see if they really did support the theories. We must remember that at this time he was still an undergraduate working for his schools. He also obtained access to the three other known English specimens: two in the British Museum and one at York. He states the 'Tritubercular Theory' advanced at that time by Osborn, Cope

and other American palaeontologists and then characteristically writes: 'Let us now examine the facts.'

All through his life's work that phrase, or some other like it, recurs again and again; he states the generally accepted theory and then examines the facts: the actual specimens concerned. So often, as here, he proved the theory false, or else greatly enhanced its value. The then widely accepted American view was that the Tritubercular tooth, with cusps arranged in a triangle, was derived from a Triconodont type, with the three cusps in line, by the shifting outwards of the median cusp; the Triconodont condition was in turn considered the first step towards the more complex mammalian molar by being derived from the simple reptilian cone by the addition of an extra cusp in front and behind. 'Professor Osborn', writes Goodrich, 'in his illustrations of the theory . . . has made large use of the Mesozoic mammals found in England; one can therefore stand on firm ground while criticising his conclusions and his interpretations of the facts.' By carefully working away the matrix Goodrich exposed new cusps to some of the teeth and in some cases new teeth. His re-examination demolished the supposed evidence upon which Osborn's theory was based and led him to conclude 'that the common ancestor of Marsupial and Placental mammals had teeth with many cusps of the Tritubercular sectorial pattern' and that it 'seems extremely probable' that the molars of the earliest ancestral mammal 'were of an indefinite multituberculate pattern'.

In the meantime he had in 1893 published his discovery of the dorsal ciliated organ in *Nereis* and found it in other closely allied polychaetes but not in genera of other families; he states his reasons for considering it 'as a genital duct not fully developed'. He also gives a beautiful description of the nephridium of *Nereis*. This is the beginning of that magnificent series of studies on nephridia and coelomoducts to which he returned and added to so often throughout his life until the very end. When he wrote this, his first contribution to the subject, it was generally believed that genital ducts and nephridia were homologous structures; here he points out the difficulties of this view and with remarkable insight tentatively foreshadows the

conclusions which he was subsequently to establish beyond doubt.

Two years later, in 1895, came his classic 'On the Coelom, Genital Ducts and Nephridia'. It is written with his typical lucidity and beautiful economy of words; in a text of only twenty-six pages, in which he refers to 116 other published researches, he compares all the main groups of the triploblastic Metazoa and shows the thread of homology running through them. The significance of this paper cannot be better expressed than in his own words taken from its introduction:

'An unprejudiced review of the well-established and recently ascertained facts concerning the development of the excretory organs and genital ducts of the Coelomata must, I think, inevitably lead us to the conclusion that we have been confusing two organs of totally different origin under the one name nephridium—the one organ the true nephridium, the other the morphological representative of the genital duct, which may be called the peritoneal funnel, to avoid confusion. Further, that while on the one hand in certain groups such as the Planaria, Nemertina, Hirudinea, Chaetopoda, Rotifera, Entoprocta, besides the genital ducts or peritoneal funnels, we find true nephridia in the adult; on the other hand, in such groups as the Mollusca, Arthropoda, Ectoprocta, Echinoderma, and Vertebrata, there are in the adult no certain traces of true nephridia. In these latter groups, as we shall see, the peritoneal funnels (primitive genital ducts) take on the excretory functions of the nephridia which they supersede.'

It will be remembered that at this time Goodrich had not yet discovered the nephridial nature of the excretory organs of Amphioxus.

He continues:

'In the following brief review of the various classes of Coelomata, I shall endeavour to show that the two kinds of organs can always be distinguished; that the first, the nephridium, is primitively excretory in function, is developed centripetally as it were, and quite independently of the coelom (indeed, is probably derived from the epiblast), possesses a

lumen which is developed as the hollowing out of the nephridial cells, and is generally of an intracellular character, is closed within, and may secondarily acquire an internal opening either into a blood space or into the coelom (true nephridial funnel as opposed to the peritoneal funnel); and that the second kind of organ, the peritoneal funnel, is primitively the outlet for the genital products, is unvariably developed centrifugally as an outgrowth from the coelomic epithelium or wall of the genital follicle, is therefore of undoubtedly mesoblastic origin, and possesses a lumen arising as an extension of the coelom itself.

'In the series of diagrams illustrating this paper, based on the most recent and accurate researches, it has been my constant endeavour to interpret the author's results correctly and not to distort the facts in favour of the theory here advocated.'

He then proceeds to compare the conditions found in the different coelomate Metazoa group by group.

In the following year (1896) he replies in the *Zoologischer Anzeiger* to a critical review of his paper by Bergh; in this he makes a dramatic reference to his discovery of solenocytes which he had not yet announced.

'The reviewer', he writes, 'appears still to hold the view that the nephridia of the Oligochaeta are homologous not with the nephridia (excretory organs) of the Platyhelminths and Nemertines, but with the follicle-ducts of the latter; I contend that recently ascertained facts concerning the anatomy and development of these organs render the theory untenable. It may be said that if the theory which I on the other hand advocate be true, I should be able to show an Annelid with an undoubted coelom into which the "true nephridia" do not open—to this I can answer, that I believe I am now in a position to supply this long sought link in the chain of argument (*Nephtys* and *Glycera*: as I hope to show in a forthcoming paper).'

There then followed that remarkable series of papers 'On the Nephridia of the Polychaeta', Part I in 1897 dealing with

Hesione, Tyrrhena and Nephthys, Part II in 1898 on Glycera and Goniada, and Part III in 1900 dealing with the Phyllodo-
cidae, Syllidae, Amphinomidae, &c., and general conclusions. Here he describes and figures with superb drawings the minute and delicate anatomy of the excretory and genital ducts of so many different polychaetes. Here are his discoveries of the solenocytes of various kinds, the blind endings of excretory canals comparable to the flame cells of the Platyhelminths but differing from them in the possession of fine straight tubes, enclosing the flagellum, running from the cells to the lumen of the canal. Here he also describes the different conditions of combination of nephridium and genital duct or funnel that he calls the nephromixium.

