

Peter Humphry Greenwood. 21 April 1927-3 March 1995

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## PETER HUMPHRY GREENWOOD

21 April 1927–3 March 1995

Elected F.R.S. 1985

BY C. PATTERSON, F.R.S.

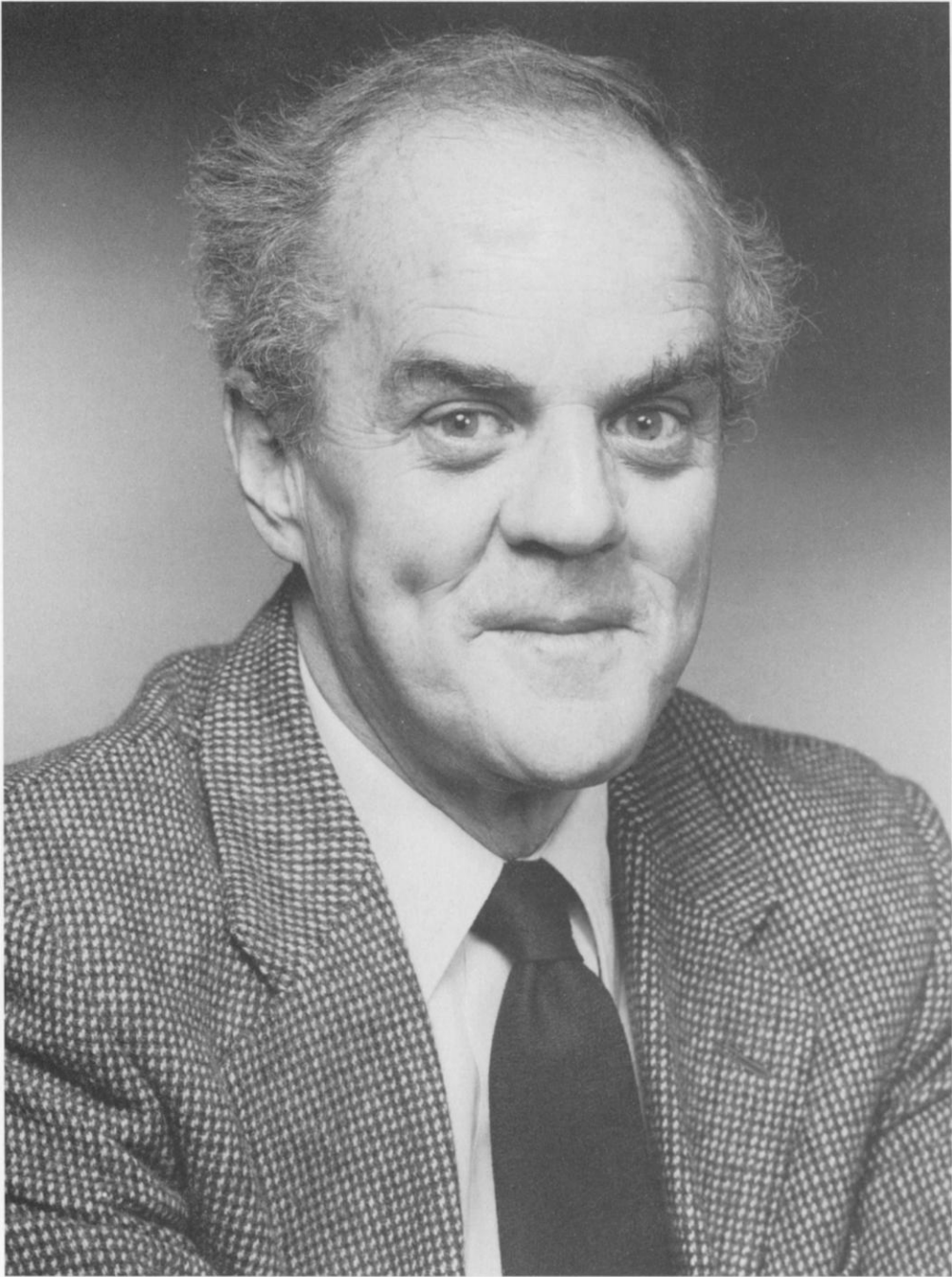
*The Natural History Museum, Cromwell Road, London SW7 5BD, UK*

Humphry Greenwood was an ichthyologist, noted in particular for his pioneering work on the species flocks of cichlids in the great African lakes, and for studies of the phylogeny and systematics of teleosts.

### FAMILY AND CHILDHOOD

Humphry's father, Percy Ashworth Greenwood (1896–1963), was a Lancastrian from Rochdale, a town full of Greenwoods. Percy Greenwood enlisted in the Lancashire Fusiliers as a private in August 1914, and after surviving the Dardanelles and the Somme, was demobilized as a captain. He then entered Camborne School of Mines, in Cornwall. The Camborne School, founded in 1859 and now part of the University of Exeter, was then a respected institution, perhaps second only to the Royal School of Mines in London as a training ground for mining engineers. Percy Greenwood was apparently the first member of his family to enter higher education.

Humphry's mother, Joyce May Wilton (1893–1957), was from a Redruth family that came to Cornwall from Wiltshire in the eighteenth century. She was musical, and first met Percy when the Redruth choral society to which she belonged came to Camborne to give a concert of selections from Gilbert and Sullivan. The two were married in 1922, and Percy left for Africa soon afterwards. There he worked for some time in the mining industry in Tanganyika before moving to South Africa, where the Greenwoods spent the rest of their lives. Percy was employed by West Rand Consolidated Mines, in the gold mines at West Rand, near Johannesburg. Custom demanded that he should accompany the morning shift down the shaft at 6 am each day, to oversee things underground before beginning his work in the office as a manager. He eventually developed pneumoconiosis, and the Greenwoods retired early to Ramsgate, on the Natal coast, where, during the 1950s, they owned a 30-foot motor launch,



complete with crew, which was used as a semi-commercial line-fishing vessel.

