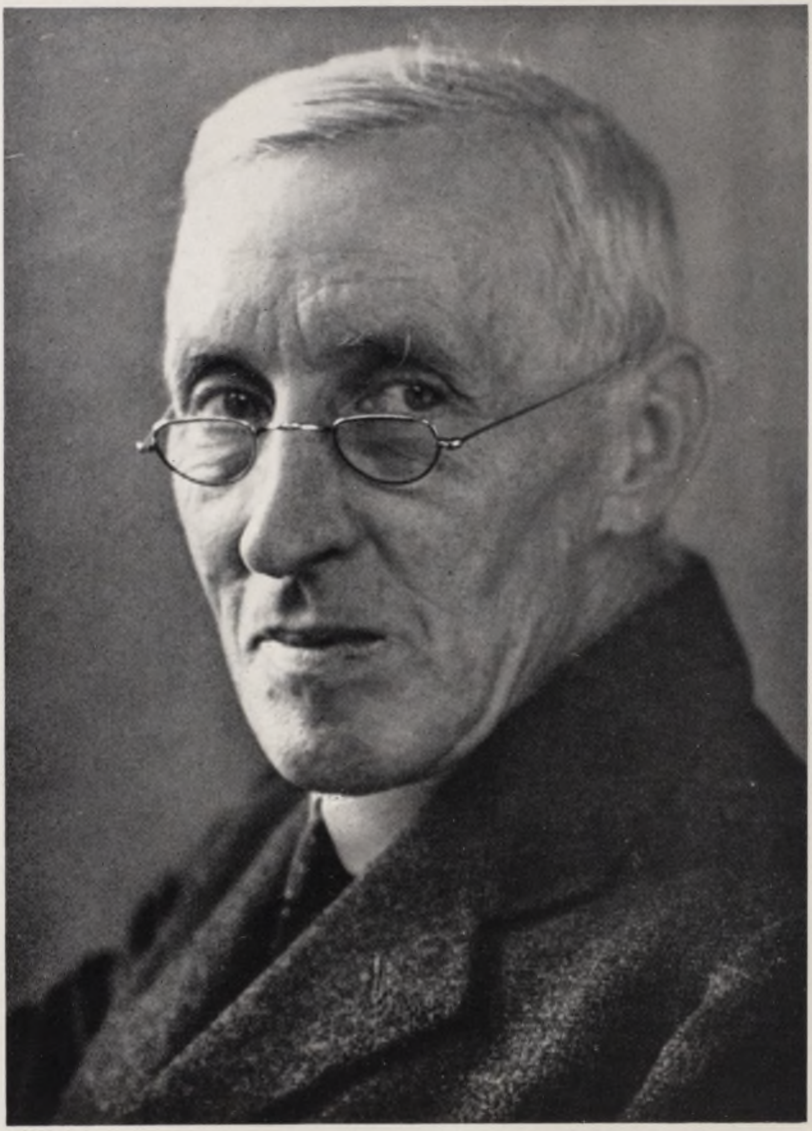
BIOGRAPHICAL MEMOIRS

James Peter Hill, 1873-1954

D. M. S. Watson

Biogr. Mems Fell. R. Soc. 1955 **1**, 101-117, published 1 November 1955



Jas. P. Hill

JAMES PETER HILL

1873-1954

James Peter Hill was born at Kennoway, Fifeshire on 21 February 1873. He was the younger son of John Hill of Langside, and his wife Catherine Campbell McInroy. Both his parents came from the highlands, his father being born at Scone in Perthshire. John Hill was a farmer, well known as an authority on the breeding of prize cattle—particularly shorthorns for which he won many medals—and as an expert judge of horses.

J. P. Hill went first to the village school at Kennoway where he was chiefly distinguished as a 'grand runner' and he showed his adventurous spirit as a boy of about ten years old by pursuading his father to allow him to sail from Leith to Archangel in a small steamer captained by an old family friend. In later years he always told of his trip as 'cabin boy' with great amusement.

Hill then went to the Royal High School, Edinburgh, and, probably because the school did not then provide science teaching, attended classes in biology at the Heriot Watt College during the years 1887-9, gaining 'qualifying teaching certificates' of the Science and Art Department, London, in 'Botany, Vegetable Morphology, Physiology and Animal Behaviour.' At school Hill was a good athlete, playing football for the 1st fifteen.

In 1889 Hill entered the University of Edinburgh as a science student, studying zoology under Professor Cossar Ewart, and botany under Isaac Bayley Balfour. But the man in Edinburgh who had most influence on him was Dr John Beard, University Lecturer in Comparative Embryology and Vertebrate Morphology. Beard was a man of originality who, having worked out in dogfish embryos the place of origin of the primordial germ cells, and their migration into the definitive gonad, went on to develop a theory of the nature of cancer, based on these observations, which has not been substantiated by later work.

It was presumably at Beard's suggestion that Hill, gaining a one-year studentship (later renewed) for teachers in training, migrated in 1890 to the Royal College of Science, London. For the summer session of 1891 he returned to Edinburgh as a junior demonstrator in zoology and botany. At South Kensington Hill was under G. B. Howes, F.R.S., the associate and successor to T. H. Huxley.

Professor F. J. Cole, F.R.S., tells me that Hill was 'one of a large group of young men who were impregnated with a love of animal morphology by the

vast and impressive erudition of G. B. Howes'. Others were Martin Woodward, W. G. Ridewood, R. H. Burne, James Johnstone, and Cole himself. At Howes's house he became friendly with (Sir) Arthur Keith.

In 1892 Professor Haswell of Sydney University wrote to Howes asking him to recommend a young man to demonstrate zoology and botany in his department. Howes recommended J. P. Hill, although he had not graduated or even completed the course. Thus, on 19 August 1892, Hill (aged 19) sailed to Australia, an anniversary he always remembered.

