The Scientific Work of Edwin Ray Lankester

THE death on August 15, 1929, of Sir E. Ray Lankester, formerly Editor of this Journal, was announced in the November number of vol. 73, 1929.[1] Lankester's long connexion, as Co-Editor, as sole Editor, and finally as Honorary Editor, with the 'Quarterly Journal of Microscopical Science' has already been dealt with by A. Sedgwick and W. F. R. Weldon in the complimentary number dedicated to him on the occasion of the twenty-fifth year of editorship (no. 141, vol. 36, 1894), and again on his seventieth birthday by G. C. Bourne (no. 253, vol. 64, 1919).

In the following pages an attempt is made to give an account of his published work. Lankester was a prolific writer. In the course of a long life he wrote some two hundred papers and books. Most of his papers are quite short, many are beautifully illustrated by his own hand. Only the more important of these works can be mentioned here.

When only sixteen years of age Lankester wrote his first contribution to this Journal, 'On our present knowledge of the Gregarinidae, with descriptions of three new species belonging to that Class', vol. 3, 1863. It is a remarkably clear historical account of the work on a group of Protozoa in which he never ceased to take an interest. It is not from lack of encouragement from him that the life-history of the new species he described from a Serpulid, a Sabellid, and Aphrodite have not yet been worked out. Lankester gave a popular account of

[1] General obituary notices appeared in 'The Times' of August 16, 1929, in 'Nature' of August 24, 1929, in the 'Journal of the Marine Biological Association', vol. 16, 1930, in the 'Proceedings of the Royal Society', B, vol. 106, 1930, and in the 'Journal of the Royal Microscopical Society', vol. 49, 1929. It may be mentioned that in the first and in the last of these notices the date of Lankester's resignation of the Linacre Chair in Oxford to go to the British Museum is wrongly given as 1892 instead of 1898.

the parasites of the Cockroach in 1865, and wrote several other papers on Gregarines during the following years, the most important being perhaps his observations on the parasites of Sipunculus made in Naples, 1873. In his masterly article on the Protozoa in the ninth edition of the 'Encyclopaedia Britannica', 1885, Lankester divided the Gregarines into two Orders: the Haplocyta including monocystid forms, and the Septata including the genus Gregarina and other polycystid forms. No better way of classifying the group has yet been found. So early as 1866 he was searching for a sexual mode of reproduction in Gregarines, and became convinced that the process must occur in the spore stages. This misconception seems to have led him later to propound theories of the nature of the sporozoites of Haemamoebae which have proved to be erroneous.

It was Lankester who recognized that the trypanosome of the frog is a protozoon with an undulating membrane and named it Undulina ('Q.J.M.S.', vol. 11, 1871). He remarked that it was 'extremely likely' that this parasite had been seen before, and in fact it had been observed some thirty years previously and was named Trypanosoma by Gruby in 1843. An intracorpuscular protozoan parasite seems to have been first recorded by Chaussat (Anguillula minima, 1850) from the blood of the frog. Lankester rediscovered this minute parasite, 1871, recognized it as a Protozoon and named it Drepanidium ranarum. Later he placed it among the Sporozoa, 1882, and here, with other Haemogregarines, it remains under the name Lankesterella.

Lankester further described several new or little known Ciliata, Lobosa, and Foraminifera. His beautifully illustrated paper on Haliphysema ('Q.J.M.S.', vol. 19, 1879) may be mentioned as a model of lucidity; it fully confirms Saville Kent's view that this form is a foraminiferon and not a sponge as held by Haeckel.

Nor was his work confined to the Protozoa among Protists, but extended to the Schizophyta and lower plants. Besides observations on Archerina (Micractinium), Golentinia, and Botryococcus, 1885, 1908, may be mentioned particularly a paper 'On a Peach-coloured Bacterium' ('Q.J.M.S.', vol. 13, 1873), in which Lankester first formulated the doctrine of pleomorphism sometimes wrongly attributed to Nägeli and others. Having shown that this bacterium, with its characteristic pigment, exists under different form-phases and that intermediate transitional forms occur, he maintained that 'the natural species of these plants are within proper limits "Protean"', and further that various cocci, bacilli, vibrios, spirilla, and leptothrix forms are but form-phases of such protean species found under different conditions. Lankester concluded that true species of Schizophyta must be defined not by simple form-features, 'but by the ensemble of their morphological and physiological properties as exhibited in their complete life-histories'.