Although Humphry's parents had been in Africa for some time before his birth, his mother decided to return home to Cornwall in 1927 to give birth. So Humphry was born in Redruth (the unusual spelling of his forename followed that of his maternal grandfather, Edward Humphry Wilton), and he did not meet his father until he was 18 months old, when his mother returned to Johannesburg. Humphry was an only child and, in fact, the last of his Greenwood line, as his one paternal aunt and one maternal uncle were both childless.

Humphry's education, like his life, began in Cornwall. His parents returned to Cornwall on long leave in 1934, and Humphry attended the Passmore Edwards school in Redruth for six months. On the family's return to South Africa, he entered St John's College in Johannesburg, where he was a day boy until the age of 12. He then went for a couple of years to Michaelhouse, an upmarket boarding school at Balgowan in Natal. His experiences there gave him a lifelong hatred of boarding schools, and ensured that when the time came for his own daughters' education, they lived within walking distance of a suitable school. But from Michaelhouse, Humphry went to an even more rigorous environment. At the age of 14 he 'ran away to sea' (as he sometimes put it) and in January 1942 joined 'General Botha', the training school of the South African Naval Forces. He found General Botha no more to his liking than Michaelhouse. A diary of his time there describes the tight routine (without complaint), but concentrates, understandably in a 14-year-old, on the highs and lows of menus. After six months he returned to a normal schooling at Krugersdorp High School. Krugersdorp, about 20 km from Johannesburg, was within a mile or two of his parents' tied house with West Rand Consolidated. However, Humphry seemed to fit no better in Krugersdorp High than in his two previous establishments; the headmaster found him unacademic and too adult for his classmates (perhaps the result of forcing on General Botha); Humphry's father disliked the headmaster; and eventually Humphry was asked to leave, apparently as the outcome of his participation in a debate on the motion 'Is this school run on democratic lines?'

#### WAR SERVICE AND UNIVERSITY

By now it was 1944, and Humphry was just 17. Expulsion from school is the traditional prelude to running away to sea, and against his parents' wishes Humphry did so for the second time, enlisting in August as an Ordinary Seaman in the South African Naval Forces. He was soon seconded to the Royal Navy, and served on H.M.S. *Ceylon*, a modern light cruiser (launched 1941). A personal log survives of his tour of duty in the Indian Ocean, from leaving Durban in December 1944 to disembarking at Colombo in September 1945. Humphry recorded a total of 294 days aboard, 178 of them in harbour, thus bearing out the adage that war is mostly waiting. He did see brief spells of action off the coast of Burma, and suffered a damaged leg from falling down an open hatch while in harbour in Colombo.

Demobilized as an Able Seaman in February 1946, Humphry (like his father after the First World War) was able to enter higher education through the arrangements made for ex-servicemen. He was exempted from matriculation on grounds of military service, and joined the University of the Witwatersrand in Johannesburg ('Wits') in March 1946. Humphry intended to study medicine (his mother was convinced that his shapely hands were those of a surgeon), but with the flood of ex-servicemen in 1946 the Medical School at Wits was already overfull. He therefore began a B.Sc. course in the Faculty of Science, hoping that success in

the Part 1 exams at the end of the first year (in botany, chemistry, physics and zoology) would get him into Medical School in the second year, when the inevitable winnowing of ill-adapted first-year ex-servicemen would have created space. Like the Medical School, the Science departments at Wits were filled to bursting with ex-servicemen (student numbers in the university increased from about 5000 to about 13 000 during 1945–46). Many classes were conducted in temporary huts, sometimes in day and evening shifts, and Humphry's first-year science course was converted from concurrent study of four subjects to botany and zoology in the first half-year, and chemistry and physics in the second. In the Zoology Department, Humphry found two influences. The first was the Professor, Cornelius Jan van der Horst (1889–1951), a distinguished Dutch zoologist who had trained at the University of Amsterdam, where he acted as assistant to Hugo de Vries. He was later a curator in the Zoological Museum of Amsterdam, and in 1920 made an expedition to Curacao. He had published on corals and hemichordates. He came to Wits in 1928 as Senior Lecturer in Zoology, and took over as Head of Department in 1933. Known as 'Pop' to the students in Humphry's time, van der Horst converted Humphry from a potential medical student into a zoologist. However, Pop's imperfect English ('some students ... found him only semi-comprehensible'; Murray 1982, p. 284) impaired Humphry's grasp of lectures on fish systematics, so he worked the subject up for himself from books.

The second influence that Humphry encountered in the Zoology Department at Wits was a demonstrator, Marjorie George. An earlier convert of van der Horst's, she completed her first degree in zoology in 1944, and while working for her honours degree was called on by Pop to help him cope with the influx of students in 1945–46. Marjorie and Humphry met at Easter 1946, on a botany excursion during his first year, and married in January 1950, after he had completed the four-year course for an honours degree in zoology. As might have been predicted, Humphry found the first year's work difficult, but got through with flying colours by hard work, and with help and encouragement from Marjorie. By his second year, Humphry was concentrating on fishes and marine biology, and Niels Bolwig, the Danish Senior Lecturer in Zoology at Wits, helped him to work as a vacation student with Dr Cecil von Bonde, Director of Fisheries, in his laboratory at Sea Point in Cape Town. Also in his second year, Humphry was President of the Council of Students in Science. A press cutting exists with a photograph of him presenting a gold watch to Robert Broom, F.R.S. (1866–1951), at a celebration to mark Broom's eightieth birthday (13 November 1946).

On graduating in 1950, Humphry won, from London, a Colonial Fisheries Research Studentship (worth £360 p.a. plus £110 marriage allowance), at least the first seven months of which were to be under the supervision of Dr Ethelwynn Trewavas in the British Museum (Natural History), and the remainder with the East African Fisheries Research Organisation, based at Jinja, Uganda.