The University to which he came was full of life. Two years before, a new building for the School of Medicine had been completed, the Department of Physiology under Anderson Stuart held in succession the future Sir Alexander MacCormick, Sir Almroth Wright, and Sir Charles Martin as demonstrators, J. T. Wilson had taken charge of anatomy, his newly built department being 'in equipment and facilities for teaching and research far in advance of any comparable department in Great Britain at this time'. The biology department was less active, but Hill immediately set to work, collecting animals of all kinds on land and in the immensely rich harbour and on the shores of Sydney. Thus in five years he published some ten papers, on abnormalities in vertebrates, on Cestodes and Zoantharia, one in which he recorded the first Enteropneust from Australia, and an admirable anatomical account illustrated by magnificent figures of another form from Funafuti.

Early in his time in Sydney Hill came under the influence of J. T. Wilson, then aged 31, who, with a small daughter whose mother had died at her birth, was living with his aged parents. In this household Hill lived until 1898 when, Wilson marrying again, he joined Professor Mills, a surgeon and later Vice Chancellor of Sydney University.

In 1897-8 Hill took leave of absence for six months, returning to Edinburgh to graduate B.Sc., being not unnaturally awarded the Bell-Baxter Scholarship for the best graduate of the year in two science subjects. He had by that time published twelve scientific papers, of which those on an early embryo of *Platypus*, and on the placentation and dentition of *Perameles* are acknowledged classics, marking a revolution in our understanding of mammals.

In 1899, after he had returned to Sydney, Edinburgh awarded to him the 'Gunning' Victoria Jubilee prize for research in zoology, and a George Heriot Research Fellowship of £100 (renewed the following year), and for four years the Government Grant Committee of the Royal Society gave him funds for the study of marsupial and monotreme development. The materials so obtained formed the foundation of much of the later work of Hill and of his school. Small money grants have seldom been used to greater effect.

After his return to Sydney, Hill published his last paper on invertebrates, a small work on zoantharian taxonomy. Then followed in 1899 and 1900 a series of papers on the parturition of *Perameles*, and on the female genital organs of marsupials in general.

On 6 January 1900, at the Presbyterian Church, Finchley, London, J. P.

Hill married Marjorie, eldest daughter of J. Steele, C.B., J.P., Chief Inspector of Inland Revenue, and returned to Sydney, setting up house there.

In 1903 Hill was a candidate for appointment to a newly established Chair of Biology in the Victoria College, Wellington, New Zealand. He submitted testimonials from John Beard, Professor G. B. Howes, Professor Cossar Ewart, Professor A. A. W. Hubrecht, and one from E. Ray Lankester so remarkable that I print it in full here:

'My dear Dr Hill,

It gives me very great pleasure to add my testimony to that of others in favour of your candidature for the Chair of Biology at Wellington College. In my judgement there is no position in the anatomical and biological world to which you might not aspire. You have alone and by your own original discoveries entirely revolutionized the views of men of science as to the history of the Australian mammals—the marsupials. This you effected by two most careful and interesting investigations—the one on the dentition, the other on the placenta of these animals. I do not know of any man of your age who holds such a record, and I consider that any University should be proud to number you amongst its professors.

With best wishes for your success now and at all times,

I am,

Yours very truly,

E. Ray Lankester,

Director (of the British Museum, Natural History).'

Such a letter from the most distinguished living English zoologist, a man whose judgment of men, as of scientific work, was notoriously critical, is a remarkable testimony to the quality and importance of Hill's work. But it did not secure his appointment to the Chair.

Hill continued to work in Sydney, now in complete association with J. T. Wilson, on the development of *Ornithorhynchus*, but published nothing for three years. Then in 1906 three Chairs of Zoology fell vacant in England: University College London; the Royal College of Science; and Oxford. Hill was a candidate for each. He was appointed to the Jodrell Chair at University College. Before this appointment was published he was selected for the chair at the Royal College, but refused it having accepted the Jodrell Chair. The Linacre Chair was filled by G. C. Bourne.

Thus in 1906 Hill returned to England and began to reorganize the department he had taken over from Minchin, a specialist on sponges and protozoa. Hill, who in Sydney had cut all his own sections and made his own drawings and photographs, realized that, with the administrative duties he had undertaken, he would not have time to do these technical things, and that the laboratory steward, Mr. H. Jessop (who was originally appointed by Ray

Lankester in the 1870's) was too busy to do much in this direction. Thus he arranged that the College should provide him with a personal technical assistant, who only did ordinary departmental work (mostly photographs) as an exceptional courtesy.

Mr F. J. Pittock, appointed to this post as an untrained lad, was originally taught by Hill and remained with him until Hill's retirement, continuing to work in the Department of Anatomy until his death in 1951. He became extremely skilful, gaining awards from the Royal Photographic Society, and acting as an adviser to a famous firm of platemakers. Thus Hill was the first British zoologist to have the services of a private technician.

From the moment of his appointment Hill devoted himself to teaching, giving four junior lectures a week throughout three terms, taking much more than his full share of senior teaching, including some demonstrating, and giving a special course of lectures and practicals on vertebrate embryology to advanced students. But the teaching was effective: most of the students who took a zoology degree under Hill stopped on in the department, working on embryology, and I believe that more than half of them did so for so long a time that they ultimately took a D.Sc. Such a record is a remarkable testimony to Hill's powers as a teacher in rousing an enthusiasm for his subject in his able students. In this teaching Hill used lantern slides extensively and the collection now in the department gives evidence of the nature of the things taught, and the changes in interest there. Thus it is shown that Hill dealt with fossil vertebrates largely in his senior classes, gaining his knowledge—as a lantern slide of *Seymouria*, made before 1910, shows—from the original papers.

In 1913 Hill, with Professor Breslau and G. S. Sansom, made an expedition to Brazil, arriving there by a fortunate accident in October, which proved to be the breeding period of the marsupial *Didelphys*. They collected much useful material especially of other South American marsupials, later described.

At the end of the first world war Sir George Thane retired from the Chair of Anatomy in University College and was succeeded by Grafton Elliot Smith, a student of J. T. Wilson who had known Hill in Sydney in the 1890's. Elliot Smith recognized that the traditional anatomy of Medical Schools could be improved by taking over histology from the physiologists, and that—becoming 'human biology'—it could play an important part in the development of medical practice. Thus when the Rockefeller Foundation, developing its world wide schemes for the improvement of human health, sent representatives to London they consulted Elliot Smith, and shortly afterwards made a great grant to University College for the erection and endowment of a new department of anatomy. This department included a Chair of Embryology and Histology, to which J. P. Hill was appointed in 1921.