Lankester's original work on Coelentera was not very extensive; he, however, contributed an excellent article on the 'Hydrozoa' to the 'Encyclopaedia Britannica', 1881. In 1880 he published papers on the newly discovered freshwater medusa Limnocodium (Craspedocustes) sowerbii, and later an elaborate study of the processes of intracellular digestion in its endoderm ('Q.J.M.S.', vol. 21, 1881). About the same time he made interesting comparisons between the larval stages of Geryonia and the Ctenophora, 1881.

Very early in life Lankester developed a keen interest in Annelids. When a mere schoolboy he gave a good account of the 'red-worm', Tubifex rivulorum in the 'Popular Science Review' (1863). Shortly after there followed a work on the anatomy of the earthworm Lumbricus terrestris ('Q.J.M.S.', vols. 4 and 5, 1864, 1865), a truly remarkable production from the pen of so young an author, combining the scattered observations of previous authors, more especially of D'Udekem, Hering, de Quatrefages, Milne-Edwards, Clarke, and Busk, with his own results into an admirably complete description of this important type. Having confirmed Hering's account of the structure of the genital organs, Lankester discussed the relation of genital ducts to 'segmental organs' (nephridia as he afterwards called them). Claparède had concluded that in Limicolae (where nephridia are absent in the genital segments) the genital ducts must be modified segmental organs. Lankester, impressed by the fact that normal nephridia coexist with genital ducts in the genital segments of Terricolae, suggested that the Oligochaeta were originally provided with two pairs of tubules in each segment, and that while one series survived in the genital segments only of both groups to form the ducts the other series persisted in these segments only in the Terricolae. But this ingenious suggestion has not stood the test of time, and the theory that the genital ducts in Oligochaeta, and indeed in Ceelomata generally, are modified nephridia was abandoned by him when it was shown many years later that they are organs of different origin, 1900. It should be mentioned that Lankester proved, in 1878, that colourless corpuscles are present in the red blood of the earthworm.

In later studies on the lower Oligochaeta, 1869–71, he showed that there are distinct 'larval' and sexual forms, and that when the larval gemmiparous form is transformed into the sexual form new special 'genital' chaetae may be intercalated in certain anterior segments.

His larger memoir on the 'Lower Annelids' read before the Linnean Society in 1867, but not published till 1870, contains an elaborate account of the chaetae, reproductive organs, and other parts of Aeolosoma and Chaetogaster, and an analysis of their mode of reproduction by fission. Developing Herbert Spencer's theory of the integration of secondary aggregates, Lankester concludes that 'there is a longitudinal cohesion or integration which counteracts this' tendency to produce a head seen in fission. 'When the longitudinal cohesion becomes weak, the tendency to anterior development prevails, and the normal head grows [forwards] and a new individual separates'. It is interesting to compare this tentative explanation of segmentation and budding with modern theories of axial gradients.

The formation of the spermatophores in Tubificids also attracted his attention, 1870, 1871. These remarkable structures, looking and behaving so like Infusoria, he showed to be moulded in the neck of the spermatheca. It was not till much later that Lankester again took up the study of Annelids when he published new observations on the microscopic anatomy of the Leech, 1880, made with his pupils, J. E. Blomfield and A. G. Bourne, which led to the appearance of the latter's monograph on the Hirudinea in 1884 ('Q.J.M.S.', vol. 24). The fine network of capillary vessels, no doubt respiratory in function, was described running between the epidermal cells; also new light was thrown on the structure and function of the botryoidal tissue, the connective tissue, and the nephridia.

His contributions on the Lithodomous Polychaeta (Sabella and Leucodore) which bore their way through limestones with the help of acid secretions; on Thalassema; on the structure of the large female and small male Hamingia; on Sipunculus, with a description of the origin of its strange free-swimming ciliated 'urns' developing from the coelomic epithelium, may here be mentioned. More noteworthy, perhaps, are his papers on the genus Rhabdopleura. Much interested in this scarce and little-known form Lankester first wrote on its affinities in 1874, and ten years later gave a beautifully illustrated account of its structure, mode of growth, and of budding ('Q.J.M.S.', vol. 24). With regard to its affinities, Lankester eventually adopted the comparison made by Caldwell, and in his article on the Polyzoa, written for the ninth edition of the 'Encyclopaedia', 1885, founded a group Podaxonia including not only the Pterobranchia (Rhabdopleura and Cephalodiscus) but the Sipunculoidea, Brachiopoda, and Polyzoa as well. Although this grouping has by no means been universally accepted, it would seem (with the exception of the inclusion of the Entoprocta) to be well-justified.