## LONDON AND UGANDA

Humphry first entered the Fish Section in the British Museum (Natural History) (B.M.N.H.) on his Studentship in March 1950, to study under Ethelwynn Trewavas ('E.T.') (1900–1993; Noakes 1994). She had joined the Museum in 1928 as personal research assistant to Charles Tate Regan, F.R.S. (1878–1943), and was appointed to the permanent staff in 1935. Humphry and his wife were immediately taken under Ethelwynn's wing, and she remained a lifelong



friend (69, 72–74).\* Humphry's brief was to study the haplochromine cichlids of Lake Victoria. Those fishes were first revised by Tate Regan in 1922, and E.T. had been publishing on them since she arrived in the Museum, both with Regan (Regan & Trewavas 1928) and on her own (Trewavas 1928). Her knowledge of the group was profound, although her major work on the group was not published until 1983, more than 20 years after her retirement in 1961. The Greenwoods, stay in London was brought to an end by the birth of their first daughter, Pamela, at the end of 1950; a small baby made their penurious life impossible. (Humphry was doubtless ready to leave because he had already learned that museum specimens alone were not enough to unravel the cichlids of the African lakes; Anon. 1952, p. 25.) They travelled by boat to Mombasa, thence by train through Nairobi, where Louis and Mary Leakey took them home for lunch, and on the following day came to Jinja on the northern shore of Lake Victoria.

The East African Fisheries Research Organisation (E.A.F.R.O.; from 1960 E.A.F.F.R.O., with the addition of 'Freshwater') was founded in 1947 (Beauchamp 1967). When Humphry joined it early in 1951, as Fishery Research Officer, there was one other member of staff with the same title, Rosemary Lowe (b. 1921, later Lowe-McConnell), now distinguished as a pioneer of tropical fish ecology (Bruton 1994), and three other scientists: a hydrologist, an entomologist and the Director, R.S.A. Beauchamp (Lowe-McConnell 1997). Humphry was to continue his work on haplochromine cichlids, while Rosemary Lowe studied the tilapiines. When Humphry began, there were thought to be about 60 species of *Haplochromis* in the lake. Ironically or tragically, during Humphry's lifetime the number of species climbed to about 300 (through improvements in sampling and systematics), and then declined (through extinction, largely man-made) to about 100. Humphry's work in Jinja can be reconstructed from the Annual Reports of E.A.F.R.O., from his correspondence with E.T. and from his publications. The first two of those were written while in London, his paper in *Nature* on the *Haplochromis* species-flock of Lake Victoria (1), and a description of Miocene fossils from in (Rusinga Island) or near the lake (2). Work for the latter paper initiated Humphry's fruitful collaboration with the B.M.N.H. fossil fish section, then staffed by Errol I. White, F.R.S. (1901–1984), and H.A. Toombs (1909–1987).

While at E.A.F.R.O. Humphry compiled parts 1–4 of his 'Fishes of Uganda' (4, 10–12), collected in 1958 as his first book (14, second edition 27). He also completed the first three of his B.M.N.H. *Bulletins* on the Lake Victoria haplochromine cichlids (7, 8, 13); these, and other papers published in Britain (3, 5, 9) were all revised and edited by E.T. He made one six-week trip to London, early in 1955, and during it worked with E.T. on paper (6). The 1953 Annual Report of E.A.F.R.O. (Anon. 1954, p. i) records one officer as having taken 'a considerable period of leave on account of dermatitis caused by formalin'. Humphry was the officer. The trouble began on his hands shortly after he began work at E.A.F.R.O.; in August 1951 he wrote of a safari to the Murchison Falls 'as part of a rest cure for my hands', and thereafter it flared up repeatedly throughout the early part of his career. In July 1953 a medical board assessed him as 'permanently incapacitated from handling formalin', and he seriously considered turning to palaeontology. But rubber gloves helped, when he eventually agreed to use them, and he was able to continue work with alcoholic specimens.

At the end of 1953 Humphry's colleague Rosemary Lowe married, and had thereupon to resign from E.A.F.R.O. because of the 'marriage bar' then in force in the Civil Service. She

\* Numbers in this form refer to the bibliography at the end of the text.

was not replaced for a couple of years, and Humphry soon found that his research time on fishes was being eroded by fisheries survey work. When a replacement did arrive, Humphry found him 'without much interest or ambition. This is really tragic since there is so much aching to be done, but which isn't going to yield its secrets to an 8.30 to 4.30 man' (in litt. to E.T., 22 January 1956). Another approaching problem was the need to find schooling for the Greenwoods' eldest daughter. As a result, Humphry began to look around, and successfully applied for a Civil Service Commission Fellowship, which turned out to be tenable in London.

### BRITISH MUSEUM (NATURAL HISTORY) I

In July 1957 the Greenwoods, now numbering five (daughters Jennifer, b. 1953, and Nan, b. 1955, having been born in Uganda), returned to London and Humphry took up a temporary appointment as Senior Research Fellow in the fish section of the Department of Zoology. The appointment was confirmed in February 1958, and in April 1959 Humphry joined the permanent staff as Senior Scientific Officer. When Humphry joined, the scientific staff of the Fish Section comprised Ethelwynn Trewavas, specializing in African freshwater fishes; N.B. (Freddy) Marshall (1915–1996, elected F.R.S. 1970), appointed in 1947 and specializing on marine fishes; and Denys W. Tucker, appointed 1949, who left in 1960. E.T. became Deputy Keeper of Zoology in April 1958, an appointment that took much of her time and left Humphry responsible for freshwater fishes, and in July 1962 Freddy Marshall achieved an Individual Merit promotion which relieved him of administrative duties, so making Humphry, by default, Head of Section.

In Humphry's early days on the museum staff he was probably free to create his own job. He continued his monographs on haplochromine cichlids (16–18, 21, etc.), and presented synthetic papers at the London International Zoological Congress in 1958 (15) and at an evening discourse in the Royal Institution in 1964 (25). He also produced (22) a revision of *A history of fishes*, a text first published in 1931 by Humphry's predecessor in the Museum, J.R. Norman (1898–1944). Humphry's version was translated into several languages, and went through another edition 20 years later (43).