There is no need here to stress the immense amount of work he has described in these and subsequent papers; as already mentioned and as all will know, he had so recently completed, just before he died, that magnificent review of all the work done in this field since the publication of his paper of 1895. It is written with the same economy of words, yet instead of twenty-six it has 266 pages and refers to 430 other papers. It is more than a review of past work for it contains many original and hitherto unpublished observations; the most important of these is perhaps his study of the early stages of the nephridioblast in *Tubifex* where he clearly shows that it was never a cell derived from the coelomic epithelium as believed by Meyer. His own work and that of others have fully confirmed the conclusions he formerly reached regarding the nature of the two kinds of ducts; in addition the gonocoel theory is accepted as the best explanation of the origin of the coelom. Professor de Beer in his Royal Society obituary of Goodrich has well said: 'Even if he had done nothing else this last paper would be sufficient to ensure his lasting reputation as a zoologist.'

In spite of this so recent review of his, we must not leave the subject of nephridia without recalling what is perhaps his most exciting discovery: the solenocytes of *Amphioxus*. In 1890 both Weiss and Boveri had independently discovered the excretory organs of *Amphioxus* but had described them as tubules opening into the coelomic cavities; they took them to be the primitive

homologues of the pronephric tubules of the higher chordates. Goodrich in his third paper on the nephridia of the Polychaeta (1900) records in a footnote how he was struck by the 'strange resemblance between the solenocytes' (which he had discovered in the Polychaetes) 'and the peculiar cells described by Boveri as surrounding the openings of the excretory tubules in *Amphioxus*'. He goes on to say: 'Some years ago, I examined these tubules in fresh specimens and came to the conclusion that the resemblance is only superficial.' The following winter, however, when working at Naples, he decided to re-examine them and was now able to show that they were indeed true solenocytes and there was in fact no funnel opening into the coelom at all. They were not homologous with the kidney tubules of vertebrates which he had shown to be coelomoducts but were true nephridia and bore a remarkable resemblance to the solenocytes he had described in *Phyllodoce*. It must have given him great satisfaction to have had the opportunity of personally demonstrating the correctness of his observations to Professor Boveri who happened to be visiting Naples at the time.

As will be seen from his list of publications he returned again and again to the study of *Amphioxus*; he made many journeys to obtain material to Sicily, Naples, Heligoland and Bermuda. His proficiency in the Italian language, as well as French, was a great help to him in his field work, for he was often out with the fishermen in their small boats going from Messina to Cape Faro at night or very early in the morning in search of *Amphioxus*. Great was his disappointment to find that the plentiful supply there earlier in the century had been exterminated by the earthquakes of 1912, probably by a wave of hot water, and had not been replenished twelve years or more afterwards. Overcoming the many difficulties, technical and otherwise, he produced further detailed studies on the nephridia of *Amphioxus* and their development in 1909, 1932, and 1934 as well as a short note on 'Hermaphroditism in *Amphioxus*', 1912, and a paper on the development of the club-shaped gland in 1930. Other beautiful studies of solenocytes in larval forms must just be mentioned: his account of the body cavities and nephridia of the *Actinotrocha*

larva of Phoronis (1908) and the nephridia of the larvae of Echiurus and Polygordius (1909).

He wrote two papers on *Sternaspis* (1898 and 1904) which, although originating in an examination of the genital organs and nephridia should be mentioned for their fine anatomical studies of the muscular and vascular systems. I cannot resist quoting from the first of these papers for quite another reason: it illustrates so well his characteristic combination of courtesy and directness in demolishing the false views of others. He begins the paper thus: 'In the beautiful works both of Professor Vejdovsky and M. Rietsch on *Sternaspis* we find certain statements which, if correct, would place that worm in a very exceptional position.' He then briefly describes the statements concerned and goes on: 'It was, therefore, with a view to either confirm or correct these descriptions that I began a study of *Sternaspis thalassemoides*, Otto, during a recent visit to Naples. I may say at once that they both proved to be erroneous.' His clear interpretations and drawings of his serial sections then supply the proof.

In 1898 with his remarkable morphological insight he cleared away much previous confusion in his essay on the segmentation of the Arthropod head and his thesis has well stood the test of time. His arguments in favour of there being six segments in the Crustacean head were largely based on evidence from the nervous system, for at that time distinct somites or coelomic cavities had not yet been traced with certainty in the development of the cephalic region. How pleased he must have been when Miss Manton in 1928 in her beautiful embryological study of *Hemimysis* clearly demonstrated six mesoblastic somites in the head.

To group after group of invertebrates he applied his skill; in the same year he solved a nice problem in the Mollusca. Again I cannot resist giving a quotation:

'Strange indeed, and happily unique in the annals of comparative anatomy, has been the history of our knowledge of the reno-pericardial canals of *Patella*. Although discovered more than thirty years ago, and investigated by many

observers since, not only is their structure insufficiently known, but their very existence has been called in question and even positively denied!

'Wishing to find out definitely whether these ducts really existed or not, I undertook this work, which was carried out in Oxford, on material obtained from Plymouth and Naples. In this short paper I hope to establish clearly, and beyond the possibility of doubt, the fact that there are reno-pericardial canals leading from the pericardium to the right kidney and to the left kidney in Patella.'

And he did.

In the following year, 1899, he made a study of the coelom and vascular system of the Leech and in 1900 came his section on the Holothuroidea in the Echinoderm volume of Lankester's *Treatise on Zoology*.

Space will not permit more than a passing reference to his keen interest in the Archiannelids and the problem of their systematic position: whether they are to be regarded as primitive or secondarily simplified; he has studies on *Saccocirrus* (1901), *Dinophilus* (1909), *Nerilla* (1912), and *Protodrilus* (1921). In the *Nerilla* paper he sums up his conclusions: 'Taken as a whole the Archiannelida form a degenerating series which can only be read one way. But very possibly the group includes three such series starting from a common Chaetopod ancestor, *Chaetogordius* and *Polygordius* forming one, *Saccocirrus* and *Protodrilus* another, and *Nerilla*, *Dinophilus* and *Histriobdella* a third.' He also wrote three papers on new or little known Syllid worms (1900, 1930 and 1933).

In a paper in 1919 he showed that the slender pseudopodia usually described and figured as projecting from the leucocytes of invertebrates are in reality the radial folds of an extensive membrane which surrounds such cells and had hitherto escaped detection. In the same year he and Mrs. Goodrich collaborated in a most interesting study of the ecological interrelationships between leucocytes and parasitic protozoa, bringing out among other things the conclusion that most such protozoa must produce some secretion which causes leucocytes to avoid them;

together they also described (1920) a new species of Gregarine, *Gonospora minchinii*, inhabiting the egg of *Arenicola*. Here too may be a convenient place to refer to one of his very recent papers, 1942, on a new method of dissociating cells: by immersing small pieces of tissue, or whole small animals such as Hydra, in a saturated solution of boric acid in normal salt solution to which a trace of Lugol's solution of iodine has been added. The cells fall apart, or may be easily separated, retaining their characteristic form; he shows many beautiful examples such as ecto- and endodermal musculo-epithelial cells of Hydra, cells of the intestine and the nephrostome of Lumbricus, cells from various tissues of the frog and rabbit: all most valuable for class work.