Much of his time during that year and the next was devoted to consideration of the departmental building then in progress, but in 1923 he moved into it, taking Mr Pittock with him.

Elliot Smith's idea in so appointing Hill was to free him from administration and much teaching so that his own research should go on the quicker; histology was to be dealt with by a 'subordinate'. But, very characteristically, Hill decided to do the work himself, giving a massive series of lectures and supervising the practical work, and especially the making of preparations used in it. These were extraordinarily good, of a different quality altogether from those then customarily used in 2nd M.B. classes.

But the new post made a gap of two years in Hill's list of publications, and the next work is Hill's first one on the embryology of Primates, its predecessor on *Tarsius* being a critical discussion of the literature. From this time on Hill was largely devoted to primate embryology, his Croonian lecture of 1932 being a treatment of the whole subject which reduced a vast literature to comprehensible order.

In 1930 T. T. Flynn, who had been a student of Hill's in Sydney, was appointed to the Chair of Zoology in Belfast, bringing with him vast collections of the eggs and embryos of monotremes and marsupials. These were added to those Hill possessed, and Flynn and Hill together began an extended investigation of early monotreme embryology to supplement 'Wilson and Hill', 1907.

Hill retired from his Chair at University College in 1938, but continued to work there as a 'Halley Stewart' Fellow for some time. The outbreak of war in 1939, followed by the evacuation of the College, raised the problem of housing Professor Hill's very large collection of slides and materials. The slides on which he was actually working were taken to Hill's residence at Finchley, the best of the slides and the spirit material were placed, along with valuable specimens from the British Museum of Natural History, in the cellars of the Rothschild Museum at Tring.

Thus Hill was enabled to continue his work, two vast papers by Flynn & Hill, published in 1939 and 1947, giving a most detailed account of the establishment of the primary germ layers in monotremes. After the war Hill received grants from the Wellcome Trustees, and continued to work in his own house and at the Department of Anatomy. This work continued almost uninterruptedly to the end of his life: he was busy at his microscope until the hour of his death, on 24 May 1954.

J. P. Hill's scientific work

Hill's first six scientific papers, though accurate, deal with matters of no present interest, but the seventh, written in association with C. J. Martin, is the beginning of that investigation which occupied him for the rest of his life—for sixty years. It is a description of the structure of an embryo of *Platypus* (*Ornithorhynchus*) taken from an egg in the uterus nearly ready to be laid: the mother had been shot by one of the authors on 1 October 1894. The description is clear and precise and the figures admirable, and it was the first in the field, for the great collection made by Caldwell in 1884 had, and has,

yielded little beyond the celebrated cable 'Ornithorhynchus oviparous ovum meroblastic'.* The paper is full of new facts, and of novel interpretations, which time has justified.

The authors showed that the egg (with its shell) had greatly increased in volume since it was shed from the ovary. That the vesicle, of whose surface the embryo was part, completely filled the eggshell and was itself full of a nutrient solution, yolk, added to by the secretion of the uterine glands. That this rapid increase in volume by imbibition explains the delayed upgrowth of the embryo pressed by it against the shell, the albumen layer being of no thickness, and these qualities are therefore not found in the sauropsidan egg with its enormously greater yolk supply. They recognized that the blastoderm was mammalian in character with special resemblance to the marsupial vesicle.

Exactly one year later Hill read to the Linnean Society of New South Wales a paper describing the occurrence of an allantoic placenta in the marsupial *Perameles*, thus breaking down a universally recognized character of marsupials. Another characteristic of marsupials in general was the fact that only a single tooth in each jaw was changed. This fact produced an abundant literature, including many investigations into the dental lamina and the mode of formation of teeth in mammals in general. Much confusion resulted from this work, ending in the 'discovery' in mammals of a pre-milk and a post-permanent dentition which have no real existence.

With Wilson, Hill investigated this matter in *Perameles*, concluding that the marsupials had been derived from a stock with the normal milk and permanent dentitions of the Eutheria by the almost complete suppression of the milk series following on the adoption of the permanent attachment of the pouch young to the teat immediately after birth. Eleven years later Wilson and Hill found evidence of small transient teeth anterior to those discovered by Poulton in *Platypus*, which suggested that at some remote period the monotreme conformed to a normal mammalian pattern.

Next year came a full paper on the placentation of *Perameles*, followed by others dealing with the corresponding structure in other marsupials. Meanwhile Hill discovered that *Perameles* is born by rupturing the connective tissue between the median vagina and the perineum, the passage so formed healing up after each parturition. That this strange phenomenon was present in the marsupials of South America as well as those of Australia interested Hill for many years (from 1898-1926).

In a preliminary note in 1903 Hill, in association with J. T. Wilson, returned to monotreme embryology, and in 1907 published a great paper in which for the first time a connected account of the development up to and including the neurula stage was given. Unfortunately in this paper a 'yolk navel' was incorrectly taken to be a primitive knot, so that, despite the perfect accuracy of the individual description of stages, the general pattern

* The cable was sent by Caldwell in the field to the President of the Zoology Section of the British Association then meeting.

of development is confused. In 1915 Wilson & Hill corrected this error, and in 1939 and 1947 Hill, in association with T. T. Flynn, wrote a great monograph in which the establishment of the 'germ layers' is traced in the greatest possible detail.

In the 1907 paper Wilson & Hill re-examined the *Platypus* embryo described by Hill & Martin in 1894. They now produced a new interpretation of one obtrusive feature of that embryo. Here, on each side of the flat forebrain, there is an immense thick mass of cells lying between the ectoderm and a thin layer of scattered mesenchyme cells overlaying the endoderm. This mass was originally described as 'head plate' mesoderm, and carefully distinguished from the walls of the 'amnio-cardiale vesicles' and from the somitic mesoderm. It was recognized that it was homologous with a similar structure found by Selenka in the opossum. Now Wilson & Hill, examining an embryo somewhat younger, discovered that the mass was in continuity with the brain, and interpreted it as neural crest, the primordium of the gasserian ganglion, despite the fact that in the original later stage each head plate was of greater volume than the whole forebrain! Had they examined the next later developmental stage of a marsupial they could not have escaped the conclusion that the mass not only produced the ganglion but also gave rise to the whole mesoderm of the mandibular arch. That it was in fact neural crest mesoderm, now known to be of almost universal occurrence.