Keith Thomson (b. 1938), who went on to become Dean of the Graduate School at Yale and President of the Academy of Natural Sciences of Philadelphia, was an undergraduate vacation student with Humphry during his early days in the Museum (summer 1959; their collaboration resulted in paper 19). Thomson writes with keen appreciation of his experience, recalling the 'untrammelled collegiality' of Humphry's museum environment: 'Instantly, this was home. From that day onwards I have always worked in Museums and the memory of Humphry will always be conjured up by the special "feel" of a research museum'. Humphry, Thomson feels, was then 'both brash and unsure, but obviously very ambitious. That he made time for me was a constant surprise, but he always had a wonderful way of making people feel as though their problems and issues were terribly important. His working style was fascinating. He alternated periods of deep still concentration—poring over bottles of cichlids—with intervals of frenetic activity. One measure of Humphry's intensity is the amount of work we got done, squeezed in amongst all his other duties.'

Humphry's work with Thomson on the osteoglossoid *Pantodon* was one sign of a broadening of his research interests. Another avenue opened in 1959 with the arrival in the museum of some puzzling fossils from lacustrine deposits at Singida, Tanzania. Fortunately,

in the same year was published an account of the Denticipitidae, a new family of primitive Recent teleosts from streams in Nigeria (Clausen 1959). Humphry's fossils proved to be almost identical to *Denticeps clupeioides*, only living member of the Denticipitidae, and he named them *Palaeodenticeps tanganikae* (20). Dr H. Stenholt Clausen at the Zoological Museum in Copenhagen supplied Humphry with specimens of *Denticeps*, and these, together with his experience of osteoglossoids (19) and notoapteroids (23, 24) gave him ammunition for the next major step in his career.

#### THE NEW CLASSIFICATION OF TELEOSTS AND NEW YORK

In 1966 a substantial paper under the title 'Phyletic studies of teleostean fishes, with a provisional classification of living forms' (26) was published, with four authors, P.H. Greenwood, D.E. Rosen, S.H. Weitzman and G.S. Myers. Donn Rosen (1929–1986) was at the American Museum of Natural History in New York; Stan Weitzman (b. 1927) at the National Museum of Natural History (then the United States National Museum), Washington, D.C.; and George Myers (1905–1985) at Stanford University. This 1966 collaboration is the most important and influential of Humphry's contributions to science (by 1990 it was judged a 'Citation Classic'; T.W. Pietsch, in litt. April 1988, rates it 'the most important ichthyological contribution of this half-century'), and the background to it merits space. The Foreword of the paper states that it originated from talks and correspondence between Greenwood, Rosen and Myers at and following the 16th International Congress of Zoology in Washington, D.C. (20–27 August 1963). Attendance at that meeting was Humphry's first visit to North America; he travelled by ship, to New York, and there met Donn Rosen for the first time. Humphry was quickly persuaded to forget the hotel room that he had booked, and stayed instead with Donn and his family for a day or two before travelling to Washington. After the Congress, Myers wrote (12 September 1963) to Rosen, with copies to Greenwood and Weitzman, setting out his ideas about a new classification of fishes. The most recent comprehensive classification was by the Russian, Leo S. Berg (1940, revised 1955). Myers's idea was that a tentative 'skeleton' classification or 'list of categories' be produced for publication by a small group; 'Perhaps a new one could be gotten out every few years'. His original ideas for the team included (in addition to Greenwood, Rosen and Weitzman) several others, such as a palaeontologist and specialists on chondrichthyans. By the end of September the three had replied to Myers's letter, and it was agreed that the group should restrict themselves to actinopterygians, leaving out agnathans, chondrichthyans and sarcopterygians (lungfishes, coelacanth). In the event, lower actinopt (sturgeons, holosteans, etc.) were also left out. The composition of the group was still under discussion, with Warren C. Freihofer (1922–1989, at Stanford with Myers) and Bobb Schaeffer (b. 1913, in New York with Rosen) as the most likely candidates; both evidently dropped out or were dropped, though after a long silence Freihofer felt he might be included as late as February 1965. Myers began allotting tasks (25 September 1963), with Greenwood to tackle what became the osteoglossomorphs and gonorynchiforms, Weitzman to take on the ostariophysans and stomiiforms, Rosen to do what became the atherinomorphs, and the percomorphs left aside for the moment. In April 1964, Donn Rosen came to London for a month to work with Humphry for the first time, and in October 1964 and February 1965 Humphry spent two months with Rosen in New York. By January 1966 they were correcting proofs on the new classification. The bulk of the paper is



the work of Greenwood and Rosen. Weitzman was responsible for the sections on ostariophysans and stomiatooids, and for the 412 thumbnail sketches (charts 1–32) of a representative from each recognized family. George Myers, although he initiated the project, actually took little part, apparently because of family problems (his wife left him in 1964). Before his withdrawal, judging by the extant correspondence, leadership had already passed to Donn Rosen, who threw himself into the project with his usual energy. All four contributors met once only, in New York early in 1964. Greenwood, Rosen and Weitzman got together three or four times, and Rosen and Weitzman met in New York on several occasions working through the final manuscript and with the proofs. Humphry produced the sections on what became Elopomorpha, Clupeomorpha and Osteoglossomorpha, and the germs of the idea of gonorynchiform/ostariophysan relationships. He also ‘rewrote much of the text into a more or less single style’ (Weitzman, in litt., April 1988). Weitzman (in litt., July 1996) recalls the ‘delightful stream of humor’ that Humphry brought to the collaborators’ meetings, and Humphry’s skill as a tactician in keeping reins on the profusion of ideas that Donn Rosen would produce. The major innovation in the new classification was to dismember the old basal teleostean group variously named Isospondyli, Malacopterygii or Clupeiformes, and distribute its members among four new taxa, Osteoglossomorpha, Elopomorpha, Clupeomorpha and what was later (28) named Euteleostei. An analogy is to imagine the situation in mammalogy if monotremes, marsupials and placentals were not distinguished until 1966. As Humphry ‘conceived and wrote the first drafts of what became the Clupeomorpha, Elopomorpha and Osteoglossomorpha’ (in litt. to T.W. Pietsch, April 1988) he was responsible for the major innovation in the classification, though doubtless the sparks struck by Rosen helped bring the ideas to fruition.