During the recent war the importance of studying and controlling the insect pests infesting grain and other stored products has been fully realized and many have been engaged in such researches. In the previous war Goodrich was a pioneer in this field; he sought to find out how the presence of parasitic Hymenoptera (Chalcidae) may affect the various grain-infesting beetles. First he showed that some species of beetle were parasitised and others not, and that those which were, were attacked in the larval stage. He then showed that the Chalcids could not be effectively used in keeping down these beetles because, as he discovered, they themselves were in turn parasitised and kept in check by an acarid *Pediculoides ventricosus* Newport which had not hitherto been known to attack hymenoptera. Rarely in an official report (1921) do we see such a vivid description as he gives:

'In a grain of wheat are often found the shrivelled remains of the Calandra larva on which the hymenopteron larva has fed, the dead or dying Chalcid imago, and the *Pediculoides* attached to it. Thus the whole series of events is permanently recorded in chitin, and the complete tragedy can be unfolded, even from unpromising material, by soaking it in a strong solution of potash.'

Up to here, the only vertebrate work of his we have noted is his study of the fossil mammals of the Stonesfield Slate. If a

novice in Zoology should read this article thus far, he would get the impression that Goodrich was mainly an invertebrate specialist; we must now correct that impression. Great as have been his contributions to invertebrate Zoology, still greater are his achievements among the vertebrates.

In 1901 in making a study of the pelvic girdle and fin of the fossil fish *Eusthenopteron* he came to compare the pelvic girdles and fins of all groups of fish. There was at that time considerable confusion regarding the morphology of the pelvic supports; it was commonly held for example that a true pelvic girdle was present in the Selachii, Holocephali and Dipnoi but that the supports in the Crossopterygii and Actinopterygii were derived from the fin skeleton itself. 'Let us see what difficulties such views lead us into', he says, and at once proceeds to one of his masterly analyses of the different theories side by side with a study of the actual specimens concerned. The logic of his argument inevitably leads us to the 'conclusion that the pelvic supports, whether paired or unpaired, are homologous throughout the fish series'. He now became greatly interested in the fins of fish and the importance of their differences in structure in classification. In 1903 he published his beautiful studies of the dermal fin rays of both living and fossil forms. Having clearly distinguished the four different kinds: the ceratotrichia of the Elasmobranchii and Holocephali, the actinotrichia and lepidotrichia of Teleostomes and the camptotrichia of the Dipnoi, he then proceeds to discuss their origin and homologies. He shows that the lepidotrichia are of quite a different nature from the horny ceratotrichia and actinotrichia and are undoubtedly derived from modified body scales. Further, although not conclusively proved, he shows it likely that the camptotrichia of the Dipnoi are homologous with the lepidotrichia of the Teleostomes but have sunk deeper and been overlaid by a secondary extension of the body scales.

The two foregoing papers, important in clearing up much confusion, were but the prelude to his grand attack on the problem of the origin and nature of the paired fins in 1906. It was a major problem of the time, for there was little doubt that the paired fins of fish and the limbs of the higher vertebrates were

homologous. Zoologists were divided into two camps: those who followed Gegenbaur in believing the paired fins to be derived from gill structures (the gill-arch theory) and those who followed Balfour, Thacker and Mivart in the view that they were derived from paired longitudinal fin folds of a similar nature to the median fins (the lateral fin-fold theory). 'Each of these theories', he says, 'may claim to have among its numerous supporters the names of some of the most eminent exponents of the morphology of the vertebrates.'

The literature on the subject had been extensive, but it practically came to an end when Goodrich stepped in and settled the matter for good and all. It is impossible in a brief review to do justice to his case, but let us just remind ourselves of some of the more telling points he made in this which was another of his classic papers. The paired fins develop on the whole just like median fins: the muscle buds grow out from the myotomes, divide into upper and lower halves to supply each side of the radials which are differentiated between them. There is a remarkable resemblance in detail of structure between the paired and unpaired fins. If the paired fins had developed from vertical gill septa they would in the first instance have hindered forward locomotion and the two pairs would have been close together one behind the other and so mechanically ineffective. In development the fin never appears as a dorso-ventral fold, but always as a longitudinal one. There is no evidence, either from primitive living fish or early fossil forms, of a more anterior pelvic fin which might be expected if it was derived from a gill arch; in those Teleosts where the pelvic fin is far forward, there is good evidence that this is a recent and secondary development. The presence of rudimentary muscle buds in front of the pelvic fins had been supposed to indicate a backward migration of the fin from a primitively more forward position; Goodrich, however, showed that rudimentary muscle buds may also be found *behind the fin*. The gill-arch theory does not account for the large number of segments often contributing to the muscle buds of the fins and the fact that usually more segments are concerned in the more primitive forms. And then the *coup de grâce*: the gill arches are morphologically in the wall of the ali-

mentary canal and are supplied by visceral muscles innervated here by *dorsal roots* (vagus) whereas the paired fin muscles are derived from myotomes and innervated by somatic motor nerves from the *ventral roots*.

This same paper did much more than clear up the question of the paired fins; it dealt also with the development, structure and origin of the median fins. He showed how the 'concentration' of muscle buds and radials found in the fins (both median and paired) came about: the muscle buds having been nipped off from the myotomes, the body of the fish now grows faster than the fin so that the series of muscle buds no longer corresponds in length with the series of myotomes which gave rise to the buds but appears as a concentration.

His studies of the nerve supply of the muscle buds of fins and limbs led him to enunciate a general principle which is of great importance in helping the comparative anatomist in the correct interpretations of evolutionary morphological problems: that the motor nerves always remain faithful to their particular myotomes or their derivatives even, as he says 'throughout the vicissitudes of phylogenetic and ontogenetic modification'. It seemed to him, both on physiological and anatomical grounds, highly improbable that a motor nerve could forsake the muscle in connection with which it was originally developed to become attached to another muscle of different origin. All his work on the development of the limbs supported this. They are supplied by branches from a number of segmental nerves forming a plexus, but such a plexus can be shown to be 'brought about, not by the nerve deserting one muscle for the sake of another, but by the combination of muscles derived from neighbouring segments'. He tested this experimentally in the living skate by observing the separate contraction of the different muscle elements of the plexus when their corresponding nerves were stimulated by electrical and mechanical means.