A paper 'On some undescribed points in the Anatomy of the Limpet, Patella vulgata', published in 1867 (Ann. Mag. N.H.', vol. 20), is his first work dealing with the Mollusca. In it are described a small left and a larger right kidney, and the reno-pericardial duct. This discovery of paired kidneys was later confirmed by V. Jhering and extended to Haliotis and Fisurella, and led Spengel to formulate his theory of the torsion of the visceral hump of Gastropods. It may be considered as the first step in the elucidation of this interesting problem.

Lankester's studies on the early development of Loligo and various Gastropods and Lamellibranchs (1871–7) brought out many new and important results. With the very limited technical means at his disposal, he described the ovum, its cleavage, the formation of the germ-layers, the influence of yolk on development, the inpushing of the hypoblast by 'invagination', the closure of the orifice of invagination for which he proposed the name 'blastopore' ('Q.J.M.S.', vol. 15, 1875), the formation of a closed two-layered 'planula', the fact that in Paludina the blastopore coincides in position with the anus, the ingrowth of the ectoderm at the mouth to form an ectodermal region of the alimentary canal he later called the 'stomodaeum' (1878) and a similar ingrowth at the anus to form the 'proctodaeum', the multiple origin of the mesoblast, and the development of a trochosphere stage, with preoral ciliated ring later to become the 'velum'. His discovery of the early-formed 'shell-gland' enabled him to define the important later 'Veliger' larval stage characteristic of Mollusca in general.

From these embryological researches and those of Kowalevsky and other contemporary workers, Lankester drew material for two noteworthy essays, landmarks in the history of Embryology. The first, founded on lectures delivered in Oxford and published in 1873 ('Ann. Mag. N.H.', vol. 11), but the substance of which was written before the appearance of Haeckel's famous 'Monograph on Sponges', 1872, and Gastraea theory, 1873, is entitled 'On the Primitive Cell-layers of the Embryo as a Basis of Genealogical Classification of Animals, and on the Origin of Vascular and Lymph Systems'. Having reviewed the relations of Evolution to phylogeny and ontogeny, and described the development of Metazoa from the single cell through the 'Polyplast' stage (Morula of Haeckel) to the 'Planula' (Gastrula of Haeckel) either by direct growth (later called 'delamination') or by invagination, he divides multicellular animals into 'Diploblastica' (Coelentera and Sponges) and 'Triploblastica'. This latter name for the forms provided with a mesoblastic layer is really preferable to Coelomata, later adopted, since the coelomic body-cavity is scarcely recognizable in the lower groups. Lankester then maintained that the Planula is common to all the Metazoa, that there is no fundamental difference between its origin by invagination and by direct growth or delamination, and that the former method may well be due to a shortening of the developmental process. (Invagination is an economy of material, a mode of rapidly filling in the outline of an organ in the embryo leaving it in a hollow condition for subsequent completion, 1874.) He pointed out that whereas the otocyst and to some extent the ganglia arise by invagination in Loligo, in Nudibranchs and other Gastropods they may arise as solid thickenings. The relation of the various tissues to the germ-layers, the development of blood and lymph spaces in the mesoderm, the origin of corpuscles from their walls, the distribution of segmental organs, are discussed. A figure of the 'Archiscolex' or primitive worm-like form is given, no mean precursor of the more famous 'Archimollusc'. A very important passage occurs in the discussion on the nature of the Prostomium: 'The segmentation of the prostomial axis in Arthropoda and some Annelids, which has an appearance of being a zooid-segmentation comparable to that of the metastomial axis on account of the identity in the character of the appendages with those of the metastomial axis, has yet to be explained. It may be suggested that it is due to a distinct breaking up of this axis like the posterior one into zooid-segments: there is much against this supposition. Much more likely, it seems, is the explanation that the oral aperture shifts position, and that the ophthalmic segment alone in Arthropoda represents the prostomium, the antennary, and antennular segments being aboriginally metastomial and only prostomial by later adaptational shifting of the oral aperture'. This bold suggestion, as we shall see later, was to give the clue to the morphology of the Arthropod head.