Before the 1966 paper was published, Humphry and Donn Rosen had already begun to collaborate on other projects, a partnership that was to last almost until Rosen’s death in 1986, with annual or more frequent visits by Rosen to London and by Greenwood to New York. Their first joint publication (32) grew from ideas proposed in the 1966 paper, and resulted in a new classification of ostariophysans in which gonorynchiforms were included within the group. This proposal has stood the test of time (Fink & Fink 1996), and the evidence for it has grown with subsequent analyses. Greenwood and Rosen worked next (35) on alepocephaloids and argentinoids, two groups of lower euteleosts. They were able to show that the two are related because they share a dorsal diverticulum of the gill-chamber, named the crumena organ. Again, these ideas have stood the test of time and been reinforced by subsequent work (Johnson & Patterson 1996). The third joint paper by the pair (44) deals with synbranchoids, a difficult group of eel-shaped fishes. After that 1976 publication the two discussed various possible collaborative projects, but each increasingly found their time eaten up by other matters. They met enthusiastically during Humphry’s trips to North America and Rosen’s trips to London, but published no further work together, and Humphry’s transatlantic collaborations shifted north to Harvard (51, 54, 56). Humphry last visited Donn in June 1986, during Donn’s final illness and a few weeks before his death in August 1986. Humphry was appointed a Research Associate in ichthyology at the American Museum in 1967, and maintained that appointment until his own death.

## HARVARD

Humphry first visited Harvard in October 1964, at the invitation of Ernst Mayr (elected For.Mem.R.S. 1988), then Director of the Museum of Comparative Zoology (M.C.Z.). Humphry spent a week at M.C.Z. and gave three lectures on aspects of evolution in African cichlid fishes. Soon afterwards, Humphry was offered a job at M.C.Z. and responded positively. By mid-1966 Mayr's offer was still open and Humphry was still responding positively. There are gaps in the correspondence, much of which must have been carried out from Humphry's home address, but in 1970 negotiations were reopened by the new Director of M.C.Z., A.W. Crompton, a fellow South African who succeeded Ernst Mayr in 1970. The stakes were now higher, as the M.C.Z. had acquired endowment for the Bigelow Professorship of Ichthyology. Humphry revisited M.C.Z. in October 1970, submitted a detailed memorandum on the condition of the Fish Department there, and subsequently again responded positively to Crompton's proposals. By March 1971 the Dean of Arts and Sciences at Harvard offered Humphry the Bigelow Chair, but in June Humphry turned down the offer because of his responsibility for the I.B.P. team on Lake George (below). However, Humphry returned to M.C.Z. in 1979, when as Bigelow Visiting Professor he gave a series of lectures as part of the course on biology of fishes. He did the same in 1983, teaching the course with his friend, collaborator (51, 56) and fellow-prankster Karel F. Liem, who had been appointed to the Bigelow Chair in 1972. In the Harvard students' annual evaluation of courses, Greenwood and Liem received the highest rating of any course in science (mysteriously, Humphry's forename becomes 'Martha' in the published evaluation), and Karel Liem recalls their cooperation as a wonderful experience, and comments on the inspiration that students received from Humphry's catalysing energy.

## I.B.P. AND LAKE GEORGE

In 1963 the Royal Society set up a National Committee for the International Biological Programme (I.B.P.). It established subcommittees for each of the main areas of research, including productivity of freshwater communities (P.F.), under the chairmanship of J.W.G. Lund, F.R.S. Humphry was appointed to the P.F. subcommittee in 1964. In 1965 that subcommittee budded off an *ad hoc* committee to establish a research team on Lake George, Uganda, to study organic production in the lake. The first members of the team arrived on Lake George in November 1966, where they took over some derelict accommodation beside the factory of the Uganda Fish Marketing Corporation. The team members spent their first few months building and restoring the accommodation, but by March 1967 they were able to begin research. Humphry visited the newly established team for a month in March–April 1967, working on the lake cichlids with Ian G. Dunn, the team leader. The team then included four other scientists and five locally recruited staff.

Early in 1968, J.W.G. Lund resigned the chairmanship of both the P.F. subcommittee and the African Freshwater Team *ad hoc* committee, and in May 1968 Humphry was appointed to the *ad hoc* committee as chairman. This appointment occupied a great deal of his time for the next five years, an effort documented by the mass of papers in his files. He acted as manager of a team of five or six scientists and up to eight local employees, dealing with every aspect of the project: budgets, management of research, welfare and frequent local catastrophes, such

as thefts, accidents, personality clashes, etc. Humphry visited the team several times (March 1970, April–May 1971, May–June 1972) and both he and they seem greatly to have enjoyed these interactions. The team was wound up in the middle of 1972, when the buildings and equipment were passed to the nascent Uganda Institute of Ecology. The team's baggage, including most of their primary data, was left with agents to be air-freighted to London, unfortunately just before Idi Amin decreed that all Asians be expelled from Uganda. The resultant exodus led to chaos at Entebbe airport, and the loss (temporary or permanent) of the team's baggage. Most of it eventually arrived at London airport, where in November 1972 Humphry spent a day with a team member searching through five tons of 'unidentified rubbish, mostly rotting foodstuffs' that had been shovelled out of two aircraft from Entebbe. Their search for missing data recovered only one notebook and a few sheets of paper and index cards.

The results of the Lake George programme were summarized in a discussion meeting at the Royal Society on 14 February 1973 (40). Authors of the published papers included 10 who had been team members for all or part of the project's existence. Its results included four doctoral theses, two master's theses and about 40 scientific papers.

#### LINNEAN SOCIETY

Humphry gave much time to the Zoological Society of London, serving on the Publications Committee (for nine years), Education Committee (six years), and Medals and Awards Committee (three years), but he regarded the Linnean Society as his true 'scientific charity'. He served on Council 1964–71, was Zoological Secretary 1967–70, Vice-President 1970–71, and President 1976–79. Professor Brian Gardiner (P.L.S. 1994–97), Zoological Secretary during Humphry's Presidency, recalls those years as his happiest period of Linnean Society service, and comments on Humphry's 'brilliant performance' as President, on the hilarity and fun he brought to Officers' Meetings, on 'the breath of fresh air' of his period of office and how he (B.G.) would never have taken on the Presidency without Humphry's example and his support.