All through Goodrich's work we see his curiosity being aroused by points which set him off on fresh lines of fruitful investigation; he had a remarkable gift for picking out problems of importance, the significance of which had been missed by others. We now come to the puzzle of *Polypterus*. In his paper

of 1901 on the pelvic fins and girdles he draws attention to the position of this fish which for so long had been placed with the Crossopterygii and hints that he considers it not unlikely that it is really an Actinopterygian. In 1907 he read a paper to the Zoological section of the British Association on 'The Systematic Position of *Polypterus*' in which he develops the thesis more definitely. It had been placed in the Crossopterygii by Huxley on account of its lobate paired fins, paired gulars, rhomboid scales and outwardly diphycercal tail. Goodrich had already shown that internally its paired fins were of quite a different structure from those of the Crossopterygians to which they had but a superficial resemblance. He now showed the same thing for the scales, the two kinds look alike but those of *Polypterus* are not covered with cosmine but are of a true ganoid type resembling closely those of the fossil Palaeoniscoids. The paired gular plates might just as well be compared with the anterior members of the lateral series of plates of an Actinopterygian (such as the branchiostegal rays of *Amia*) as with the more median pair of gular plates of the Crossopterygians—indeed he pointed out that among the fossil Actinopterygians there are the Palaeoniscidae which in fact have just such anterior lateral plates enlarged. Again internally the caudal fin of *Polypterus* shows evidence of being a modified heterocercal tail. He now definitely believed it should be regarded as an Actinopterygian—but he was cautious about going further at that time, although reading between the lines one can sense his leaning to the belief that it is really a living Palaeoniscid. In his great book on the Cyclostomes and Fishes published in 1909 he still places *Polypterus* among the Crossopterygians but at their end, next to the Actinopterygians, and indicates his belief that they will be proved to belong to the latter; here however we see a certain caution owing to his having seen the resemblance of *Polypterus* to *Tarrasius problematicus* which was then regarded as an Osteolepidotid Crossopterygian. But I must cut a long, and exciting, story short. It was not until 1927 that Goodrich published his '*Polypterus* a Palaeoniscid?' in which he fully gives the reasons with which he had 'ventured to suggest that the Polypterini are survivors of this large and varied group

hitherto supposed to be extinct'. His brilliant pupil, the late Mr. J. A. Moy-Thomas, now put the finishing touches to the story; his tragic death in the war, such a great loss to Zoology, was a personal grief which Goodrich felt very deeply.¹ Moy-Thomas published his study² of the development of the chondrocranium of *Polypterus* in 1933 and compared it with the development of the chondrocrania of other fish; he ended by saying 'the view of Goodrich is thus afforded additional support'. In the following year he, Moy-Thomas, proved that *Tarrasius problematicus* was actually a Palaeoniscid.³ Goodrich's suspicions were confirmed in both directions: *Polypterus* resembled both *Tarrasius* and the Palaeoniscids for the now simple reason that the two were shown to be of one and the same Actinopterygian group.

In 1939 Moy-Thomas in his book *Palaeozoic Fishes* (p. 117) definitely refers to '*Polypterus*, itself a palaeoniscid derivative' and ends his book with these words:

'The African *Polypterus* is probably directly descended from the Palaeoniscids in the Cretaceous, and has retained the Palaeoniscoid scales, but has become rather specialized in other ways, especially in the nature of its fins.'

The puzzle of *Polypterus*, indeed an exciting story of detection, is ended. We have here a living fossil, almost as remarkable as the living *Coelocanth Latimeria*, discovered not, as was the latter, by its sudden appearance in a trawl, but by the methods of comparative anatomy of which Goodrich was the master: the comparison of both living and fossil forms together.

Again one thing leads to another. Both his work on the dermal fin-rays of fish and his interest in the scales of *Polypterus* led him on to another of his major contributions to vertebrate morphology: his study 'On the Scales of Fish, Living and Extinct, and their importance in Classification', published in 1908. Here he gave us his beautiful drawings of sections of the

¹ See his obituary notice of Moy-Thomas in *Nature*, April 8, 1944.

² *Q.J.M.S.*, 76, 209.

³ *Proc. Zool. Soc. London*, 1934, 367.

different kinds of scale and his interpretations of them. Williamson half a century earlier had shown that some of the so-called ganoid scales of Agassiz, those of fossil osteolepidotid fish such as *Megalichthys* were of what he called a cosmoid type, formed by a layer of fused denticles—the cosmine layer—becoming attached to an underlying bony plate, the so-called 'isopedin' layer. Goodrich largely confirmed Williamson's findings and called attention to his somewhat neglected work which had been hidden by the more recent and, as Goodrich showed, erroneous theories of Oscar Hertwig. He distinguished the cosmoid scales of Williamson from the true ganoid scales and further subdivided the latter into those of the Palaeoniscoid type, found in the fossil Palaeoniscids and the living *Polypterus*, and those of the Lepidosteoid type found in *Lepidosteus* (and the *Amioidei*). The former he showed to be evolved from the cosmoid type by the addition of layers of ganoin on top: a sandwich of cosmine between the ganoin and bony isopedin plates. The Lepidosteoid scale he showed to be similar but lacking the intermediate layer. He went on to demonstrate the great value of these different scales as an aid to classification.

This work in turn led to an interesting discovery he published in 1913 but which is best mentioned here: one concerning the structure of bone in fishes; a 'contribution to palaeohistology' he called it. In addition to the differences between the palaeoniscoid and lepidosteoid scales just referred to, it was now found that the bony layers of the latter were quite different from those of the former; in the lepidosteoid scale the layers of bone are traversed at right angles by peculiar tubules which in the living tissues are filled with the long protoplasmic processes of large cells situated on the surface of the scale. He now discovered that this condition was also present not only in those dermal bones of the skull originally derived from scales but in the *whole endoskeleton* as well, that is of those Actinopterygian fish which have Lepidosteoid scales (the *Amioidei* and *Lepidosteoides*) and in those fish alone. He gives a list of the fish of many groups he has investigated. 'It follows that, from the examination of the minutest fragment of the skeleton of a living or extinct species of fish we can decide whether it belongs to these two orders or

to some other group. The histological structure of the bone may therefore be of the greatest practical value for the identification of fragmentary specimens.' He had placed a new tool in the hands of the phylogenetic 'detective'.