The second essay, 'Notes on the Embryology and Classification of the Animal Kingdom, comprising a Revision of Speculations relative to the Origin and Significance of the Germ-layers', contains an elaboration of some points and a revision of some conclusions ('Q.J.M.S.', vol. 17, 1877). By this time Haeckelismus dominated embryology; but, although Lankester greatly admired some of Haeckel's zoological work, he preserved his independent judgement. He did not accept the Gastraea theory, pointed out objections to it, maintained that the blastopore is not identical with and is not represented by the mouth as held by Haeckel and Huxley, that the gastrula with its archenteron can be formed by delamination (as in Geryonia) or by invagination, and that the former is probably the more primitive method. Figures are given in this essay to show the possible phylogenetic stages from a 'monoplast' ingesting solid particles of food, to a polyplast or morula in which the particles pass to the interior, and finally to a diblastula in which the food enters a central digestive cavity surrounded by endoderm. Stomodaeum and proctodaeum erupting into the enteron are later formed in relation to mouth and anus. Regarding the blastopore as an orifice of secondary nature existing temporarily and solely in relation to the invagination process, he explains its occasional coincidence with mouth or anus as cases of secondary adaptation. A new and important conception of 'precocious segregation' is invoked to explain differentiation of the blastomeres in cleavages, and differences between epibolic and embolic invagination.

Discussing the origin of the coelom this principle of Precocious Segregation is again called upon to explain its different modes of development. Huxley had distinguished between enterocoel and schizocoel. Lankester here maintains that there is no fundamental difference between the nipping off of hollow diverticula of the archenteron and the hollowing out of the solid mesoderm. Less happily he further holds that the former is the more primitive mode of origin; a view inconsistent with the modern Gonocoel theory which seems to be far nearer the truth.

It is in this essay that Lankester introduced his well-known nomenclature for the various parts of the vertebrate kidney; the whole individual series of tubules he called the archinephron with its longitudinal archinephric duct, while to the successive portions which succeed each other in development he gave the names pronephron, mesonephron, and metanephron with their respective ducts. Here also he proposed the name nephridium for the excretory tubules generally known as segmental organs and for the genital ducts throughout the Coelomata. It was then held that these excretory and genital ducts are all more or less modified nephridia; but, when it was shown many years later that two quite different sets of organs, the true nephridia and the coelomoducts, had been confused under the one name, Lankester readily accepted the new interpretation, 1900. ('Treatise on Zoology', Part 2.)

After discussions of various morphological subjects including larval forms and the modifications of the primitive ciliated band or 'architroch', the paper ends with a tabular statement of classification in which the new term 'Grade' is introduced to indicate marked advance in differentiation along a phyletic branch. These two essays together occupy only some 70 octavo pages.

Among Lankester's other contributions to our knowledge of the Mollusca may be mentioned his exposure of the fallacy that water is taken in and expelled from the vascular spaces, 1884; his observations on the development of the yolk-sac, otocyst, eye, ganglia, and pen-sac of Loligo, 1873, 1875; the paper written in collaboration with A. G. Bourne on the 'Osphradium' and genital ducts of Nautilus, 1883; and the publication under his direct guidance by his pupil R. H. Peck, 1878, of an important memoir on the gills of Anodon. Having described in detail the minute structure of these complex lamelliform gill-plates, it was shown how step by step they could have been derived from the more primitive 'ctenidium' of Mytilus by the concrescence of the free axis with the body and of the simple separate filaments with each other.

To the ninth edition of the 'Encyclopaedia Britannica', 1883, he contributed an admirable article on the Mollusca. Although now out of date in some respects, notably in regard to his own later work on the coelom and vascular system, it remains the most comprehensive and illuminating account of the whole group ever written in so short a space. Here is built up the schematic 'Archi-mollusc', not a phantastic ancestor derived from some embryonic or larval stage according to Haeckelian doctrines of recapitulation, but a viable adult creature embodying all the essential organs which, according to the evidence of comparative anatomy, the primitive Mollusc must have possessed. The modifications of this type in adaptation to various modes of life Lankester traced along the diverging branches of the phylum with convincing lucidity.