#### COELACANTHS

Under this heading are gathered a few disparate parts of Humphry's career. In 1967 the Royal Society established a Coelacanth *ad hoc* Committee, with F.C. Fraser, F.R.S. (1903–1978), as chairman, to discuss a joint (France, UK, USA) study of *Latimeria*, the living coelacanth. Humphry joined the Committee in 1967, and in 1968 it became the Coelacanth Research Committee whose aims were: (i) to encourage, promote and coordinate research on *Latimeria*, including the acquisition of specimens; and (ii) to advise Council concerning research on other creatures of long lineage (nothing came of this). The Coelacanth Research Committee existed until 1976, under Humphry's chairmanship from 1974. It had two main achievements. First, in January–February 1969, it organized a 6-week fishing trip by F.R.V. *Manihine* out of Mombasa, to search for *Latimeria* around the islands and banks to the north and west of the Comores, from which come all but three of the known specimens of *Latimeria*. The expedition was named the Royal Society Indian Ocean Deep Slope Fishing Expedition, to camouflage its

real intention. Of the five participants four were British and one was from USA (Forster *et al.* 1970). The method was night long-lining, as used by the Comorans who take *Latimeria* as a by-catch when fishing for oilfish, *Ruvettus pretiosus*. *Ruvettus* were taken, but no *Latimeria*. The Coelacanth Research Committee's second achievement was a 3-month (January–March 1972) French/UK/USA expedition to the Comores, and was much more successful. A large, ripe female coelacanth was caught off Anjouan on 5 January, when only half the expedition had arrived; Professor Jean Anthony chartered a plane and brought it back to Grande Comore. Then, on 22 March, when most of the expedition had left, a second fish was brought alive to the surface off Grande Comore, near the expedition's base, and in the dawn was photographed and filmed in motion. These two fishes were dissected while fresh, and fixed or frozen tissues distributed to many specialists. The two fishes eventually reached the B.M.N.H., and Humphry exhibited the tennis-ball-sized eggs from one at the Society's soirée in 1972. Over 45 scientific papers resulted from the capture of these coelacanths (listed in Locket 1980).

Mode of reproduction in *Latimeria* had long been a puzzle, and the 20 huge eggs found in the 1972 female spurred further speculation. In 1975, dissection of a specimen in the American Museum of Natural History, New York, disclosed five near-term fetuses, 30–32 cm long, each with a large yolk sac. The American Museum gave one of these pups to B.M.N.H. (I carried it to London), and Humphry exhibited it at the Society's soirée in 1976.

In 1991 a Japanese trawler took a female coelacanth off the coast of Mozambique, the second fish to be found outside the Comores (J.L.B. Smith's 1938 specimen was the first). When dissected at the Natural History Museum of Maputo, Mozambique, the female was found to contain 26 pups, 31–36 cm long, all without external yolk sacs and apparently ready for birth. Ten of these pups were donated to the J.L.B. Smith Institute of Ichthyology, where Humphry then was, and he published (60) an account of their viscera, which clears up a number of controversial points. He also wrote a booklet (59) to accompany a B.M.N.H. exhibition marking the golden jubilee of *Latimeria* (reprinted as 62), and a number of articles on the fish (61, 67, 68).

## BRITISH MUSEUM (NATURAL HISTORY) II

Humphry received an individual merit promotion to Senior Principal Scientific Officer in 1967. Although such appointments are supposed to relieve the holder of administrative duties, he continued as Head of the Fish Section in the Museum. Notable work in the late 1960s and early 1970s includes his 1968 paper on *Denticiceps* (30), demonstrating that the fish is a clupeomorph, the sister-group of all others; his 1970 papers on the skull and swimbladder in tarpons (33), and on the Mesozoic fossil *Lycoptera* (34), demonstrating that it is related to the living osteoglossomorph *Hiodon*; and his 1971 paper (36) on gill-arch musculature in osteoglossomorphs. In 1972–73 he took a major part in organizing the Linnean Society symposium 'Interrelationships of fishes' and in editing the resulting volume (38). That volume is something of a landmark, not only in ichthyology ('one of the most influential books in the modern literature'; Stiassny *et al.* 1996, p. xi) but in systematics, as the first multiauthor treatment of a major group in which the orientation was phylogenetic or cladistic. Humphry's contribution to the book was an important synthesis on osteoglossomorphs (37). He continued his series of monographs on the haplochromines of Lake Victoria (29, 31, 45), covered also those of Lakes George (39) and Rudolf (41), and in 1974 produced a major

phylogenetic analysis on the Victoria species flock (42). However, he soon found those results inadequate and returned to the problem in 1979–80 (46, 48). In the late 1970s his time was much occupied by Presidency of the Linnean Society, and he ended his 3-year period of office with a Presidential Address on ‘Macroevolution—myth or reality?’ (47), giving some of his views on the evolutionary process, as mediated by his experience with cichlid species-flocks (his answer to the rhetorical question was ‘myth’). He was influenced here by Gould and Eldredge’s theory of punctuated equilibria, a theme to which he returned in several papers in the early 1980s (49, 53, 55, 57, 58).

In October 1980, together with Marjorie, he visited Hong Kong and China for a month, under the Royal Society’s agreement with the Chinese Academy of Science. Despite ‘the 17-hour day’ which he found to be the norm on the trip, and the 3- to 4-hour duration of his lectures (through a translator), he enjoyed the visit enormously. He lectured in Hong Kong, Beijing, Xian, Shanghai and Wuhan, and was greatly impressed by the ‘enthusiasm and capacity for work’ of the many ichthyologists he met. He concluded his report on the trip with the words ‘probably the most memorable experience of my life’.

Humphry made one further trip to the Far East. In 1985 he was nominated by the Royal Society for the newly established International Prize in Science of the Japan Academy. Although he did not win (the prize went to E.J.H. Corner, F.R.S., 1906–1996), he was invited to sit on the jury for the 1986 prize, and spent three weeks in Japan, lecturing in Tokyo and Kyoto in addition to his jury duty. Humphry received VIP treatment in his Tokyo hotel after the Crown Prince (whom he knew as an ichthyologist) sent an aide to collect him for an evening at the Palace.