In 1909 came his *magnum opus* on the 'Vertebrate Craniata: Cyclostomes and Fishes' forming Part IX of Lankester's *Treatise on Zoology*. All will know that it has been, and will continue to be for very many years, the standard text-book on the morphology of fish. While a literature of over 500 items is referred to, it is no mere compilation of the work of others; it is threaded through and through with his original observations on both recent and fossil forms, and the majority of the observations of others have been checked by him personally. Here, in addition to the results of his researches on scales and fins already referred to, are his masterly accounts of the skull and axial skeleton, the segmentation of the head, the nerve components, the nature and development of the coelomoducal kidneys, the vascular system and the air bladder; this is to mention only some of the many subjects all treated from the evolutionary point of view and clarified by his peculiar morphological insight. More than 150 of the illustrations are original, and many of them are those semi-diagrammatic but nevertheless accurate figures showing the three dimensions of space which are such a godsend to the student. Flesh and fossil, Science and Art have rarely been combined as here. It is superfluous to say more when the fame of the book is world-wide; I will just add a quotation from an appreciation of Goodrich by Dr. Julian Huxley in *The Times*:

'As an example of the international esteem in which he was held, I should like to record what Professor Berg, the leading Russian authority on fishes, said to me in Leningrad this summer, in asking me to take charge of a book for presentation to Goodrich: "Please tell him that, though neither I nor my colleagues have ever met him, we all regard ourselves as his pupils."' '

Following a laudatory review of this book, 'W. E. A.' in *Nature*. 1909 (vol. 82, p. 152), among a very few 'points of minor importance which call for criticism', writes:

'On p. 116 we read, as one of the *primitive* characters of the Pisces (which group here does not include the Cyclostomes), that the pericardium may communicate with the abdominal coelome. In view of the fact that this communication in Elasmobranchs is formed secondarily in ontogeny after the two cavities have been completely separated from each other, it would have been better not to have included it in the list of characters "considered primitive" without a qualifying note.'

I mention this 'minor point' because it has an interesting outcome. Goodrich did not reply for nine years, not until he had characteristically had an opportunity of re-examining the facts, and when he did he made no reference to 'W. E. A.'s' criticism. In 1918 he published his study, with some of his best three-dimensional reconstructions of sections, 'On the Development of the Pericardiac-peritoneal Canals in the Selachians'. I quote the two opening sentences of his summary:

'Balfour's suggestion that the canal leading in the adult Selachii from the pericardial to the peritoneal coelom, and opening into the latter by paired apertures, is a remnant of the wide communication between these cavities in the embryo is correct. The canal openings are not new formations as Hochstetter maintained, but are derived from the pericardiac-peritoneal passages above the mesocardia lateralia.'

In 1910 he took part, with the other leading zoologists of the day, in the famous two days' debate, recorded in the *Proceedings of the Linnean Society*, on Gaskell's theory of the origin of the Vertebrates from Arthropod ancestors, which of course he opposed. The Vertebrates cannot be descended both from a form like Amphioxus and from an Arthropod; the supporters of Gaskell's heterodox views regarded Amphioxus not as a primitive form but as a secondarily simplified degenerate vertebrate. Although Gaskell's theory, that fascinating but gigantic folly of phylogenetic speculation, appears to-day to be dead and forgotten, there may still be a misguided few who prefer to regard Amphioxus as degenerate rather than primitive. If there

are, let them for a moment listen to Goodrich making some of his telling points in the debate:

'Now, although *Amphioxus* is doubtless in some respects a very specialized animal—as for instance in the possession of an atrial cavity—yet it preserves many primitive characters. Judging from its structure, we must conclude that the ancestral Vertebrate was still more uniformly segmented than the primitive Craniate. The head-region was scarcely differentiated at all, there was no skull (probably no cartilaginous axial skeleton at all), a quite rudimentary brain, no specialized cranial nerves, no cephalization due to the presence of large paired organs of sense. It is possible that *Amphioxus* is somewhat degenerate; but it cannot seriously be urged that it once possessed in well-developed condition those paired sense-organs which have so profoundly modified the structure of the head-region in the Craniata. For it would be ridiculous to suppose that the modified segments could be restored to their original condition of uniformity with the trunk segments; no trace of the disturbance appearing in either adult or embryo.

'Further, in *Amphioxus*, there is no dermal or epidermal armour, and primitiveness is shown in the structure of the endostyle, which becomes modified into the thyroid gland in higher forms. Lastly the presence of true nephridia, a type of excretory organ which has been lost in other Vertebrates, links *Amphioxus* to the lower Invertebrate Coelomata.

'Thus can be traced an irreversible series of stages in the differentiation of Vertebrate structure, at the bottom of which we find a much simpler, but still essentially Vertebrate ancestor, probably already extinct in Silurian times.'

In the 1906 paper on the development of fins Goodrich first pointed out a most important conclusion that I have not hitherto referred to; I have delayed mention of it because it was in two later papers, in 1911 and 1913 that he developed these conclusions to their full and surprising significance. In 1906 he had shown that in the paired fins, as in the median ones, different series of segments were involved in different species of fish. In

the course of evolution there had been a change in the position of the fins up and down the body; this he showed was not due to an actual migration of the fin material itself, but was brought about by the incorporation of fresh segments to the front of the fin and a reduction of those taking part behind or vice versa: so producing an apparent 'migration'. In 1911 in his paper 'On the Segmentation of the Occipital Region of the Head in the Batrachia Urodela' he showed the same thing taking place in the hind region of the head. The problem he tackled had arisen thus. The occipital region of the Amniota includes behind the vagus nerve four scleromeres enclosing three roots of the hypoglossal nerve, thus making at least five segments between the auditory capsule and the Atlas; in the fish the post auditory region while less definite always includes at least seven segments; but in the Batrachia the skull appears to end immediately behind the vagus foramen. He writes thus:

'These facts immediately suggest several questions:—Does the occipital region of the Amphibian really include fewer segments than that of the other Gnathostomes, or have certain segments been telescoped and practically crushed out? Are the hypoglossal segments of the Gnathostomes really represented by the first three trunk-segments of the Amphibian, or have these simply assumed the function originally fulfilled by others farther forward? Further, if the Amphibian head includes fewer segments, it may be asked whether this condition is primary, or due to the return of segments to the trunk which formerly held a place in the head.'