His most important work on Crustacean morphology is contained in a paper entitled 'Observations and Reflections on the Appendages and on the Nervous System of Apus cancriformis' ('Q.J.M.S.', vol. 21, 1881). A careful description of the appendages and detailed comparison with those of other Crustacea is followed by an interpretation of the significance of the structure of the nervous system of peculiar interest and novelty. In the description of the nervous system of Apus given by Zaddach in 1841 (for Lankester's own specimens were badly preserved), he finds striking confirmation of the suggestion made in his essay of 1873 that there has been a relative shifting backwards of the mouth and forwards of the segmental appendages in Arthropods. For whereas in higher Crustacea both first and second antennae are innervated from the preoral brain, in Apus not only the second but even the first pair of antennae is supplied from post-oral ganglia, a condition approached by Limulus whose cheliceral nerves come off from the lateral nerve-cords posteriorly to the brain. Lankester concluded that there is a progressive tendency for the cephalization of the anterior segments of segmented animals, that in Arthropods the paired originally post-oral ganglia tend to move forward with their appendages and fuse with the primary median brain, his 'archi-cerebrum', situated in the prostomium; and further, that while this primitive archi-cerebrum remains pure in Annelids, in Arthropods it becomes more and more complex by the successive addition of ganglia from behind to form a 'syn-cerebrum'. This simple but brilliant suggestion, explaining at once the presence of preoral appendages and the complex structure of the brain in Arthropoda, has been generally accepted, and much work has since been done in the attempt to make out exactly how many segments make up the head in the various diverging branches of the phylum.

One of his most remarkable achievements was the proof that Limulus is an Arachnid closely related to Scorpio in a celebrated paper entitled 'Limulus an Arachnid' ('Q.J.M.S.', vol. 21, 1881). Straus Durkheim, 1929, had long ago maintained that the 'King Crab' should be placed in the Arachnida, since it has no antennae, legs radiating from a common sternum, and an internal cartilaginous sternum. But, in spite of his arguments, Limulus was always classified either with the Crustacea or in a special group. Lankester, in the paper mentioned above, compared Limulus and Scorpio organ by organ, segment by segment, and with irrefutable logic brought forward overwhelming evidence that these two Arthropods so different in appearance are not merely allied but closely related forms, the one more primitive and adapted to aquatic life, the other more specialized and modified for life on land. The evidence was completed in other publications on the respiratory organs, 1881, the excretory organs, 1882, 1884, the endoskeletal and muscular systems, 1885 (written with the assistance of W. B. Benham and E. J. Beck), and particularly the eyes (with A. G. Bourne), 1883.

In these and a later valuable article on the 'Structure and Classification of the Arachnida', written for the 'Encyclopaedia Britannica', 1902, and reprinted in vol. 48 of this Journal, Lankester showed that the Arachnida form a degenerating series leading from the more primitive fully segmented and earliest forms to the Acari in which segmentation is almost completely lost. These writings not only greatly advanced the knowledge of Arachnids, but incidentally threw welcome light on the evolution of the Arthropoda in general, and the interrelationships of the various groups included in that large phylum, a subject which he discussed in two other publications, 1897, 1902.

We may turn now to his later work on the coelom and vascular system. In a note appended to Gulland's paper on the coxal gland of Limulus and other Arachnida ('Q.J.M.S.', vol. 25, 1885) Lankester compared this gland to the nephridia of Chaetopods and the so-called 'nephridium' of Peripatus, suggested that the genital ducts of Molluscs, Arthropods, and other Coelomata might be modified nephridia, and further maintained that 'the blood-system in larger Arthropoda . . . is altogether distinct from the general system of lacunae of the connective tissue' and end-sacs into which the excretory tubes open. This important conception led to the enunciation at the British Association meeting at Manchester in 1887 (published in 'Nature', 1888, and the 'Q.J.M.S.', vol. 34, 1893) of one of his most illuminating contributions to Invertebrate Morphology. The nature of the body-cavities in Molluscs and Arthropods had hitherto seemed very obscure. It was generally held that their body-spaces were continuous; vague notions prevailed that the coelom and vascular space had either not yet been differentiated from an ancestral original space, or had become secondarily fused. Lankester showed that in Arthropods and Molluscs the main body-cavity is not coelomic but distended blood-vascular space to which he gave the name 'haemocoel'. By expansion chiefly of the venous vessels the haemocoel has (except in Cephalopods) almost obliterated the coelom leaving remnants here and there. In Molluscs the coelom is represented by the pericardial and perigonadial spaces ('generative glands' or 'gonads'). The kidneys were later recognized as excretory chambers of the coelom. His observations and experiments on the red-blooded Solen legumen by injections and silver impregnations showed that complete arteries, veins, and capillaries still persist in certain regions and that coelomic and haemocoelic spaces do not communicate.