Humphry had a long-standing collaboration with a group of cichlid workers in Leiden, led by Dr C.D.N. (Kees) Barel, who published a brief but heartfelt account of his experience with Humphry (Barel 1996). Beginning in 1971, he made many trips to Leiden, usually only for a day or two, interacting with the *Haplochromis* Ecology Survey Group (H.E.S.T.), which conducted fieldwork at the southern end of Lake Victoria from 1977 to 1992.

In March 1985 Humphry was elected to the Royal Society, and in July was awarded an individual merit promotion to Deputy Chief Scientific Officer (the first B.M.N.H. member to achieve that distinction). With these honours, his retirement, due in April 1987 on reaching 60, was deferred for two years. After retirement he was appointed a Visiting Research Fellow, and until his death spent several months each year in the Museum.

#### THE J.L.B. SMITH INSTITUTE OF ICHTHYOLOGY

The J.L.B. Smith Institute (J.L.B.S.I.), Grahamstown, was created in 1968 to replace the Department of Ichthyology at Rhodes University, after the death of Professor J.L.B. Smith (63), who established the Department in 1946 and was renowned as describer of *Latimeria*, the living coelacanth. Humphry first visited J.L.B.S.I. in 1975, during a 2-month tour of South Africa, but he had corresponded with the first Director, J.L.B. Smith’s widow Margaret, and as early as 1969 she offered him a job as Senior Research Fellow. In 1983, after the retirement of Margaret Smith, Humphry began negotiations with the new Director, Dr M.N. Bruton, over the possibility of moving to Grahamstown in a research position as Deputy Director. Serious negotiations continued for some time, but in 1985 London became more attractive with his election to the Royal Society and his promotion to Deputy Chief Scientific Officer. However,



he visited J.L.B.S.I. for five weeks in 1984, six weeks in 1985, and for a month or more in 1986–88. Eventually, on his retirement from B.M.N.H. early in 1989, he left immediately for Grahamstown, but elected to take an honorary position so that he would have freedom to spend half the year in South Africa and half in London. He bought a house in Grahamstown across the road from J.L.B.S.I., and as the years passed spent less and less time in London.

In addition to his research in Grahamstown, Humphry played a full part in the work of J.L.B.S.I., teaching courses, supervising students, helping colleagues, enjoying field trips and making frequent contributions to the Institute's newsletter (e.g. 64–66, 71). He was held in the highest regard by staff and students (Ribbink 1995*a–c*; Skelton 1995).

### FINIS

In July 1989 Humphry visited the Lofoten Islands, in northern Norway, to take part in a symposium organized by the Norland Academy of Arts and Sciences on 'Contemporary problems in the border zone between evolutionary science and philosophy'; his topic was the species problem (70). On that trip he also lectured at the University of Bergen and, as usual, established cordial relations with his hosts. He returned to the Lofoten Islands in 1991, and from then on made annual visits to the University of Bergen, staying for about a month and teaching a course on fishes. He was due in Bergen on 6 March 1995; travelling from Grahamstown he stopped off in London en route. He came into the Natural History Museum on 1 March and worked with Dr Nigel Merrett, his successor as head of the Fish Section. Merrett left for home at about 5 pm, but Humphry stayed on to continue work. He was found next morning, collapsed in Nigel Merrett's room; as the lights were not on, the stroke that felled him must have occurred before dark, perhaps at about 6 pm. Humphry was immediately taken to hospital, but did not regain consciousness and died in the early hours of 3 March 1995. The room in which he suffered the fatal stroke had been his own for the greater part of his career in the Museum.

A celebration of Humphry's life and achievements was held at the Linnean Society on 21 April 1995, which would have been his 68th birthday. A memorial issue of the *South African Journal of Science* is expected in December 1997. He is survived by his wife Marjorie, a researcher on fossil insectivores, four daughters (the youngest, Pippa, b. 1961, is now a public figure through her regular appearances in gardening programmes on radio and television), and four grandchildren.

### INFLUENCE

Humphry's principal publications can be divided, with a few loose ends, into two categories: work on African cichlids; and on higher-level teleostean systematics. The cichlid work is certainly seen as his main contribution, and this 'brilliant work' was picked out in his citation on election to the Royal Society. I believe that history will judge his higher-level systematics as more important. There are at least three reasons (which Humphry would acknowledge) why the cichlid work seems an attempt on the unattainable.

Humphry's cichlid work was firmly grounded in his early days of fieldwork on Lake Victoria. Van Oijen (1996) (who collaborated with Humphry since the 1970s (45)), gives a

critical account of this work:

The species descriptions of Greenwood, the first ichthyologist involved in fieldwork on Lake Victoria, were quite different from preceding ones. They were ... much more detailed, but they also contained information on the ecology .... and often, on live coloration' (p. 76).

But Humphry's systematics, for at least the first 15 years of his cichlid studies, was set in a framework that he later rejected, the 'evolutionary systematics' universal in the 1950s and early 1960s. Humphry was an early convert to cladistics, or Hennigian phylogenetic systematics (Hull 1988, p. 144), and this changed his view of such basic principles as the meaning of 'monophyly' and 'relationship'. In the Introduction to the collected reprints of his monographs on haplochromines (50) in 1981 he wrote: 'whenever phrases with the word "related" (or its derivatives and synonyms) are used ... the words should be taken to mean "resemblance" or "similarity" in a strictly phenotypic sense'. Attempting a cladistic analysis of the Lake Victoria haplochromines in 1974 he produced 'Greenwood's wheel' (42, figure 70), which provided tentative phylogenies for six groups of species, but no link between any two of them. A few years later (48, p. 3) this scheme was 'seen to be quite inadequate, and in many respects misleading when taxa from the historically related lakes Edward and Kivu are taken into account'. At issue here was the phyletic integrity of the lake Victoria 'species flock': was it monophyletic or not? Later (52) he decided that it was not. Attempting to generalize on the evolutionary processes responsible for the cichlid species flocks of the African Great Lakes he came up with 'cladistic gradualism' (47, p. 297; 49, p. 70 and elsewhere), a concept that seems not to have been taken up by others.