During the antipodeal winters of the years 1899-1901 and 1904 Hill bred *Dasyurus viverrinus* in captivity and thus made a great collection of eggs covering the period of early development. At that time the only publication dealing with that matter in marsupials was an old paper by Selenka (founded, in fact, entirely on abnormal materials of *Didelphys*), and a statement by Caldwell that the egg in the uterus was enclosed in a shell. In 1910 Hill gave a magnificent description of this material, beginning with the ovarian egg. During its passage down the Fallopian tube the fertilized ovum is surrounded by a layer of albumen, and this in turn by an egg shell, which are as Hill showed usual in marsupials and exactly comparable to those of *Platypus*, and imply their descent from a prototherian stock. Cleavage produces an upper ring of four cells which alone give rise to the embryo and the whole endoderm, and a lower ring which forms only the 'trophoectoderm' of which the remainder of the blastoderm is formed, the two regions meeting in a junction which remains recognizable for some time, until in fact the spread of the endoderm obscures it. Here the description ends, and in a lengthy but lucid discussion it is shown that, so far as our limited knowledge of early eutherian development permitted a judgment, the early marsupial process provides an admirable intermediate stage between a monotreme and that of a eutherian.

In two papers published in 1894 and 1897 W. Heape showed that primates had a definite oestral cycle in the behaviour of the female and in the reproductive apparatus. Not until 1903 did F. H. A. Marshall describe the oestrous cycle and the formation of the corpus luteum of the sheep, in a paper which first introduced the idea of hormonal control of this series of changes. It is

therefore remarkable that from 1899 to 1904 Hill should have kept such accurate records of the condition of his breeding *Dasyurus* from day to day (and preserved all the necessary parts of their genital apparatus) that it was possible to work out from them, in 1911-1913, the oestrous cycle and the changes in the corpus luteum and Graaffian follicle, and of the mammary glands, work done by Hill & O'Donoghue, and by the latter alone.

Much later, in 1926, with J. B. Gatenby, Hill described the growth and decline of the monotreme corpus luteum, showing that it contains two histologically distinct kinds of secretory cells, and that it is in full regression by the time the egg is laid, but conforms in general to the normal mammalian pattern.

In 1909, when he was writing up the *Dasyurus* development, Hill found that the then existing knowledge of the early stages of placentals did not reach the standards he desired. So he began to collect cat embryos. After examining several hundred females over a period of ten years Hill obtained a series which enabled him in collaboration with Dr Tribe to write what is in effect a cell lineage, which establishes the existence of a determinate cleavage back to the second or third cleavage generation. He had previously shown that this condition existed in *Dasyurus* from the fourth, and in *Didelphys* from the first cleavage.

In the cat, as in all Eutheria, one cell, passing early in development into the centre of a sphere of cells tightly packed round it, divided in such a way that its progeny remains in a tight packed mass attached to one pole of a sphaerical blastocyst undergoing enlargement by imbibing uterine secretion, exactly as do the corresponding stages of monotremes and marsupials, as Hill had earlier shown. In the cat, and in the members of the other two groups, two different types of cells arise in this cell mass, and by active migration the smaller of them spread outwards to line the blastoderm, and form the embryonic endoderm, whilst the remainder form the embryonic ectoderm, which in the cat, by disappearance of the thin layer of cells (Rauber's membrane) which overlies the embryo, comes to form part of the sphaerical outer surface of the blastocyst.

By this time Hill had effectively provided that knowledge of the early development of some member of each of the three classes of mammals necessary to answer the question which he posed to himself thirty years before. He had shown that not only the general plan, but many details of the early development of monotremes, marsupials and eutheria are only to be explained by an ultimate derivation of each of these stages from that before it. Thus he settled, I think for all time, a problem which arose when matters of phylogeny were first discussed, and which cannot be determined by consideration of adult morphology, nor from fossil materials.

But one possible uncertainty remained: the cat is not a very primitive eutherian, and its development, so comparable with that of a marsupial, may be a secondary condition, that found in 'rodents with inversion', and higher Primates, being antecendent to it in a phylogenetic sense. This latter

view was, in fact, the opinion predominantly held amongst embryologists in 1918. Thus it became necessary to investigate this problem, which was in essence the phylogeny of eutherian orders and some of their divisions. Hill had already begun to do so. In 1919 he discussed the literature about the development of *Tarsius*, and in 1922, with his old fellow student R. H. Burne, described the foetal membranes and placentation of a nearly full-term foetus of the lemur *Chiromys*. In 1928, with F. E. Ince and A. Subba Rau, he described the development of the foetal membranes of the Indian lemur *Loris*, showing that the animal resembled *Nycticebus*, earlier described by Hubrecht, but that the greatly extended knowledge acquired by the authors added the further evidence that, in general, the early development of *Loris* agreed with that which study of the cat had shown Hill to be the primitive eutherian pattern.

Meanwhile in 1915 Huber had described the early development of the white rat, and Hill's student, G. S. Sansom, in 1922 published an admirable detailed study of implantation in the vole *Microtus*. The story is added to by a joint description by Hill & Sansom of the implantation of the blastocyst of *Cavia*, the guinea-pig, not closely related to *Microtus* and *Rattus*. This paper, illustrated by superb micro-photographs made by Dr Sansom, was published in 1931. It showed that the three 'rodents with inversion' discussed in it exemplified three different ways in which the 'inversion' is brought about, and suggested that the condition, so far from being one primitive for mammals in general, was evidently a highly specialized device to secure an advantage to the rodents possessing it.