In Arthropods, also, the blood-vessels, especially the veins, have swollen to large spaces obliterating the original coelom which persists only in the perigonadial space, and the end-sacs and the small lymph-spaces in the connective tissues into which the excretory tubules open. These conclusions were soon confirmed by the work of Sedgwick on the development of Peripatus, of Weldon, Marchal, and Allen on the body-cavity and excretory organs of Crustacea, and of numerous workers on the development of Arthropods.

It was to a great extent Lankester's attempt to understand the origin of the unique structure of the Arthropod heart that led him to this view. This heart, lying in a pericardial blood-space into which it opens by paired ostia, he successfully explained as derived from the Annelid longitudinal dorsal vessel receiving segmental afferent vessels by enlargement and fusion of the latter vessels, the accompanying obliteration of the pericardial region of the coelom, and the final enclosure of the longitudinal muscular tube in a continuous haemocoelic space. The ostia represent the original afferent openings. Rarely can so short a paper have so successfully solved a number of puzzling morphological problems!

Lankester delighted in the use of the microscope; it was his custom always to examine the body-fluids and blood of the animals he dissected. Hence he made many important observations on the cells and special corpuscles floating in these fluids (1870), but especially did he take up with enthusiasm the new method of examination with the micro-spectroscope introduced by Hoppe Seyler and Stokes, and apply them to the study of pigments, particularly respiratory pigments, in Invertebrates. In these pioneer researches, from 1867 onwards, he established the presence of true haemoglobin in the blood-plasma of the Nemertean Polia sanguirubra, of Lumbricus, Eunice, Nereis, and other Annelids, of Planorbis among Molluscs, of Cheirocephalus, Daphnia, and the larva of Cheironomus among Arthropods; also in the coelomic corpuscles of Glycera, Capitella, Thalassema, and Phoronis, and the Lamellibranch Solen legumen. Moreover, he found haemoglobin in the pharyngeal muscle of Littorina and other Gastropods, and in the nerve-cord only of Aphrodite; and noted that it is absent in the abundant blood-corpuscles of the transparent Leptocephalus larva of the eel. In the green-blooded Chlorhaemidae he discovered a new respiratory pigment, chlorocruorin, allied to haemoglobin and of similar properties, and a pink pigment in the coelomic corpuscles of Sipunculus. In a valuable discussion of the significance of these observations and on the apparently capricious distribution of respiratory pigments ('Proc. R. S.', vol. 21, 1873), Lankester 'suggests the hypothesis of the existence of various bodies not necessarily red, possibly colourless, which act the same physiological part in relation to oxygen as does haemoglobin'—a suggestion which seems to bring him near to Keilin's recent discovery of the existence of a generally distributed cytochrome.

Lankester's interest in these questions lasted throughout his life, and his latest contribution on the subject is a lecture delivered at the Royal Artillery Institution, Woolwich, October 26, 1916, on blood, 'A wonderful fluid' ('Journal of the Royal Artillery', vol. 43).

Here we may allude to Lankester's observations on chlorophyll bodies in Spongilla and Hydra, which for long he maintained are products of the animals themselves, on 'Green Oysters', 1886, and to his description of 'chaetopterin' from the intestinal wall of Chaetopterus, 1897, and 'stentorin' the colouring matter of Stentor caeruleus, 1873.

Although the bulk of Lankester's researches were concerned with Invertebrates he did not neglect the Vertebrates. He was much interested in Amphioxus, wrote a short paper on it in 1875, and a more serious contribution some years later ('Q.J.M.S.', vol. 29, 1889), in which many new points were described and several excellent diagrams given illustrating its anatomy. However, his 'brown tubes', so-called 'atrio-coelomic funnels', which acquired considerable notoriety, have turned out disappointingly to be merely blind pockets of the atrial wall. In collaboration with his pupil, A. Willey, was published an important description of the later larval development, including a new version of the development of the atrium ('Q.J.M.S.', 1891). This paper together with Willey's previous one on the earlier larval stages stand as classical contributions to our knowledge of Amphioxus.