The second reason for dissatisfaction with the cichlid work is the recent history of the African Great Lakes, Lake Victoria in particular. From the perspective of the 1990s, the years of Humphry's fieldwork on Lake Victoria in the early 1950s seem like a golden age. Subsequent events (Lowe-McConnell 1997) include introduction of exotic *Tilapia* (1950s) and of *Lates niloticus* (1960s), eutrophication (1960s or earlier), population explosion of *Lates* (1970s), overfishing, etc. One result of these events is extinction of perhaps two thirds of more than 300 endemic species of haplochromine cichlids in Lake Victoria. Humphry's species flock is already a thing of the past.

The final reason for dissatisfaction is the development of molecular systematics, applied extensively to African Great Lakes cichlids in the 1990s. Humphry (48, p. 3), regretting the failure of morphology to resolve relationships among the Great Lakes haplochromines, wrote 'there would seem to be great scope for developing biochemical techniques directed towards that end'. They were soon developed (e.g. Meyer 1993; Kocher *et al.* 1993; Sülmann *et al.* 1995). Although the molecular phylogenies of cichlids are not always congruent (Stiassny 1997), problems like the monophyly of Lake Victoria haplochromines, which Humphry was unable to settle after 30 years of morphology (52), are now more likely to be resolved in a few months by a graduate student and an automatic sequencer.

Humphry's work in higher-level teleostean systematics is a much happier story of solid achievement. His major contributions here are recognition and characterization of the clades Osteoglossomorpha, Elopomorpha and Clupeomorpha; his work on fossil and Recent osteoglossomorphs; his work on elopomorphs and the primitive clupeomorph *Denticeps*; and his work with Rosen on gonorynchiform/ostariophysan and alepocephaloid/argentinooid relationships. All this has stood the test of time, and will ensure his scientific immortality.

Humphry influenced generations of students by personal contact rather than through his

publications. Throughout his career he was ready to accept invitations to lecture, and regularly travelled to speak to bodies of students or to local societies, as well as taking part in formal university courses. His skill as a speaker is exemplified by the ratings awarded by students at Harvard (above). Humphry was also happy to take on wider exposure to the public, and broadcast frequently during the later stages of his career. He supervised about a dozen doctoral students in B.M.N.H., most of them jointly with Professor Brian Gardiner, Queen Elizabeth and (later) Kings College. The most successful of these in a professional sense are Dr Melanie Stiassny, who now holds Donn Rosen's job as chairman of ichthyology in the American Museum of Natural History, and Dr Gordon McGregor Reid, who is Director of Chester Zoo.

### PERSONALITY

Obituaries and tributes after Humphry's death (Anon. 1995; Barel 1996; Howes 1995*a,b*; Reid 1996; Ribbink 1995*a-c*; Skelton 1995; Smith 1995; Stobbs 1995) referred, without exception, to his infectious sense of humour and the fun and merriment that surrounded him. Ribbink's (1995*c*) 'irrepressible naughtiness' puts it particularly well. Most of Humphry's friends will have enjoyed or endured the discomfiture of telephone conversations apparently with a Chinese laundry, Indian restaurant or foreigner eager for information on an obscure topic, all revealed eventually as facets of Humphry's remarkable gift as a mimic.

Beneath the superficial wit and charm, there was a complex and elusive personality. Humphry was reputed to have a short and ferocious temper, though I never saw it in 35 years of collaboration with him. He was ambitious, and (perhaps like most of us) was anxious to be liked and admired. As a result, he found it hard to say no and took on many jobs that he could have avoided. In working through his correspondence I am struck by the inordinate trouble he would take over enquiries that could have been turned aside; the pains he took obviously won him many friends. It is clear from the correspondence that he liked to be at the centre of things, for in cases of conflict he would play off one correspondent against another, so that each thought Humphry agreed with their own view. An extreme instance of his failure to say no, or his desire to be at the centre, was his inability decisively to turn down offers of jobs. At one point, around 1970, when Harvard were fully expecting him soon to arrive as an employee, he had given some reason for the same expectation to at least three other institutions! From the early 1960s until the mid-1980s, there was hardly a time when Humphry was not playing some potential employer with an angler's skill. Obituarists and others comment on his ability to convey enthusiasm to students, and to convince them of the value of research as a way of life.

Humphry was a balletomane, a collector of books and a serious collector of pictures. Himself no artist (and with execrable handwriting), his long-term assistant and colleague Gordon Howes, who is now a professional painter and who illustrated many of Humphry's publications, noted Humphry's 'acute artistic eye' and called him 'a shrewd and discerning critic of visual art' (Howes 1995*a*).

## HONOURS AND AWARDS

In addition to his Fellowship of the Royal Society, Humphry received the Scientific Medal of the Zoological Society of London (1963); Linnaeus Medal, Linnean Society of Sweden (1978); Linnean Medal for Zoology, Linnean Society of London (1982); and an honorary D.Sc. from Rhodes University (1991). He was elected Honorary Foreign Member of the American Society of Ichthyologists and Herpetologists (1972) and Foreign Member (Class VII), Royal Swedish Academy of Sciences (1984).

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The frontispiece photograph was taken by the Godfrey Argent Studios, and given to the Society in 1985. It is reproduced with their permission.

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**Peter Humphry Greenwood**

**Bibliography**

Greenwood 1



## Peter Humphry Greenwood—Bibliography

The list is in two parts: scientific papers (nos. 1-166) and book reviews, obituaries, abstracts, semipopular contributions, etc. (nos. 167-278). The distinction is mainly Humphry's own, with the first part containing publications that he chose to include in his professional CVs. I believe that the first part is complete, but I am sure that the second is not. Humphry was a prolific book reviewer, and kept no record (so far as I know) of his reviews or other minor contributions. Many of the listed book reviews were found by leafing through likely journals. Other contributions were traced through hints in correspondence records; some of those hints could not be followed through, and the second part of the list is therefore incomplete.

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