Thus, when in 1929 Hill delivered his Croonian lecture on 'The developmental history of the Primates' (published only on 19 May 1932), he was not troubled by the idea that the haemochorial type of placenta found in the higher monkeys was the original pattern, but could set out in order, and describe as consecutive 'evolutionary stages' of early development and placentation, the conditions found in lemurs, *Tarsius*, pithecoids (platyrrhine and catarrhine monkeys) and anthropoids. These descriptions were all original, essentially every fact set out and discussed had been observed by the author himself in original materials. *Loris* was from materials collected by a friend of Dr Subba Rau, *Nycticebus* and *Tarsius* were based on Hubrecht's materials, *Hapale* was collected by Hill himself, other platyrrhines came from Selenka's collection, *Cebus* and *Chrysothrix* from Bluntschli's collection. Thus Hill gathered into his laboratory all the relevant materials known to exist in the world, and based his argument on direct personal knowledge, taking nothing for granted from the papers of any other worker. None the less he read all their papers with great conscientiousness and gave them full credit for all the facts they had recorded, differing from their interpretation apologetically when necessary. The whole work (133 quarto pages and 117 figures) is most impressive. It makes clear the nature of the problem, and then plunges directly into detail. Each stage of development of each animal is described and illustrated, earlier interpretations by other authors are dis-

passionately considered, then either accepted or refuted for reasons precisely stated. The whole is then summarized concisely in absolutely clear language, and finally definite conclusions based on the facts so set out are stated in the clearest possible way.

With this paper Hill in effect completed the investigation he had begun thirty-eight years before. He had shown, by a completely new line of evidence, that man shared with the anthropoid apes a unique, highly advanced type of early development and placentation, which could only have been derived from that found in catarrhine monkeys. That the catarrhine early development and placentation differs in small details from that of the platyrrhines in ways which render it unlikely that either of these groups could have been derived from the other. But both could have come from an animal unknown allied to the still living *Tarsius*. *Tarsius* in turn could only have come from the lemurs. The lemurid conditions are found as a pattern in many other primitive Eutheria, and are in effect foreshadowed by those in such a marsupial as *Dasyurus*. The lemur *Loris* even shows signs that its ancestors once possessed a yolk-laden egg. The marsupial egg has even more yolk, and in its passage down the oviduct becomes surrounded by an albumen layer and an egg shell, some kind of a placenta—even including an allantoic contribution—existing. '*Platypus*' has a shell, 'white', and a large yolky egg, but the egg imbibes nutrient solution on its way down the genital tract, so that it is more advanced in a mammalian direction than that of any 'sauropsidan'; but it is laid as an egg.

In University College Hill taught a number of men and women who proceeded to that Special Honours degree in zoology the course leading to which included (largely because he urged it on the 'Board of Studies' of the University) a written paper and practical examination in a 'Special subject' at a very high standard. In his hands this subject was 'vertebrate embryology', the field becoming more and more restricted, but the course requiring from the candidate a wide study of original papers and materials. Thus his students, on graduation, wished to settle for themselves questions which had come into their minds during his teaching, and Hill gave them materials on which they could work, usually on the development of some organ in which they were interested. Very commonly one or more of the resulting papers were published as joint work.

With Dr E. A. Fraser (1915) he wrote an elaborate account of the development of the thymus, epithelial bodies and thyroid in *Trichosurus*, to which Dr Fraser alone added an account of these structures in other marsupials. From the same materials she also showed that the marsupials alone amongst mammals possessed large 'anterior head cavities' from whose walls the eye muscles innervated by the oculomotor nerve arise. In this they agreed with lower vertebrates from elasmobranchs onward.

Somewhat later (1917) Dr K. M. Parker, working on the development of

the marsupial pituitary body, showed that these head cavities arose as outgrowths of the extreme anterior end of the fore gut, from the prochordal plate. Much earlier it had been recognized that the anterior head cavities were connected with one another by a canal in many lower vertebrates.

In 1924 Hill, with Dr Tribe, emphatically states his belief that the prochordal plate is a surviving relic of a premetameric stage of vertebrate development, and presumably ancestry. It was thus a structure of very great interest and Hill returned to its consideration in human embryos, with Dr Florian, in a paper published in 1931.

For some years, as student and colleague, Hill had the pleasure of a scientific association with his daughter, C. J. Hill, who in 1933 published an account of the histology of the monotreme oviduct during gestation, to which he added an account of the development of the egg shell.

With G. R. de Beer, who succeeded him in the Department of Anatomy, Hill described the vestiges of the egg tooth and analogous structures found in marsupials.

Thus, taken as a whole, the work of J. P. Hill and his school has made a unique contribution to descriptive embryology. To it we owe what is essentially all our knowledge of the early development of the monotreme and marsupial mammals, and much about their organogeny which cannot be found elsewhere. It is Hill's work that has established beyond dispute that Monotreme, Marsupial and Eutherian represent essentially definite evolutionary stages through which the higher mammals have all passed, and to him we owe the best evidence which exists to show that we ourselves, man, have been derived from ancestors which, traced backward, are anthropoid, pithecoid, tarsioid and lemurine in the plan and details of their early development. Though this work is descriptive the discussion of detail is full of suggestions as to the functional significance of unusual conditions, of the retention, for example, of a flat brain plate in marsupial embryos to a stage of morphological and histological development found in sauropsids and eutherian mammals long after closure of the brain vesicles.

Hill was a teacher who took his work very seriously. When I succeeded him at University College he lent me his notes for the Intermediate course in zoology. These showed that in his first session, 1906-7, he had written out not notes but a full hour's lecture for each meeting of the class. He revised these every year, correcting anything which he felt to be misleading, or out of date. But very often the effect was to introduce more matter into each lecture. In fifteen years they were in effect an unusually detailed text-book, including a mass of morphological facts impossible of immediate comprehension. The students' only hope was to get it all down verbatim, and then study it at leisure. But to the morphology some physiology came to be added. His senior lectures on both vertebrates and invertebrates were similar, full of detail and kept entirely up to date. They were illustrated by lantern slides and by splendid blackboard drawings, made in advance and sometimes labelled 'keep', so that they went on from one

meeting to the next. When he came to teach histology to medical students he followed the same plan.