He now makes his careful and as usual beautifully illustrated study of the development of the Amphibian head and comes to this conclusion:

'Now, in the case of the fins of fishes, I have already shown that it is not possible to account for variation in position by the theory of inter- and excalation. Growth and transposition from one segment to another alone account for the facts. The same is probably true of the occipital condyle. There is not the slightest trace of the disappearance of segments behind

the vagus in the ontogeny of the Amphibia. We are familiar with the variation in the extent of the gill-region in Vertebrates by mere growth. Obviously the hind limit of the series of gill-slits varies backward or forward, according as certain segments cease to develop gills or take on the function of gill-formation. The posterior limit of the skull is doubtless altered in the same way, and the position of the occipital condyles may shift up or down the segmental series. There should, therefore, be no theoretical objection to accepting the anatomical and embryological evidence that the occipital region of the head in Amphibia contains only three segments. If segments could really disappear, leaving no trace behind, it would be hopeless to attempt to homologise segments in any two forms.'

This leads to his very important 1913 paper on 'Metameric Segmentation and Homology' where he develops this thesis to the full. As with fins, so with paired limbs. No one will deny that the fore limbs or hind limbs are homologous throughout the Tetrapods and that they can be traced back in an uninterrupted series to some common ancestral form; yet they are not necessarily made up of the same segments. The hind limb of the frog for instance occupies segments 8, 9, and 10, that of the salamander 16, 17, and 18, and that of *Necturus* segments 20, 21, and 22. These and many other facts are considered and lead him to give us this new conception of homology:

'In the Vertebrates, as in other animals, the organs and parts of two individuals are to be considered as homologous when they can be traced back to corresponding parts in a common ancestor, and not because they occur on the same segments. The homology is independent of the number and ordinal position of the segments which take a share in the formation of the organs. Any structure may apparently shift from one segment to another; and this is brought about neither by intercalation or excalation of segments, nor by redivision, nor by migration, but by a process of transposition. Organs may be homologous when they are composed of few or of many, of the same or of different segments, or are

not segmented at all. There are degrees of homology; it may be general or more special, complete or incomplete. The homology of two organs is complete when all their parts have been derived from corresponding parts in a common ancestor.'

When discussing vertebrate segmentation we should recall that he made an even more detailed study of this in the head of *Scyllium* in 1918.

In 1915 he published an account of a most delicate piece of work on the development of the chorda tympani (that twig of the hyomandibular branch of the facial nerve which supplies the organs of taste and salivary glands in the region of the lower jaw) in relation to the tympanic membrane and the structure of the middle ear in reptiles, birds and mammals. Its position in relation to the tympanic membrane had been a difficulty in accepting the conclusions of Reichert that the auditory ossicles of the mammal, stapes, incus and malleus, were derived from the columella, quadrate and articular respectively. If the tympanic membrane corresponded to the spiracle as had been thought, how is it that the chorda tympani passes above and in front of the former whereas it passes behind and under the spiracle? Goodrich clears up the whole matter in confirmation of Reichert's views. He shows that the tympanic membrane although now actually occupying the former position of the original spiracle, does not represent a covering of that opening; the tympanum develops as a separate diverticulum of the spiracular cleft (tympanic cavity) rather below and behind the spiracle proper which is more and more reduced as the diverticulum (tympanum) swells up to *take its place*. It swells up not only below and behind the spiracle but also below and behind the chorda tympani, so now this nerve passes above and in front of it. The difficulty is resolved. His paper is illustrated by plates of superb reconstructions of sections in which the different elements are shown in shadings of five different colours.

There are too many good things to look at all at once. In viewing any exhibition of works of art or science there comes a time when we must stop; there is a limit to what we can appreciate at one time, even if the works are familiar to us. We have

the catalogue; we know where they are to be found for future study. We must leave ourselves time, and here space, to consider our general impressions.

But there is still his greatest work of all, and we must hurry through the gallery of his vertebrate studies to reach it. As we pass we just note 'The Classification of the Reptilia', 1916 (also 1942), in which he points out the systematic value of the fifth metatarsal which is hooked in some and straight in others, and a kindred study of syndactyly as a key to the phylogeny of the Marsupials, 1935. We see his notes on the reptilian heart, 1919, and on the blastocoelic and enteric cavities in Amphibia, 1935.

His 'Proboscis Pores in Craniate Vertebrates', 1917, is a suggestion of the homology of the connections linking the coelom of the premandibular somites with the hypophysis, as found in the development of *Torpedo* and of the duck, with the opening of Hatschek's pit in *Amphioxus*, the proboscis pores of *Balanoglossus* and the water pores of Echinoderms, all to be regarded as coelomoducts. Here too are further studies on the Cyclostomes and fish: on the head of *Osteolepis*, 1919, the pectoral girdle of young Clupeids, 1922, the cranial roofing bones in the Dipnoi, 1925, the relationship of the Ostracoderms to the Cyclostomes, 1930, the spinal nerves of the Myxinoidea, 1937, and on the denticles in fossil Actinopterygii, 1942. We see his work on the vertebrates, as on the invertebrates, going on to the very end.

We now come to his *maximum opus*, that masterpiece: *Studies on the Structure and Development of Vertebrates*. It is all that his Cyclostomes and Fishes volume is, only more so: full of his own original work and his careful checking of the work of others. He refers to no fewer than 1,186 other works and it is illustrated by 754 text-figures of which again so many are his own. 'This work has been written', he says, 'in the hope that it may help advanced students and others engaged in teaching and research.' Every serious student of the vertebrates will acknowledge how fully his hope has been realised. His book is indispensable and it cannot be an extravagant prophecy to say that it will still be so in a hundred years' time. A senior zoologist in a recent letter

expresses the feelings of all: 'I never use his comparative morphology of the Vertebrates without an increasing admiration for the mind that conceived it or the hand that illustrated it.'

As with his Cyclostomes and Fishes volume it is so well known that any description of it in the space available would be superfluous. I prefer to use that space in quoting from his preface to show in his own words his grand conception; it will be useful too because so often the student dives at once into the text for the facts he wants and leaves the preface unread.