The structure of the heart of Ceratodus, Protopterus, and Chimaera, and of the valves in the conus arteriosus of these fishes was the subject of a communication to the Zoological Society published in 1879.

In a series of three papers on the structure of the heart of Monotremes and Apteryx, 1883–5, Lankester corrected a strange mistake made by Owen, and gave an accurate description of the auriculo-ventricular valve of the right ventricle of Ornithorhynchus and Echidna, pointing out certain primitive characters, and the fact that the almost total absence of a septal flap distinguishes the heart of Monotremes from that of the Ditrematous mammals.

Among other things may be mentioned that the peculiar villi borne on the pelvic fin of the female Lepidosiren were first described by Lankester in 'Nature', 1894, and later he published correct descriptions and figures of the externals of Lepidosiren and Protopterus. The affinities of the interesting carnivore Æluropus were the subject of a paper in 1901. His monograph on the newly discovered Okapia was never completed; but a part containing many beautiful plates appeared, 1910, and observations on the 'ossicones' or bony cores of the frontal processes, 1901. The comparison of these with the similar processes of the Giraffe and related forms is a valuable chapter in the history of horns and antlers.

Owing possibly to Huxley's encouragement Lankester from his boyhood collected fossils with enthusiasm. The Red Crag of Suffolk was a happy hunting ground where he discovered various new mammalian species and forms new to the locality, 1864–70. But the remains of those earliest Vertebrates now generally known as Ostracodermi attracted him most. A short communication to the 'Geologist' on Pteraspis, 1862, is Lankester's first appearance in print. It includes a restoration of the dorsal shields and a figure of some of the pits of the lateral line organs. His later description of scales on the body, 1864, set at rest all doubt as to the piscine nature of these obscure fossils, which had by some been considered as shells of Cephalopods and by others as remains of Crustacea. The publication of his classical monograph on the 'Cephalaspidae' in 1868, marked a great advance in our knowledge of these palaeozoic fishes. Besides giving a systematic and fully illustrated account of all known forms, he described many new species, and gave excellent reconstructions of Pteraspis and Cephalaspis. Lankester definitely separated the Pteraspids from the Cephalaspids, placing them in two groups which he named 'Hetero straci' and 'Osteostraci' respectively. He considered them to be true fishes, but cautiously concluded that the evidence did not warrant the close association of the Osteostraci, and still less of the Heterostraci, with any known group of Pisces refusing to accept Huxley's opinion that they are allied to the armoured Teleosts. It should be noticed that Lankester had failed to recognize that the separate shields to which he gave the name Scaphaspis are merely the ventral shields of Pteraspids. This was not established till some years later when Kunth and Schmidt found them in association. A remarkable Heterostracan dorsal shield was described, figured, and named Holaspis by Lankester in 1873; it shows the complete course of the lateral-line system. Quite lately Stensiö has made use of this figure to support his contention that the Pteraspids are closely allied to the Cyclostomes, a view Lankester had energetically opposed in 1897.

We may now turn to some of Lankester's more general contributions to zoological literature. He had no liking for mere controversy, but was ready to attack what he considered to be false doctrine, and to help in clearing up ambiguities. Speculation remote from facts did not appeal to him, nor far-fetched theories, however popular. He lived through the stirring times when the battle for Evolution was being fought, and was intimately acquainted with many of its most prominent protagonists. A convinced evolutionist and Darwinian, his life-work was to a great extent devoted to the application of the new doctrines to comparative anatomy and embryology, to the tracing of phylogenetic affinities, and the improvement of classification based on evolutionary principles.

In addition to the two essays already noticed, may here be mentioned an important essay on 'Comparative Longevity', 1870, and a lecture on 'Degeneration: a chapter in Darwinism', delivered at the British Association meeting in Sheffield in 1879 (republished in 'The Advancement of Science', 1890). Also his theory of the evolution of blind cave animals, owing to the constant wandering out of the darkness of those individuals which can see best. In an essay, 'On the Use of the Term "Homology" in Modern Zoology, and the Distinction between "Homogenetic" and "Homoplastic" Agreements" ('Ann. Mag. N.H.', vol. 6, 1870), Lankester redefined Owen's terms Homology and Analogy in the light of Evolution. Structures genetically related and traceable to a common ancestor are 'homologous', or, as he preferred to call them, 'homogenous'. Further, parts generally homogenous may, along different phyletic branches, be differentiated similarly, giving rise to similar parts which are merely 'homoplastic'. Thus, agreement between bones of the skull, or muscles of various regions in different groups may be due to 'homoplasy'. Likewise, the correspondences arising between 'serially homologous' parts are homoplastic. 'Analogy' has a wider meaning, and is applied to any two organs having the same function but no genetic affinity.