Hill was thus a very busy man, but he worked long hours. He was in the department from 9 a.m. to 6 p.m. every day except Saturday, when he left at midday. And he spent the whole of this long day at work, for he usually lunched on sandwiches eaten in his laboratory, and seldom visited the 'Professors' Smoke Room'. At any time when you went to see him you expected to find him sitting at a bench with a microscope, sometimes with a binocular embedding an embryo and determining the proper plane of section, usually with a set of slides hunting some fact. He often took slides home, where he kept a microscope in his study, and there he read the literature, regularly working steadily up to midnight. But he was a keen golfer, playing at most weekends and during the summer vacation, when he took a six weeks' holiday with his family, sometimes at Elie in Fifeshire, near his old home, or latterly more frequently at Seaford in Sussex. His golf appears to have been good, and he believed in its therapeutic effect.

Nearly all his published papers were written in collaboration, at first with a senior man, especially J. T. Wilson; after he came to London he was the senior author. This collaboration was genuine, both authors studied the materials as intensively as if each were writing independently, and they discussed the work in very great detail, down to the point of whether an individual cell should be included in the neural plate of a flat embryo being graphically reconstructed, or not. Thus Hill secured a very high accuracy of statement of fact. Then arose discussion of the significance of the facts so discovered. Here also both authors contributed; in the early days, as Hill himself records, it was reputed that the discussions between Wilson and Hill could be heard a quarter of a mile away, and as Elliot Smith said to me, these two 'wrangled like a pair of Scots'. But such discussion of particular problems, known to both authors not only from a study of sections, but of the whole literature, seems to have been useful to 'J.P.' (as he was always known at University College) in enabling him to make up his mind.

Then came the drafting of the text, written and corrected until it had become lucid and precise. There is a story that when E. S. Goodrich was applying for appointment as professor in Oxford, Hill and F. J. Cole drew up a document which was widely signed and sent to the Electors. Cole drafted it with immense care, and stopped with Hill to discuss its wording. After dinner Cole gave his draft to Hill, who read it, said nothing, but some time later suddenly remarked—'damn it, man, at least let's have that comma out.' Determination of the text of a joint paper was a similar process.

In contrast to this pernickety attitude toward the written word he was apt at times to lapse into complete informality in speech. On one occasion he put his head round the door of the senior laboratory and asked a class within, 'have ye finished the bleeding things with legs?'—thus referring to the Arthropoda, a phylum for which he had a distaste.

Hill possessed more knowledge of embryology, and probably of zoology in

general, than any of his contemporaries in England, but his contributions to public discussion were always marked by extreme diffidence. In work with research students he was wont to express a view with great finality, but was always ready to alter it on satisfactory evidence being shown.

Hill had a very great personal charm of a kind which is difficult to make evident to anyone who did not know him. I do not think he knew that he possessed it: certainly he never traded on it, and some people did not recognize its existence. It depended in part on that complete sincerity which informed all his scientific work, accompanied by a lack of any sense of urgency: that a thing should be done as well as possible far outweighed any sense that, if its completion should be deferred from year to year it might (even if ultimately achieved) appear after general interest had passed far beyond the matter involved. His relation to his research students and associates was close, and, after a first period, a relation of equals, with whom everything must be discussed in the greatest detail. Everything in which they were concerned was present in Hill's mind, and led him to make interjections deprived of their context. 'I see you've got your head back and I thought it would take two men and a boy,'—spoken from a slightly opened door to a research student who, rearranging the departmental museum, had had difficulty in reinstating a hippopotamus skull on an upper shelf.

Such an account of Hill's life may give an impression of a somewhat inhuman character, but any such belief is entirely mistaken. Hill thoroughly enjoyed the expeditions in Australia, and later in Brazil, when he collected materials and lived in camp with friends. Writing of those days in New South Wales Hill says 'those were years of intensive activity, with the days often prolonged far into the night and relieved by 'working holidays'' in the Blue Mountains during the long summer vacations and by camping expeditions into the bush in search of monotreme and marsupial material during the short winter breaks. These camping trips were memorable and joyous occasions when we reverted to the primitive life—shot and cooked our own food, hunted by day and yarned over the camp fire by night.' I remember walking through the departmental museum with him when he suddenly pointed to a mounted skeleton of an agouti and without any preface remarked, 'that provided the second best soup I ever made.'

Hill's tenure of the Jodrell Chair ended very soon after the first world war and covered a time when the College funds were very small, when an additional binocular microscope was a very serious expenditure, and when there were (except for the small Derby Scholarship) no funds available for the support of research students. Only late in J.P.'s time did the parents of a research student who died young, Percy MacGregor, give to Hill a small scholarship to support a research student. He was, perhaps, a little unworldly in his apparent belief that all new graduates could be expected to continue to work with him without any grant. And with his women students not every post was suitable. But he did his best to make financial

provision for those whose work was good. After the war the D.S.I.R. came to the rescue.

Thus, that so many of those who took their degree under Hill stopped on in the department and worked with him on his material is a testimony of the affection which he inspired in them. They were worked hard, they had to be prepared to discuss in detail the evidence for every point in a graphical reconstruction. They were expected to have read all the literature, and to make use of it. And when the work was done and written up the hope that further material would come from some unknown source 'further to paint the lily' might defer publication from one year to another, so that, for instance, what was really conclusive evidence of the neural crest origin of the marsupial mandibular arch, recognized in 1918, still lacks publication.

Hill's judgment of men was almost always kindly: he recognized before others the uncanny genius of Robert Broom, who of all men was the most unlike himself in scientific method. He had an admiration of the work of Spemann and was delighted to recognize in him a man who had himself cut every section he had used in his work on the embryology of newts. But although he was peculiarly well fitted to do such experimental work he never did so. He respected and admired Hubrecht, although he steadily corrected his conclusions until nothing was left, and his relationship to J. T. Wilson, shown so well in his obituary notice of his old friend, was delightful.

One of Hill's former colleagues most justly sets out traits which won their affectionate regards for the man himself. His courtesy and unfailing readiness to give time to a junior colleague who stood in need of the illumination of J.P.'s keen mind. That he could meet on their own ground and in a foursome beat his students in a staff-student golf match. That in his latter years he refreshed his spirit by listening to Beethoven late at night at the end of his day's work. And the pleasure of visiting him and his family in a house significantly called 'Kanimbla', the Australian name of a beautiful former camping ground in New South Wales which means 'Valley of the Kangaroos'.