'It is not a complete treatise, but deals with certain subjects and problems of special interest and importance, some of which receive but scant notice in current text-books. My original intention was to cover the whole range of vertebrate morphology; but the preparation of this volume has taken so many years, that I thought it better to publish what is ready than to wait for the remainder which might possibly never be completed. The literature dealing with the Morphology of the Vertebrata is so vast, the accumulation of known facts so large, that students are apt to feel discouraged from the start, and to turn perhaps to some newer branch of zoological science. On the one hand, they may think that little remains to be done in so ancient a study; or, on the other hand, that its conclusions, for instance in Phylogeny, are so insecure that they afford little trustworthy evidence concerning the process of Evolution. It has, therefore, been my endeavour not only to give an account within reasonable compass of the facts already known and to discuss their significance, but also to point out where our knowledge is deficient; and where further research is desirable. During the last fifty years or so much has been accomplished, many old theories have been overthrown, some new conclusions have been firmly established; yet a great deal remains to be done, and new fields for research are continually being opened up.'

While not a complete treatise it deals very fully with the vertebral column, ribs and sternum, the median fins and paired limbs and limb girdles, the segmentation of the head, the skull, the skeletal visceral arches, the middle ear and ear ossicles, the

visceral clefts and gills, the vascular system and the heart, the air bladder and the lungs, the subdivisions of the coelom and the diaphragm, and the excretory and genital ducts. The nervous system and sense organs are less fully dealt with; but here he gives important new views on the evolution of the autonomic system. In the detail in which he planned it, no one person could have done more.

Some of the younger generation whose main interest is focused on the rapidly growing physiological, genetical or ecological branches of zoology may be inclined to think of Goodrich as an out-of-date morphologist—out of date because they regard morphology as a worked-out mine with little more to yield. His pupils never thought this. While Goodrich was largely engaged in morphological studies, he was never a morphologist pure and simple, in the sense of one who delights in unravelling and describing details of bodily structures as an end in itself. This end is of course important, but he was primarily a comparative anatomist and there is a big difference between being that and being a pure morphologist. The former compares animal structures with a view to discovering the course of evolution, tracing lines of phylogeny and building a classification as far as possible upon true relationship. Goodrich's passionate interest was not just in the details of the different kinds of nephridia and coelomoducts or scales and fins which he discovered; it was always centred upon the homologies they might reveal linking group with group: their evolutionary significance. Let me again quote from the preface of his great book:

'The triumph of the doctrine of Evolution has owed much in the past to the study of the structure and development of the Vertebrates, and the correct interpretation of their morphology still plays an important part in the elucidation of the evolutionary process. No other group of animals presents us with so complete a record of the divergent phylogenetic lines along which they have evolved.'

The elucidation of the evolutionary process—meaning the elucidation of the paths the process has taken rather than the causes underlying it—that was what he strove for all the time

and how remarkably successful was his quest. He had a genius for seeing the essentials and so selecting the profitable lines of attack. In that I think we see Goodrich the artist. Great landscapes are never photographic reproductions of nature; the artist emphasises those features which are essential to the beauty or character of his composition and lays less stress on others. Goodrich did not look at his animals with just the photographic eye of the pure morphologist. He saw much more; he had the insight enabling him to pick out from among the details those points which had significance for his picture; his evolutionary theme. Perhaps all great scientists are artists in their particular medium, but they become great only when, like Goodrich, they subject their artistic insight to the discipline and rules of the scientific method.

Goodrich never allowed himself to be carried away on wild flights of phylogenetic fancy; he was ever critical of those plausible speculations on descent which, often based only on flimsy similarities, bring discredit on the comparative method when they are held almost as creeds instead of being put forward as tentative hypotheses. He was always cautious. We have seen that in his 1907 paper on the phylogenetic position of *Polypterus* one can sense his leaning to the belief that it is a living Palaeoniscid; but he does not jump to this conclusion; he tests it step by step. In the paper of the following year on the scales of fish he writes: 'Not for a moment is it asserted that *Polypterus* is a living Palaeoniscid; but it is probably in the neighbourhood of this family that it will eventually find its place in the system of classification.' It was another twenty years before he allowed himself to write '*Polypterus* a Palaeoniscid?' and still with a question mark; it was another ten years before it seemed certain.

The discoveries Goodrich continued to make should show that comparative anatomy is not yet a worked out field. It is true that to-day it does not have the same attraction that it had; the new growing branches of biology are discovering more and more about the causes underlying the evolution, development, mechanism and behaviour of living things, so that it is natural that they should draw towards them those most curious about the nature of life. But the work of the great comparative anatomo-

mists like Goodrich is not obsolete and dead ; it has been providing a more and more reliable chart of the animal kingdom based on the course evolution has taken in the different phyla. It forms the essential background in the education of the zoologist, no matter in what particular field of research he intends to work. It makes sense of the diversity of form ; it shows what achievements the process of evolution is capable of.

While his research was mainly concerned with tracing the course of evolution it would be the greatest mistake to suppose that he was not interested in the causes underlying the process. In 1912 he wrote a little book in the People's Series called *The Evolution of Living Organisms* (second edition 1920) and in 1924 enlarged it considerably under the title of *Living Organisms: their Origin and Evolution*. No clearer accounts of our knowledge of the process of evolution had been written at the time these books were published and in spite of recent additions to the theory of the subject his *Living Organisms* is still one of the best introductions to evolution for the student. In the original 1912 edition see how clearly he emphasised the importance of both heredity and environment :

'An organism is moulded as the result of two sets of factors: the factors or stimuli which make up its environment, the conditions under which it grows up ; and the factors of inheritance, the germinal constitution, transmitted through its parent by means of the germcells. No single part or character is completely "acquired", or due to inheritance alone. Every character is the product of these two sets of factors, and can only be reproduced when both are present. Only those characters reappear regularly in successive generations which depend for their development on stimuli always present in the normal environment. Others, depending on a new or occasional stimulus, do not reappear in the next generation unless the stimulus is present. In popular language the former are said to be inherited, and the latter are said not to be inherited. But both are equally due to factors of inheritance and to factors of environment ; in this respect the popular distinction between acquired and not acquired characters is illusory. In every

case it is the capacity to acquire, to become modified or to respond, which is really transmitted; the direction and extent of the modification depends on the stimulus. The presence of a given hereditary factor cannot be determined by mere inspection of the characters of an organism; the factor may be present, but the corresponding character fail to show itself owing to the absence of the necessary stimulus. On the other hand, dissimilar stimuli acting on different factors may give apparently similar results. Heredity must be defined afresh as the transmission of the factors of inheritance, and not as the reappearance of characters in successive generations.'