In letters to 'Nature', 1894, Lankester discussed 'Lamarckism' and 'acquired characters', and, with his usual insight, went at once to the root of the matter. He pointed out that changes induced in an organism in a new environment are of the nature of responses to the new conditions; that the potentiality to respond of an individual is transmissible by heredity; that 'potential' may be distinguished from 'actual' characters. The term 'acquired character', he held, should be limited to Lamarck's definition indicating acquisitions under new conditions, though 'actual' responsive characters are of the same order as 'potential' characters. He then pointed out that Lamarck's First Law, that new external conditions give rise to new characters, is inconsistent with his Second Law, that such new characters are transmitted by inheritance. 'Since the old character had not become fixed and congenital after many thousands of successive generations of individuals had developed it in response to environment, but gave place to a new character when new conditions operated on an individual (First Law), why should we suppose that the new character is likely to become fixed after a much shorter time of responsive existence or to escape the operation of the first law?' This question still remains unanswered by the supporters of Lamarck.

During his brief residence in Cambridge, before migrating to Oxford, Lankester wrote a paper 'On the Cerebrum of the Entellus Monkey: Semnopithecus entellus', 1865. Many years later he returned to this subject in a communication on 'The Significance of the Increased Size of the Cerebrum in Recent as compared with Extinct Animals' read before the Société de Biologie in Paris, 1899. Having pointed out that generally speaking recent Reptilia and especially Mammalia have larger cerebral hemispheres than their early Tertiary or Mesozoic predecessors, and that a similar but greater relative increase appears when man's brain is compared with that of anthropoid apes, he maintains that, nevertheless, the earlier and more primitive forms cannot be considered as defective in the essential control by the brain, and were no doubt efficient and adequate mechanisms. Man, however, is born with relatively fewer ready-made 'instincts'—performances of inherited nervous mechanism—than lower mammals, but man is endowed with greater capacity for 'learning' and the storing of individual experience, for developing in the course of his individual growth similar nervous mechanisms in response to new and diverse conditions. This 'educability', or adaptability by means of mental powers, is what man possesses in excess as compared with apes. There is a tendency to substitute the more valuable educability for mere inherited brain-mechanisms. Hence selection was probably transferred to the cerebrum, the all-important organ of educability. Although the results of education are not transmissible, yet 'educability' is inherited.

Lankester again developed this theme in his well-known 'Romanes Lecture' delivered in Oxford in 1905.

Before closing this notice something may be said about Lankester's work on Flint Implements. In his later years he became keenly interested in Prehistory and collected objects of the Stone Ages. As an archaeologist he will particularly be remembered for his championship of what he called the 'rostro-carinate' implement of Pliocene date, first described by J. Reid Moir. Lankester published papers upon this type of implement in the 'Phil. Trans.', B, vol. 290 (1912) and B, vol. 367 (1920), and in the 'Proc. Royal Soc.', B, vol. 91 (1920) and B, vol. 92 (1921), and elsewhere. With characteristic vehemence and detailed argument he supported Reid Moir's contention that the rostro-carinates were of human manufacture. It may be said that it is in great part due to Lankester's advocacy that these rough and early implements are now accepted as artifacts by a large number of archaeologists.

Little has been said in the foregoing pages about Lankester's more general works. Some of his articles in the 'Encyclopaedia

Britannica' have already been alluded to, but there remain to be mentioned the article on 'Vertebrata', and on 'The history and scope of Zoology', and the very interesting 'Introductions' to Parts I and II of the 'Treatise on Zoology' of which he was general editor.

In his later years Lankester wrote a series of semi-popular books, such as 'Extinct Animals', 'Science from an Easy Chair', 'Great things and Small', full of interesting information.

This brief review of Lankester's writings may help to show how wide was the range of his researches, and how great was the part he played in the progress of zoological science.

EDWIN S. GOODRICH.