These things add to our understanding of a man whose life was devoted to a single problem, pursued over a period of very nearly sixty years.

Hill was elected to the Royal Society in 1913, served on the Council 1925-27, and was Darwin Medallist in 1940. He was D.Sc.(Hon.) of the Universities of Dublin and Belfast, and Honorary Member of many foreign societies, including the National Academy of Sciences, U.S.A. (1940), Hollandsche Maatschappij der Wetenschappen, Haarlem (1925), the Sociéte Royale de Bohême, the Sociéte Portugaise des Sciences Naturelles (1921), and the Royal Society of New South Wales (1929) and the Linnean Society of New South Wales (1923). He was also a Founder Member of the International Institute of Embryology. He was awarded the Mueller Medal of the Australian Association for the Advancement of Science in 1906, and the Linnean Gold Medal in 1930.

This biographical sketch of J. P. Hill's life and work is founded on knowledge gained from a forty-four year friendship. But it has been controlled,

added to and greatly improved by the advice of many of his students and associates.

To Dr Catherine J. Hill (Mrs Kirkham Jones), Dr Elizabeth Fraser, Dr Margaret Tribe and Dr Katherine M. Parker (Mrs Watson) I owe some family history, many reminiscences and a check of my memory of J.P.'s activities. Professor F. J. Cole, who alone remembers the days of Professor Howes's department at South Kensington, gave me some knowledge of that stage in Hill's career. Professor P. D. F. Murray gave me some records of Sydney. I am indebted to Drs Abercrombie and Newth who read my account of Hill's scientific work.

The photograph illustrating this notice was taken by F. J. Pittock in 1935.

D. M. S. Watson

BIBLIOGRAPHY

1892. (With G. B. Howes.) On the pedal skeleton of the Dorking fowl, with remarks on hexadactylism and phalangeal variation in the amniota. *J. Anat., Lond.* **26**, 395-403.

1893. Note on an abnormal connexion of the renal-portals of a young male frog (*Lymnodynastes peronii*). *Proc. Linn. Soc. N.S.W.* (2), **8**, 222-224.

1893. Preliminary note on a Balanoglossus from the coast of New South Wales. *Proc. Linn. Soc. N.S.W.* (2), **8**, 324.

1893. Note on the presence of vestigial Müllerian ducts in a full grown male lizard (*Amphibolurus muricatus*). *Proc. Linn. Soc. N.S.W.* (2), **8**, 325-326.

1893. (With W. A. Haswell.) On *Polycecus:* a proliferating cystic parasite of the earthworms. *Proc. Linn. Soc. N.S.W.* (2), **8**, 365-376.

1894. A contribution to a further knowledge of the cystic cestodes. *Proc. Linn. Soc. N.S.W.* (2), **9**, 49-84.

1895. (With C. J. Martin.) On a Platypus embryo from the intra-uterine egg. *Proc. Linn. Soc. N.S.W.* (2), **10**, 43-74.

1895. On a new species of Enteropneusta (*Ptychodera australiensis*) from the coast of New South Wales. *Proc. Linn. Soc. N.S.W.* (2), **10**, 1-42.

1895. On a Fiddler (*Trygonorhina fasciata*) with abnormal pectoral fins. *Proc. Linn. Soc. N.S.W.* (2), **10**, 206-208.

1895. Preliminary note on the occurrence of a placental connection in *Perameles obesula*, and on the foetal membranes of certain macropods. *Proc. Linn. Soc. N.S.W.* (2), **10**, 578-581.

1897. (With J. T. Wilson.) Observations upon the development and succession of the teeth in *Perameles;* together with a contribution to the discussion of the homologies of the teeth in marsupial animals. *Quart. J. micr. Sci.* (N.S.) **39**, 427-588.

1897. The Enteropneusta of Funafuti. *Mem. Aust. Mus.* **3**, 205-210; 325-346.

1898. The placentation of *Perameles* (Contributions to the embryology of the Marsupialia, I). *Quart. J. micr. Sci.* (N.S.) **40**, 385-446.

1899. (With T. Whitelegge.) Zoantharia of Funafuti. *Mem. Aust. Mus.* **3**, 385-391.

1899. Contributions to the morphology and development of the female urogenital organs in the Marsupialia. I. On the female urogenital organs of *Perameles*, with an account of the phenomena of parturition. *Proc. Linn. Soc. N.S.W.* (2), **14**, 42-82.

1900. Contributions to the morphology and development of the urogenital organs in the Marsupialia. II. On the female urogenital organs of *Myrmecobius fasciatus*. III. On the female genital organs of *Tarsipes rostratus*. IV. Notes on the female genital organs of *Acrobates pygmaeus* and *Petaurus breviceps*. V. On the existence at parturition of a pseudovaginal passage in *Trichosurus vulpecula*. *Proc. Linn. Soc. N.S.W.* (2), **15**, 519-532.

1900. On the foetal membranes, placentation and parturition, of the native cat (*Dasyurus viverrinus*). *Anat. Anz.* **18**, 364-373.

1901. Contributions to the embryology of the Marsupialia. II. On a further stage in the placentation of *Perameles*. III. On the foetal membranes of *Macropus parma*. *Quart. J. micr. Sci.* (N.S.) **43**, 1-22.

1903. (With J. T. Wilson.) Primitive knot and early gastrulation cavity coexisting with independent primitive streak in *Ornithorhynchus*. *Proc. Roy. Soc.* **71**, 314-322.

1907. (With J. T. Wilson.) Observations on the development of *Ornithorhynchus*. *Phil. Trans.* B, **199**, 31-168.

1907. (With J. T. Wilson.) Observations on tooth development in *Ornithorhynchus*. *Quart. J. micr. Sci.* **51**, 137-165.

1910. Contributions to the embryology of the Marsupialia. IV. The early development of the Marsupialia, with special reference to the native cat (*Dasyurus viverrinus*). *Quart. J. micr. Sci.* **56**, 1-134.