In 1921 he was President of Section D (Zoology) of the British Association at its meeting in Edinburgh and chose for the title of his presidential address: 'Some Problems in Evolution'. Here we find he had already appreciated that the genes form an interacting system subject to selection, so foreshadowing the conception of the gene-complex which has been so much developed in recent years, for he says:

'Thus natural selection preserves those factorial complexes which respond in a favourable manner. In other words an organism to survive in the struggle for existence must present that assemblage of factors of inheritance which under the existing environmental conditions will give rise to advantageous characters.'

During Goodrich's tenure of the Linacre Chair the Oxford department expanded both in space and scope. New laboratories for both undergraduate teaching and graduate research were added and, more important, the staff increased. Under his headship the Oxford school widened with the rapid development of zoology because he chose for his new colleagues young zoologists, all of whom were his own pupils, enthusiastic in different fields of work. Alongside his own researches were developing under his encouragement the embryological and evolutionary studies of G. R. de Beer, the work on breeding seasons and later on cytology and histochemistry of J. R. Baker, the ecological population studies of C. S. Elton, the ornithologi-

cal work of B. W. Tucker, the genetical and field evolutionary studies of E. B. Ford, the researches on nerve anatomy, physiology and regeneration of J. Z. Young and the work of the late J. A. Moy-Thomas on palaeozoic fish. More recently he had appointed H. K. Pusey, whose embryological evolutionary studies have been interrupted by war service, and P. B. Medawar who is subjecting the problems of 'growth and form' to mathematical treatment, and investigating the nature of the differences between individuals. In all this work, so much of it so different from his own, Goodrich took a great and sympathetic interest. While always ready to help with suggestions he never tried to divert the researches of his staff along lines other than of their own choosing.

He was from first to last a warm and valued friend of the marine biological stations at Naples and Plymouth; he worked repeatedly at each, and at home frequently obtained material from them.

In character Goodrich was quiet, reserved and unassuming; while those who did not know him well would have regarded him as somewhat shy and retiring, his close friends found in him a fund of amusing dry humour. In spite of his reserve he was a great teacher. We who have been his pupils will never forget his style in lecturing. As in writing, he had in speech that power of clear and logical presentation of complicated fact, and lucid explanation of theory. But the strength of his lectures was not in the spoken word; his speech was quiet, not forceful. The impression upon his students was made by a beautiful combination of verbal clarity with visual demonstration on the board. As he developed his exposition so also he developed drawings in coloured chalks; they were not just diagrams, they were not slow and laboured drawings, they were pictures, often optical sections in three-dimensional perspective, which grew before our eyes to build up the animal structures he was describing. Bones, blood vessels, nerves, were put in in just the right sequence to make understanding easy, put in, as he spoke, with the rapid sure touch of the artist. He made easy all those difficulties of visualising what is really happening in an animal's development when organs are being formed by the folding of

surfaces or the nipping off of this or that bud or diverticulum; with a growing series of sketches giving all the impression of solidity, we could not fail to follow the changing and subtle relationships of form he was describing. His drawings had life and reality in them; they made his lectures vivid and unforgettable. Story has it that on one occasion his Honours class asked permission for the rubbing out of his drawings to be delayed while they had them photographed; all enquiries I have made to try to obtain that photograph have failed. I should much like to see it reproduced and placed on record.

Another feature of his lectures should be specially mentioned because it was so much a part of his character: his extreme modesty. When he was describing his own contributions to zoology, and we have seen how many and great they were, he never gave the slightest hint to the student that they were indeed his own discoveries.

He took the keenest and kindest interest in the practical work of his class; he was always tolerant and sympathetic to the young student in difficulties and always ready to show him how to make closer observations and better drawings of what he saw. He encouraged his pupils to go out into the field; when the course on Protozoa came round he used to offer a book prize in the Honours class for the student who had collected and made drawings of the largest number of specimens; it was keenly competed for.

A great deal of his time must have been taken up by editing the Quarterly Journal; so many have testified to the unstinted help and advice which he gave towards the improvement of the papers they had sent him for publication.

Apart from his teaching and research he took an active part in the work of the University, serving on many committees. He was always much interested in the affairs of his College and for a time was Garden Master and Librarian. One of the senior Fellows in a letter writes of his life at Merton as follows: 'He never had an enemy and he is the only one I can remember who, in that somewhat strange life of a college, never lost his temper or fell out with anybody. He was the gentlest and kindest of men, but quite inflexible in following the course he felt right.'

His advice was of the greatest value in all artistic and architectural questions. He made a collection of photographs of all views of the precious parts of the college buildings, details of old and decaying stone carvings, woodwork and in fact anything that he considered would form a useful record to be of service to succeeding generations of students. He himself designed many new details, for example: common room chairs, fireplaces and brackets for lights in the quadrangle; it was he also who rescued from a lumber attic the remains of Wren's chancel screen of carved wood and had it adapted, according to his own designs, to beautify the reading rooms below the library.

It was in painting and travel that he sought relaxation from his scientific work. He travelled extensively and always returned home with a series of striking water-colours. He delighted in the play of strong sunlight and shadow on buildings, the more delicately graded light and shade on Alpine snows, or the subtle colourings in reflections. His clear colours and bold draughtsmanship captured the atmosphere of Venice, southern Italy, Greece, Tunis and Egypt, far away Java and Malaya, and many another scene of his many vacational wanderings. His sense of composition was just as keen. Occasionally he had exhibited in Bond Street, but it was only his intimate friends who realized the full scope of his power and versatility with the water-colour brush.

In this impression of his character and work I have reserved till the end that which is most personal: his very happy partnership with his wife, Dr. Helen Pixell Goodrich. Except in the two papers already referred to, in which they collaborated, they worked independently while sharing common scientific interests. They were devoted companions in their happy home and their wanderings together abroad. It is his work we are reviewing, not hers, yet no tribute to his life and achievement would be complete without a tribute to her as well. I am sure he would like it to be said, and I am sure it is the truth, that for his continued achievements in zoology up to the very end of his life we have in no small measure to be grateful to her. Those who him knew well from early years at Oxford, and with whom I have discussed his life, have each stressed the noticeable change

in health and happiness that came to him on marriage. Our deep sympathy goes out to her in her great personal loss and we admire her courage as she continues her work in his old department.

Edwin Goodrich has gone from us; his work and influence live on. All are agreed that he was the greatest comparative anatomist of his day; in the history of science his achievements will, I believe, rank as high as those of any predecessor in his field of work, surpassing even those of the great master who inspired him, Edwin Ray Lankester.

A. C. HARDY

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