1913. (With C. H. O'Donoghue.) The reproductive cycle in the marsupial *Dasyurus viverrinus*. *Quart. J. micr. Sci.* **59**, 133-174.

1915. (With E. A. Fraser.) The development of the thymus, epithelial bodies and thyroid in the Marsupialia. I. *Trichosurus vulpecula*. *Phil. Trans.* B, **207**, 1-85.

1915. (With J. T. Wilson.) The embryonic area and so-called 'Primitive knot' in the early monotreme egg. *Quart. J. micr. Sci.* **61**, 15-25.

1918. Contributions to the embryology of the Marsupialia. V. Some observations on the early development of *Didelphys aurita*. *Quart. J. micr. Sci.* **63**, 91-139.

1919. The affinities of *Tarsius* from the embryological aspect. (In discussion on the zoological position and affinities of *Tarsius*.) *Proc. Zool. Soc., Lond.* pp. 476-491.

1922. (With R. H. Burne.) The foetal membranes and placentation of *Chiromys madagascariensis*. (With an appendix on the external characters of the foetus, by R. I. Pocock, F.R.S.) *Proc. Zool. Soc., Lond.* pp. 1145-1170.

1924. (With J. Brontë Gatenby.) On an ovum of *Ornithorhynchus* exhibiting polar bodies and polyspermy. *Quart. J. micr. Sci.* **68**, 229-238.

1924. (With M. Tribe.) The early development of the cat (*Felis domestica*). *Quart. J. micr. Sci.* **68**, 513-602.

1925. (With E. A. Fraser.) Some observations on the female urogenital organs of the Didelphyidae. *Proc. Zool. Soc. Lond.* pp. 189-219.

1926. (With J. Brontë Gatenby.) The corpus luteum of the Monotremata. *Proc. Zool. Soc. Lond.* pp. 715-763.

1928. (With F. E. Ince and A. Subba Rau.) The mode of vascularization of the chorion in the Lemuroidea and its phylogenetic significance. *C. R. Ass. Anat.* 1-5.

1929. (With F. E. Ince & A. Subba Rau.) The development of the foetal membranes in *Loris*, with special reference to the mode of vascularization of the chorion in the Lemuroidea and its phylogenetic significance. *Proc. Zool. Soc. Lond.* pp. 699-716.

1929. (With G. S. Sansom.) Observations on the structure and mode of implantation of the blastocyst of *Cavia*. *J. Anat., Lond.* **64**, 113-115.

1930. (With J. Florian.) The development of the head-process and prochordal plate in Man. *J. Anat., Lond.* **65**, 242-246.

1931. (With G. S. Sansom.) Observations on the structure and mode of implantation of the blastocyst of *Cavia*. *Trans. Zool. Soc. Lond.* **21**, 295-352.

1931. (With J. Florian.) A young human embryo (Embryo Dobbin) with head-process and prochordal plate. *Phil. Trans.* B, **219**, 443-486.

1931. (With J. Florian.) Further note on the prochordal plate in man. *J. Anat., Lond.* **66**, 46-47.
1932. The developmental history of the Primates. (Croonian Lecture.) *Phil. Trans.* B, **221**, 45-178.
1933. The development of the Monotremata, II. The structure of the egg-shell. *Trans. Zool. Soc. Lond.* **21**, 443-456.
1935. (With J. Florian.) An early human embryo (No. 1285, Manchester Collection), with capsular attachment of the connecting stalk. *J. Anat., Lond.* **69**, 399-411.
1938. (With J. H. Woodger.) The origin of the endoderm in the sparrow. (Demonstration.) *Biomorph.* **1**, 326.
1938. (With T. Thomson Flynn.) The growth of the oocyte, maturation, fertilization and early cleavage in the Monotremata. *Biomorph.* **1**, 327-329.
1938. The macroscopic features of the placentation of the water-shrew (*Potamogale velox*). *Biomorph.* **1**, 331-332.
1938. Implantation of the blastocyst in *Galago demidoffi*. (Demonstration.) *Biomorph.* **1**, 333.
1939. (With T. Thomson Flynn.) The development of the Monotremata. IV. Growth of the ovarian ovum. Maturation, fertilization and early cleavage. *Trans. Zool. Soc. Lond.* **24**, 445-622.
1942. (With T. Thomson Flynn.) The later stages of cleavage and the formation of the primary germ layers in the Monotremata. (Preliminary communication.) *Proc. Zool. Soc. Lond.* A, **3**, 233-253.
1947. (With T. Thomson Flynn.) The development of the Monotremata. VI. The later stages of cleavage and the formation of the primary germ-layers. *Trans. Zool. Soc. Lond.* **26**, 1-151. (This paper contains a section by J. H. Woodger and J. P. Hill on 'The origin of the primary germ-layers in birds' (pp. 128-132).)
1949. The allantoic placenta of *Perameles*. *Proc. Linn. Soc. Lond.*, Session 161, 1948-49, pt 1, pp. 3-7, Pl. I.
1950. (With G. R. de Beer.) Development of the Monotremata. VII. The development and structure of the egg tooth and the caruncle in the monotremes and on the occurrence of vestiges of the egg tooth and caruncle in Marsupials. *Trans. Zool. Soc. Lond.* **26**, pt 6.
1955. (With W. C. Osman Hill.) The growth-stages of the pouch-young of the native cat (*Dasyurus viverrinus*) together with observations on the anatomy of the new-born young. *Trans. Zool. Soc. Lond.* **28**, pt 5, 349-425, Pls I-XIII.
1925. Obituary Notice. The late Emeritus Professor Nicholas Kulchitsky. *J. Anat., Lond.* **59**, 336-339.
1925. Obituary Notice. W. A. Haswell. *Proc. Roy. Soc.* B, **97**, 12-14.
1925. Obituary Notice. Richard Assheton. *Proc. Roy. Soc.* B, **97**, 1-6.
1932. Obituary Notice. Albert A. T. Brachet. *Obit. Not. Roy. Soc.* **1**, 64-70.
1941. J. T. Wilson. A biological sketch of his career. *J. Anat., Lond.* **76**, 3-8.
1949. Obituary Notice. J. T. Wilson. *Obit. Not. Roy. Soc.* **6**, 643-660.